CHAPTER ONE

GENERAL INTRODUCTION

1.1 Introduction

The research presented in this thesis investigated how common marmosets (*Callithrix jacchus*) respond to two types of stimuli (aversive and pleasant) in the visual, auditory and olfactory modalities, presented individually and in various combinations. The stimuli were predator- and food-based and thus had to do with two areas vital for survival. If combinations of cues enhance a chance of survival, it is also important to know what cues might optimally achieve rapid discovery and response. How this might be achieved in environments rich in often conflicting and multimodal information has been difficult to test in the wild. In this thesis, it is addressed in captive common marmosets (*Callithrix jacchus*).

Responses to stimuli may depend on whether information is first perceived in the visual, auditory or olfactory modality, because the information contained in each may differ, despite originating from the same source (Møller and Pomiankowski, 1993). It is known that information from one sensory modality may alter the way in which information from another sensory modality is processed (Stein and Meredith, 1993). Although responses to specific sensory cues have been well studied separately, how a prey animal reacts to two or more different but simultaneous cues in different sensory modalities has remained largely untested. Similarly, food cues have not been well studied in different modalities. Potentially, multiple sensory cues from the same stimulus should provide an animal with a greater ability to recognise the stimulus and, perhaps, allow it to respond more rapidly than it might when presented with a single sensory cue (Meredith and Stein, 1983; Partan and Marler, 1999; Stein *et al*., 1988). The questions addressed here are whether recognition of stimuli by common marmosets is enhanced or altered by the use of multiple cues from the same type of stimulus, or altered by conflicting cues from different stimuli.

The three main aims of this thesis were: 1) to determine whether responses of common marmosets to stimuli presented individually differ depending on the sensory modality; 2) to determine whether the combination of related sensory cues enhances or alters the responses shown to individual stimuli; and 3) to determine whether one stimulus has a greater influence on the response of the marmosets when the stimuli presented simultaneously represent a conflict of interest. That is, how a prey species is able to respond to a predator when it is also receiving cues producing conflicting motivations, such as in finding food or being engaged in sexual communication. Such situations represent a conflict of interest, but animals must face these regularly (Skals *et al.*, 2005).

The common marmoset is an ideal species in which to test sensory perception in the three modalities and, in particular, to study the response to predator-based (aversive) stimuli. The Callitrichids, New World primates, to which *C. jacchus* belongs, are susceptible to a diverse range of potential predators (e.g. raptors and other birds, snakes, felids and tayras) due to their small body size (Bartecki and Heymann, 1987; Bezerra and Souto, 2008; Corrêa and Coutinho, 1997; Emmons, 1987; Heymann, 1987, 1990; Peres, 1993; Rylands, 1981; Stafford and Ferreira, 1995; Sussman and Kinzey, 1984). *C. jacchus* range in weight between 350 g and 450 g, making them an ideal prey size for many predator species (Clarke, 1994). They also show defensive or anti-predator behaviours to coatis (Rylands, 1981), tufted capuchins (Peres, 1993) and a variety of birds, including vultures, toucans and parrots (Heymann, 1990; Peres, 1993; Rylands, 1981). Marmosets are particularly vulnerable to predation while foraging for insects (Caine, 1996), and they may spend up to 30% of their day engaged in this activity (Caine, 1996; Rylands and de

Faria, 1993). Their visual, olfactory and auditory sensory systems are well developed, are known to be important in social and sexual communication (Barton, 2006; Lazaro-Perea *et al.*, 1999; Rylands, 1993; Sussman and Kinzey, 1984), and should also be essential to food and predator detection, as explored in the research conducted for this thesis.

1.2 Sensory systems of primates, specifically of marmosets

Probably more is known about vision in primates than any other sensory system. Since primates have been typically regarded as visual animals (Buchanan-Smith, 2005; Laska *et al.*, 2000), this is hardly surprising. The eye structure of marmosets has been described as being very similar to that of humans (Ordy and Samorajski, 1968; Troilo *et al.*, 1993) and therefore marmosets have been used largely as research species for their eyes. As a haplorhine primate, the common marmoset has specialised vision, including greater acuity and orbital convergence, and a larger visual cortex than strepsirhine primates (Ross, 1995). Both dichromatic (two visual pigments) and trichromatic (three visual pigments) vision are found in common marmosets, with all males and approximately one third of females dichromatic (Jacobs, 1998; Surridge, *et al.*, 2003; Travis *et al.*, 1988). Dichromatic vision is thought to be an advantage in detecting camouflaged predators (and food in shaded conditions) (Caine *et al.*, 2010; Morgan *et al.*, 1992; Saito *et al.*, 2005), whereas trichromatic vision is thought to have an advantage in detecting ripe fruit, particularly red fruit, and young leaves amongst a foliage background (Caine and Mundy, 2000; Pessoa *et al.*, 2005). However, given that common marmosets live in dense tropical rainforests, viewing opportunities can be limited by many obstructions (Dominy *et al.*, 2001).

Primates are said to have a poorly developed sense of olfaction, but this is not actually true of prosimians and New World primates (Barton, 2006; Hübener and Laska, 2001). The olfactory bulb – the part of the brain principally involved with olfaction – represents 0.18% of the total brain volume in New World primates, and is even larger in prosimians (1.75% of the total brain volume: Stephan *et al*., 1970). In non-human great apes the olfactory bulb is only 0.07% of the brain volume and in humans this structure represents merely 0.01% of the total volume (Stephan *et al*., 1970). To my knowledge, only three primate species – two Callitrichids, the red-bellied tamarin (*Saguinus labiatus*) and the cotton-top tamarin (*S. oedipus*) – and one species of prosimian – the gray mouse lemur (*Microcebus murinus*) – have been studied in some depth for their ability to identify predatory cues via olfactory means (Buchanan-Smith *et al*., 1993; Caine and Weldon, 1989; Sündermann *et al*., 2008) and they found that these primates do respond to the odours of predators.

As for auditory capacity, Seiden (1958) determined that the high-frequency limit of sound detection of *C. jacchus* is 30 kHz but a more recent study by Osmanski and Wang (2011) suggests that this limit may be as high as 36 kHz. This is substantially higher than that of humans at 17.6 kHz (Heffner, 2004). Indeed, the hearing of marmosets is oriented towards high-frequency sounds (Seiden, 1958), and so is specialised for their generally high-frequency vocalisations (up to 22 kHz). Both Seiden (1958) and Osmanski and Wang (2011) also determined that the marmosets' best frequency hearing was at 7 kHz (once again higher than humans at 4 kHz), with an optimal sensitivity as low as 9 dB. The hearing capabilities of marmosets allow them to communicate above ambient, low-frequency background noise, around 4 kHz, improving the likelihood of being heard (Snowdon, 2003). In fact, *C. jacchus* appears to have a reduced sensitivity to sounds below 6 kHz (Heffner, 2004; Osmanski and Wang, 2011).

Given that, in marmosets, vision, olfaction and audition are highly developed and capable of fine discrimination, the marmoset is a particularly good model species to test the response to stimuli in any of these modalities individually and in combination. The experiments in this thesis use all three modalities individually and in combination to test the theoretical model of multimodal signalling posed by Partan and Marler (1999) which will be discussed in more detail below (Section 1.5).

1.3 Predator recognition in captive animals

Predation has long been regarded as a major force in shaping the behaviour of animals (Caro, 2005; Lima and Dill, 1989), including behaviour that assists in the detection, recognition and avoidance of predators, and in defence against predators (Apfelbach *et al*., 2005; Kats and Dill, 1998). Many studies have tested the ability of captive Callitrichids to recognise predators visually, using either artificial or taxidermic models (e.g. Barros *et al*., 2000, 2002; Caine, 1998; Clara *et al*., 2008; Dacier *et al*., 2006; Hayes and Snowdon, 1990). However, to my knowledge, for Callitrichids there have been only two studies on olfactory recognition and two studies on auditory recognition of potential predators, both of which were undertaken in captive environments (olfactory predator recognition: Caine and Weldon, 1989; Buchanan-Smith *et al*., 1993; auditory predator recognition: Friant *et al*., 2008; Searcy and Caine, 2003). In the experiments presented in this thesis, I used individual and combined stimuli in all three modalities building on this body of research on marmosets, but the type of stimuli that were most aversive and most pleasant to the marmosets were determined by the marmosets themselves (findings presented in Ch. 3).

The question arises, as it does in all captive studies, of what the visual, auditory or olfactory stimulus of a predator may mean to an animal that has never seen, heard or smelt a predator. One study on meerkats (*Suricata suricatta*) compared the responses of captive (one to five generations captive) and wild animals to the faeces of predatory and non-predatory (herbivorous) species (Hollén and Manser, 2007). These researchers found that captive meerkats without prior experience of predators displayed all the alarm calls documented in wild meerkats, with only slight structural differences, and produced these calls in broadly similar contexts (i.e. to the faecal scents of carnivores) to those of wild meerkats. To the faeces of herbivorous animals, however, the captive meerkats showed no aversion (Hollén and Manser, 2007). These findings suggest that the ability to identify some cues of predators may be retained in some prey species even in predator-free environments but, in certain circumstances, with relaxed selection for these behaviours, animals may eventually stop responding to some predator-based stimuli (Coss, 1999; Lahti *et al*., 2009).

Some studies have found that captive animals require training in order to associate a particular cue with a potentially predatory animal (e.g. tammar wallabies, *Macropus eugenii*, Griffin *et al*., 2001; rhesus macaques, *Macaca mulatta*, Mineka *et al*., 1984), whereas other species show spontaneous anti-predator reactions when they are faced with a predatory cue (e.g. as described above in meerkats, Hollén and Manser, 2007). Experimental studies have suggested that certain types of stimuli may require learning experiences, while others seem relatively experience-independent (Blumstein *et al*., 2008; Griffin *et al*., 2001). As an encounter with a predator can be lethal, certain types of stimuli seem to be particularly effective in triggering rapid and general anti-predator responses (Griffin *et al*., 2001). However, a predator image that can be refined with experience is advantageous (Deecke *et al*., 2002). Predator recognition and appropriate classification can improve with age and experience, as has been shown very effectively in rabbits (*Oryctolagus cuniculus*, Vitale, 1989) and vervet monkeys (*Cercopithecus aethiops,* Seyfarth *et al*., 1980). Vervet monkeys climb into trees at the sight of a leopard or hide in dense bushes when at risk of aerial predation; the appropriate referential call from a conspecific can also elicit these responses (Cheney and Seyfarth, 1992; Seyfarth *et al*., 1980). However, infants give these calls to a variety of species, including non-predators, and can respond incorrectly to the calls of adults (Seyfarth and Cheney, 1980).

Despite the amount of field time spent observing primates, predation has rarely been witnessed (Bezerra *et al*., 2009). Therefore, it is not always known which specific predators prey on which primate species. Nor are the responses of primates to natural predatory events always well known. One would imagine that prey animals first need to recognise danger, then localise the threat and distinguish it from harmless events, such as coming across a satiated predator (McLean and Rhodes, 1991; Stapley, 2003; Ydenberg and Dill, 1986). An appropriate response to a predator ought to occur on first encounter, but may require learning to associate the cue (or cues) with the predator or the state of the predator (Berger *et al*., 2001; Gil-da-Costa *et al*., 2003; Griffin *et al*., 2001).

The issue of relevance is important to my study as the marmosets tested were several generations captive. From the beginning, it was recognised that although the marmosets might show aversion and anti-predator behaviour to the stimuli presented, it cannot necessarily be concluded from this that all fear behaviour was due to the recognition of a potential predator. For example, one family in our colony showed a very strong aversion to one pair of shoes and milder reactions to other pairs of shoes (Gordon, 2007). The shoes were obviously not predatory, but the marmosets still showed a fear response. It is important to make the distinction that stimuli can be perceived as aversive without actually being predatory. Another study on the same marmosets found that the members of one family mobbed a carving of two frogs while another family did not (Clara *et al*., 2008). For the purpose of this study the stimuli tested, although predator-based, were regarded as simply ‘aversive stimuli’.

The theory that predatory sources of natural selection have a strong influence on Callitrichid behaviour has been based on the observations of these species displaying a wide array of behavioural adaptations for maximising their ability to detect predators (Caine, 1993) and minimising predation risk (Ferrari and Lopes Ferrari, 1990; Heymann, 1990). I was particularly interested in the behavioural adaptations, how they are expressed and whether the minimisation of predation risk is achieved in different ways depending on the modality of the cue (auditory, olfactory or visual).

1.3.1 Visual recognition of predators

Visual recognition of predators has been tested in wild and captive populations across a broad range of primate species, using taxidermic, 'realistic' models and silhouette models, and has been well documented in ringtailed lemurs (*Lemur catta*, Macedonia and Polak, 1989; Pereira and Macedonia, 1991), cotton-top tamarins (*Saguinus oedipus*, Hayes and Snowdon, 1990), tufted-eared marmosets (*Callithrix penicillata*, Barros *et al.*, 2002), putty-nosed monkeys (*Cercopithecus nictitans martini*, Arnold *et al.*, 2008) and others (e.g., Brown *et al.*, 1992; Caine, 1998; Coss *et al.*, 2007; Mineka and Cook, 1988; Mineka *et al.*, 1980, 1984; Murai and Tomonaga, 2009). Visual recognition of predators has been suggested to be relatively independent of experience (Blumstein *et al.*, 2000; e.g. macaques, Coss and Ramakrishnan, 2000; Davis *et al.*, 2003; Schell and Zuberbühler, 2009). Some aspects of predator morphology (e.g. size, shape, texture, speed, frontally placed eyes, short neck) have evolved convergently, allowing for some extrapolation by prey from a known predator to a novel predator (Blumstein *et al.*, 2000; Coss *et al.*, 2005; Evans *et al.*, 1993; Macedonia and Polak, 1989). Visual cues may also provide potential prey with information more indicative of a predator's current motivation and threat than do cues in other modalities (Smith and Belk, 2001). Even prey animals that are predator-naive may respond to certain general visual features of predators (Blumstein *et al.*, 2000; Coss, 1999). It has been found that, in some primate species, visual models of predators may elicit specific alarm calls and behavioural responses (e.g. vervet monkeys, Brown *et al*., 1992). These calls may denote predator type; for example, Diana monkeys (*Cercopithecus diana*) produce distinctly different calls for eagles, leopards and snakes (Riede and Zuberbühler, 2003). On the other hand, in baboons (*Papio cynocephalus ursinus*) differences in vocalisation depend on predation risk (Cowlishaw, 1997) or urgency (Coss *et al*., 2007).

Vigilance for predators has been reported to be an important priority for marmosets in the wild (Rylands and de Faria, 1993) and for other Callitrichids (Hardie and Buchanan-Smith, 1997). Vigilance is defined as the visual scanning of the environment for potential threats, in particular for predators (Bednekoff and Lima, 1998). As marmosets are thought to be particularly vulnerable to aerial predators, high levels of visual scanning appear to occur when there is a greater threat of aerial attack, and marmosets have indeed been found to express greater amounts of aerial versus terrestrial scanning (Barros *et al*., 2003). The optimality theory suggests that milder threats, such as a nearby predator sleeping, should be met with behaviour that minimises disruptions to the normal routine, in particular foraging, while not ignoring the present risk (Krebs and Kacelnik, 1991). Lima and Dill (1989) noted that prey animals can assess their risk of being preyed upon and will consider this information when making decisions. This theory has been tested with predatory and non-predatory models in captive Geoffroy’s marmosets (*Callithrix geoffroyi*, Caine, 1998). Caine (1998) found that marmosets responded to the sight of a potential predator by reducing feeding and increasing vigilance, but no such response occurred for non-predators. Once the predatory threat was removed, the marmosets quickly returned to baseline levels of foraging.

1.3.2 Olfactory recognition of predators

Olfactory cues of predators elicit anti-predator responses in many species (for a review see Apfelbach *et al*., 2005), and could be important in providing prey with long-term information regarding the movements of predators. The use of this modality in predator recognition by primates has received only limited attention, although it has been widely studied in other mammals (e.g. rats, Dringenberg *et al*., 2008, Fendt, 2006, Staples and McGregor, 2006; Cape ground squirrels, Belton *et* al., 2007; bats, Boyles and Storm, 2007; meerkats, Hollén and Manser, 2007; western grey kangaroos, Parsons *et al.*, 2007; domestic horses, Christensen and Rundgren, 2008; gray mouse lemurs, Sündermann *et al*., 2008; southern mountain cavy, Taraborelli *et al*., 2008). Yet since early mammals were most likely nocturnal (Crompton, *et al*., 1978; Geiser *et al*., 2002), olfaction may have been a particularly important modality for predator detection and may explain their highly developed sense of olfaction (Eisenberg, 1981).

Chemical communication is important in many primates, particularly in the Platyrrhini species (Ziegler and Snowdon, 2008). It is used widely in social communication, but may be used for the detection of predators as well (as found in the red-bellied tamarin, Caine and Weldon, 1989; the cotton-top tamarin, Buchanan-Smith *et al*., 1993; and the gray mouse lemur, Sündermann *et al*., 2008). The two tamarin species were tested in a similar fashion, using methylene chloride extracts of the faeces from natural predators and non-predators. Sniffing, avoidance and signs of anxiety occurred more often when the chemical cues related to predators than when those of the control and non-predators were presented (Buchanan-Smith *et al*., 1993; Caine and Weldon, 1989). Avoidance was also shown by the gray mouse lemurs when presented with the faeces of potential predators at food reward stations (Sündermann *et al*., 2008). From the responses of the captive-born tamarins the authors suggest that, in these species, experience with a predator may not be necessary for the animals to distinguish between the faecal scents of predatory and non-predatory species (Buchanan-Smith *et al*., 1993; Caine and Weldon, 1989). There were wild-born tamarins present in the group during testing, but they had been captive for many years.

My research tested whether marmosets, several generations in captivity, showed similar responses to highly aversive olfactory stimuli, some of which were expected be predator-based (the trials are presented in Ch.3). There is some evidence to suggest that even predator-naive species will respond to the faeces and urine of predators since meat digestion produces sulphuric metabolites, which are present in the faeces and urine and can be detected (Nolte *et al*., 1994). The sulphuric cues may provide a prey animal with information regarding potential predators in much the same way that certain physical features of predators can be identified as belonging to carnivorous animals, i.e. generalisations could be made from the presence of these compounds in the faeces and urine of unknown animals (Nolte *et al*., 1994). There is some debate as to whether chemical cues may cause prey animals to overestimate the current risk of predation because these cues may persist long after the predator is gone (Bouskila and Blumstein, 1992; Kats and Dill, 1998; Turner and Montgomery, 2003). However, while they are important to note and may be a factor influencing the behaviour of the marmosets in my tests, this was not a question that was tested directly here.

1.3.3 Auditory recognition of predators

There is some debate over the usefulness of presenting the vocalisations of predators as a method of testing auditory recognition of predators by prey because, as has been argued, predators tend to be silent when hunting (Arnold *et al*., 2008; for review see Blumstein *et al*., 2008). Regardless of these concerns, nearly 40 species, both wild and captive, have been studied for their ability to recognise predators through auditory cues alone (review by Blumstein *et al*., 2008; additional species: Adams *et al*., 2006; Arnold and Zuberbühler, 2006; Friant *et al*., 2008; Rainey *et al*., 2004; Reudink *et al*., 2007; Skals *et al*., 2005; Yorzinski and Ziegler, 2007). Only five species have been shown to be unresponsive to predator vocalisations (tammar wallaby, *Macropus eugenii*, Blumstein *et al*., 2000; red-necked pademelon, *Thylogale thetis*, Blumstein *et al*., 2002*a*; angoni vlei rat, *Otomys angoniensis,* Crafford *et al.*, 1999; natal multimammate mouse, *Mastomys natalensis,* Crafford *et al.*, 1999; and Cairo spiny mouse, *Acomys cahirinus,* Eilam *et al*., 1999, Hendrie *et al*., 1998).

Some birds of prey are known to use vocalisations to flush their prey from cover (Smith, 1969). Predation on common marmosets by one of these raptor species, the collared forest falcon (*Micrastur semitorquatas*), has been observed (Alonso and Langguth, 1989). Other raptors, such as the harpy eagle (*Harpia harpyja*), a suspected predator of marmosets, have also been observed vocalising prior to attacking prey (Gil-da-Costa *et al*., 2003). The recognition of these calls could forewarn primates, including marmosets, and thus avoid predation (Macedonia and Yount, 1991). For example, field studies on free-ranging blue monkeys (*Cercopithecus mitis*), red-tail monkeys (*C. ascanius*), lemurs (*Lepilemur, Eulemur, Avahi, Propithecu, Varecia* and *Hapalemur* spp.) and red colobus monkeys (*Colobus badius*) have shown these animals are able to recognise and react defensively on hearing the vocalisations of raptors (Hauser and Wrangham, 1990; Karpanty and Grella, 2001; Macedonia and Yount, 1991). Some felids are also known to use vocalisations to encourage hidden prey animals to instinctively flee, thus revealing themselves, and/or to disrupt animals already in flight move (e.g. Smallwood, 1993).

Only 12 primate species have been tested for their response to the auditory cues of potential predators; one of these was a Callitrichid (Geoffroy's marmoset; Searcy and Caine, 2003). Searcy and Caine (2003) found that captive Geoffroy's marmosets showed stronger anti-predator behaviour, such as freezing, alarm calls and increased use of safe areas in their enclosure, when played the vocalisation of a red-tailed hawk (*Buteo jamaicensis*) than when played the vocalisation of a raven (*Corvus corax*) or a recording of a power drill. The authors suggest that marmosets may use auditory cues associated with potential predators as early warning signals that a predator is in the vicinity, and this may be especially important in visually limited environments, such as a nest or dense forest (Khayutin, 1985). Whether or not marmosets also respond to feline and snake vocalisations in the same manner is addressed in this thesis.

It has also been suggested that acoustic stimuli used independently of visual cues prevent the prey species from confirming the location of the predator, which may have an impact on the type of response elicited, particularly for species that mob or approach a predator (Arnold *et al*., 2008). Acoustic cues may be detectable prior to visual cues, as these may travel around physical obstructions and may be detected from a greater distance (Dominy *et al*., 2001; Khayutin, 1985). For silent predators, other auditory indications of their presence may also serve as warning for prey. Black-mantle tamarins (*Saguinus nigricollis*), for instance, have been observed to react to the sound of wing flapping by a raptorial bird and they were able to distinguish this sound from the sound made by the wings of other avian species (Izawa, 1978). It is possible that common marmosets, as a close relative of black-mantle tamarins, may also respond to subspecific cues, but this aspect was not tested here.

In summary, initial identification of predators, be this by detection of an odour, sight or sound, leads to a suite of behavioural responses that may indicate anti-predator strategies, such as avoidance (e.g. hiding or climbing a tree), vocalisations and many other types of behaviour. If predatory cues in all modalities provide information that the prey animal can use to assess its risk of predation, it could be possible that multiple cues may improve assessment. The question then arises as to whether one modality is more important than another in eliciting anti-predator responses or stronger responses. This is discussed later in this chapter.

1.4 Use of sensory cues in food recognition

The response of marmosets, or any primate species, to food-based stimuli of any or multiple modalities has received little scientific attention. Recent studies have suggested that some primates (spider monkeys, *Ateles geoffroyi*; squirrel monkeys, *Saimiri sciureus*; and pigtailed macaques, *Macaca nemestrina*) are extremely sensitive to odours associated with natural foods (Dominy, 2004; Hübener and Laska, 2001; Laska *et al*., 2000, 2007; Siemers *et al*., 2007). Although thresholds for some food scents have been tested in these species, the behavioural responses given to pleasant (food-based) and aversive (predator-based) olfactory stimuli have not been explored. Wild marmosets have been observed to eat fruit, tree exudate and eggs, as well as live insects, lizards and small birds (Clarke, 1994), and it would be hard to believe that sounds and scents play no role in attention to potential food items.

Most reports of olfactory-guided foraging in primates are restricted to nocturnal species, particularly prosimians, and are largely anecdotal (Dominy *et al*., 2001). The use of long-range cues in food detection has been less studied than short-range food detection, despite the low-weight odour molecules of fruits and flowers most likely designed to travel long distances (Janzen, 1983). However, it is known that primates often sniff individual fruits before eating or discarding them (Kappeler, 1984). Olfactory cues may signal edibility since colour may not always be a good indicator (Dominy *et al*., 2001). In addition, food-related olfaction may improve discrimination of aversive stimuli. Some plant and animal species advertise their unpalatability and toxicity by producing specific odours that are designed to deter consumption (Dominy *et al*., 2001).

Olfactory cues of ethanol in fruits may represent sensory cues of associated caloric and physiological rewards to primates (Dudley, 2000). Low levels of ethanol exist in ripening fruits and correlate positively with concentrations of soluble sugars; frugivores may have evolved adaptations to sense and detoxify low levels of ethanol (Dominy, 2004). Therefore, ethanol could be an olfactory cue for foraging anthropoid primates, to assist in detecting and directing searches towards edible fruits (Dudley, 2000). Laska and Seibt (2002) showed that squirrel monkeys (*Saimiri sciureus*) and pigtailed macaques (*Macaca nemestrina*) have lower thresholds for aliphatic alcohols than rats, a species traditionally considered to be macrosmatic. Ethanol also produces responses in the nerve cells that convey taste and somatic sensations from the oral cavity (Dominy, 2004). In rhesus macaques, the responses of the chorda tympani, glossopharyngeal and trigeminal nerves to ethanol is far stronger than that measured in dogs, cats and Norwegian rats (Danilova and Hellekant, 2000, 2002; Hellekant *et al*., 1997). These results are consistent with the theory that ethanol is important in the regulation of primate foraging behaviour (Dudley, 2000). Being able to discern ethanol may have strong adaptive advantages for primates (Dominy, 2004).

Concerning food detection using auditory cues, much remains unknown. Some primates (including marmosets, Vitale *et al*., 2003) are known to produce food-related calls, which may serve as communication to group members regarding the discovery of food and its location, quality, quantity, type and identification (Chapman and Lefebvre, 1990; Dittus, 1984; Hauser *et al*., 1993; Kaplan, 2004; Menzel and Juno, 1985; Vitale *et al*., 2003). However, food detection via acoustic cues, such as crickets chirping, insects moving through leaf litter or even fruit falling from trees, especially in diurnal primates, has gone largely untested.

1.5 Multimodal signals

Partan and Marler (1999) theorised that animals may send and perceive information from multiple sensory modalities in any given signal. Endler had suggested in 1993 that when animals use multiple sensory channels to send a signal they would send different information through each modality. There is some evidence to support this, but it is not always the case. The meanings of components from a multimodal signal may be redundant or non-redundant (Partan and Marler, 1999). Not all components engender information (Rowe, 1999*a*) and some may be registered but not elicit a response in the receiver (Hebets and Papaj, 2005). These types of signals are harder to study and, for obvious reasons, are less represented in the literature (Hebets and Papaj, 2005).

Redundant signal components presented individually should have equivalent effects on a perceiver as they relay the same information. For example, components *a* and *b* both elicit response *x*. Combined, they may produce an equivalent (*x*) or enhanced (*X*) response from the receiver (Partan and Marler, 1999) (Table 1.1). Enhancement appears to be a more common form of redundant signalling (Partan, 2004). In this context, 'redundant' refers to the shielding of a message from possible flaws in transmission (such as ambiguity or noise) by repetition and predictability (Pinker, 1994). In this way, redundancy increases the odds of predictability of the signal's meaning, eliminating any vagueness that may be present in the message. The courtship display of the fruit fly (*Drosophila melanogaster*) has been used as an example of redundant, enhanced, multimodal signalling (Partan and Marler, 2005). Rybak *et al*. (2002) found that when only the acoustic playback of the wing-vibration song (component *a*) from *D. melanogaster* was displayed during courtship, 37% of males had a successful mating (response *x*). When only the chemicals from the male's cuticle (component *b*) were presented, 10% of males were allowed to mate (response *x*). However, when the two components of the male's courtship were presented simultaneously, there were significantly more successful matings (61%) (response X) than for the individual components alone (Rybak *et al*., 2002).

Table 1.1. Multimodal signalling classification. The information presented here is taken and summarised from Partan and Marler (1999).

Sensory Cue	Response	Multimodal signal	Response	Multimodal signal type (R = redundant; NR = non-redundant)
a	x	ab	x	Equivalent (R)
b	x		X	Enhanced (R)
c	x		xy	Independence (NR)
d	y	cd	x or y	Dominance (NR)
			$X/_x$ or $Y/_y$	Modulation (NR)
			z	Emergence (NR)

Non-redundant signalling is more complex than redundant signalling and there are fewer examples of it in the literature (Partan and Marler, 2004). Rowe (1999*b*) suggests that the small number of examples of non-redundant signalling may be a reflection of the potential detriments to this type of signalling, i.e. response time and accuracy may be affected due to the potentially conflicting information provided in the signal. This would therefore make non-redundant communication less beneficial to the sender. However, non-redundant signals also provide a means for the signaller to send more information content per unit of time (Møller and Pomiankowski, 1993; Partan and Marler, 1999, 2005).

Unlike redundant signalling, the components in non-redundant signals elicit different responses when tested individually. When the components are combined there are four possible outcomes: independence, dominance, modulation and emergence (Partan and Marler, 1999) (Table 1.1). Independent, non-redundant signal components produce the same responses in the receiver both when presented individually and when combined. For example, component *c* evokes response *x*, component *d* evokes response *y*, and combined *c* and *d* components (*cd*) produce *x* and *y* responses (*xy*). Dominance outcomes occur when the response *x* elicited from component *c,* but not *d,* is also produced when *cd* is presented. If *cd* evokes *X* response, this is a modulation of the typical *x* response from component *c* (Markl, 1985). A modulated response may be either an enhanced response (like that seen in redundant signalling) from the original behaviour observed in response to the single sensory cue, or a reduced response (not seen in response to redundant signals). A new response, or emergence, occurs when the response to components *cd* is *z*. Modulation appears to be the most common subcategory of non-redundant signalling; few examples of dominance and emergence have been found (Partan and Marler, 2005). Rowe (1999*b*) argues that dominance signalling is unlikely to exist in natural communication systems as it would not benefit the signaller to provide two cues if only one was important. However, Partan and Marler (2005) suggest that compound learning, in which one component is more intense than another and thereby overshadows the secondary component (Pearce, 2008), may be similar to the dominance category – although this, they say, appears to be rare.

Persons and Uetz (1996) found that wolf spiders (*Schizocosa ocreata)* watch prey (response *x*), such as live crickets, when they can be visually observed (stimulus *c*); however, the vibrations from substrate-borne oscillations from crickets (stimulus *d*) produces no response (response *y*). When vibratory and visual cues are combined, the length of time the spider spends watching the crickets increases (response *X*). This is an example of non-redundant modulation. Stauffer and Semlitsch (1993) tested the tadpoles of two frog species, *Rana lessonae* and *R. esculenta*, for their response to chemical and tactile cues of a predatory fish. The tactile cue – the movement of water similar to that caused by a large fish (stimulus *c*) – produced no response in the tadpoles (response *x*), while the chemical cue – water from the fish tank (stimulus *d*) – elicited an escape response (response *y*). When these cues were combined, the response shown by the tadpoles was *Y*, another example of modulation. Visual cues (stimulus *e*) were also presented to the tadpoles, but responses did not differ significantly from control treatments either when tested individually or when tested in conjunction with the tactile cues (Stauffer and Semlitsch, 1993). However, given that tactile cues alone also produced a weak response, it is possible that different outcomes would have been achieved had they tested visual cues with chemical cues, and also visual, tactile and chemical cues all together. Few primate studies have tested more than two modalities at a time (e.g. Evans *et al*., 2005; Ghazanfar *et al*., 2005), especially not in predation or food-related situations.

Modulated, non-redundant signals are implied in the 'threat-sensitivity predator avoidance hypothesis'. This theory predicts that predation risk increases with multiple predatory cues, and therefore the behavioural responses of prey animals also increase: response *X* (Helfman, 1989). That is, as prey are presented with cues representing a predator in multiple modalities, there is a potential additive effect of the cues providing additional information (Helfman, 1989; Smith and Belk, 2001). There seems to be a neurological basis for this hypothesis: the firing rate of multisensory neurons (neurons capable of carrying information from different modalities) appears to increase in an additive, or enhanced, way (Stein and Meredith, 1993), which allows stimuli to be viewed as emanating from the same source. The magnitude of the interaction inversely depends on the effectiveness of the unimodal inputs (Nakamura *et al*., 2001; Stein and Meredith, 1993). When the stimuli are spatially or temporally disparate, they trigger inhibitory mechanisms that can suppress, or dampen, the responses to either unimodal cue (Fort and Giard, 2004). Behaviourally, there is some evidence to suggest that multiple cues from a predator may have an additive effect on prey (Helfman, 1989; e.g. Amo *et al*., 2006; Ferrari and Chivers, 2006; Ferrari *et al*., 2008; Smith and Belk, 2001; Zhao *et al*., 2006). Whether simultaneous visual, olfactory and/or auditory cues from food would also have an additive affect is largely unknown; the research presented here was designed to test this.

1.5.1 Alternative terminology

The terminology used when describing the types of multimodal signalling is varied throughout the literature; the above description is that proposed by Partan and Marler (1999, 2005). Horn (1983) offers an alternative nomenclature: the term ‘trigger effect’ refers to a response controlled by different modalities successively, ‘coupling’ occurs when signals from multiple modalities are simultaneous, and a ‘compromise’ refers to a case when the response elicited is a blend of the responses produced by the individual, conflicting components of the signal. The two forms of redundant signalling have also been labelled additive (equivalence) and synergistic (enhancement) (Leger, 1993). In addition, Johnstone (1996) proposed the use of the terms ‘backup signal’ for redundant signalling and ‘multiple message hypothesis’ for non-redundant signalling, while Smith (1977) referred to these as fixed and fluid signals, respectively. Furthermore, the term ‘crossmodal’ is often used instead of ‘multimodal’, particularly in neuroscience, to describe a complex of two or more stimuli which are modality-specific (Stein *et al.*, 2010). The research presented in this thesis follows the terminology used by Partan and Marler (1999, 2005).

1.5.2 Issues in the methodology in the multimodal signalling context

In order to categorise signals, Partan and Marler (2005) suggested that research needs to test responses to each component individually as well as to the combination (the multimodal signal). However, in many cases one or more unimodal components had not been tested, or were found difficult to test (Leger, 1993). Without this information, the type of signal cannot be classified at even the broadest level (Partan and Marler, 2005). In a predation context, this also reduces our knowledge of the full repertoire that prey animals have in order to recognise and respond to a potential predator. My research addressed this by testing sensory cues in three modalities, first individually and then in several multimodal combinations.

The number of behavioural responses measured in a study may also confound accurate classification (Partan and Marler, 2005). If only one behavioural response is measured, the conclusion from the study will apply solely to that behaviour. For example, components *c* and *d* are studied separately, but only behaviour *x* is measured; *x* is present in response to both cues. The combination *cd* is then considered; the response is *X*. It would therefore be concluded that this is an example of redundant enhancement signalling. However, should behaviour *y* also be measured but found to occur only in response to *d* and *cd*, then this signal would be reclassified as non-redundant modulation (Partan and Marler, 2005). Therefore, it is important to understand all the behavioural responses to a particular individual signal first. I followed this methodological proposal closely. Threat of predation may elicit very strong, obvious reactions in prey, such as flight or mobbing (e.g. Australian magpies, *Gymnorhina tibicen*, Kaplan *et al*., 2009). However, other behavioural responses, perhaps less conspicuous, may also be displayed and could provide further insights into prey responses upon detection of a predator. These have been included in my study of responses to aversive (predatory) and pleasant (food-based) stimuli in marmosets.

Multiple social signals may be emitted simultaneously, but are not necessarily received together (Partan and Marler, 2005). Sequential receiving of components may occur because light travels faster than sound (Wickler, 1978), which travels faster than odours (Partan and Marler, 2005). Perception may also be variable due to the differing time-scale and range properties of each modality. When components are received sequentially, the first component to be perceived may have a greater effect on the behavioural response and reactions than the subsequent components (Partan and Marler, 2005). However, as modalities have varying processing times, neurons may be optimally excited when stimulated some time apart (Miller and D'Esposito, 2005). For example, in the cat brain, auditory information is apparently transmitted more rapidly than visual information (Stein and Meredith, 1990). These problems associated with multimodal signals needed careful consideration for the method used in my experiments, and great pains were taken to ensure that the sensory cues were presented as closely together in time as possible.

Few studies have considered a third signal component, if present, particularly for non-redundant signalling (component *e*). The majority of studies discussed so far have examined the responses to two sensory channels (bimodal). However, if learning is improved through the use of multiple modalities, as suggested by Rowe (1999*b*) and Stein and Stanford (2008), then it stands to reason that the more ways in which one can perceive and ultimately interpret the information, the faster and more discriminatory the learning process may be. This should be particularly important in predator recognition. The few studies to consider trimodal (and more modalities) combinations have been aimed at understanding sexual systems (e.g. Bielert, 1982; Ewing, 1983; Rybak *et al*., 2002). One of the aims of my research was to test how different and multimodal combinations of aversive (predatory) and pleasant (food-based) sensory cues influence behaviour and which, if any, modality elicited the strongest responses.

Of course, the other issue in studying multimodal signalling using predator- and food-based stimuli is that these stimuli are essentially inert. That is, a predator does not signal to its prey, nor does food signal to its predators. Instead, cues within the sensory stimuli may contain information that can be perceived and interpreted by a non-conspecific (prey or predator of a different species). A predator may vocalise, signalling its location to conspecifics and prey may then use this information to avoid the area but this cannot be studied specifically as a sender-receiver signalling system between predator and prey. Signalling is an intention to communicate and send information to a conspecific (Coss *et al*., 2005). Partan and Marler (2005) did provide predator-prey examples of multimodal signalling but this is essentially incorrect because there is no intention of sending any information that may be in the cues within the predator; however, prey may learn to read the information and use it to determine the appropriate response in the situation. Their theory was inherently socially-based, i.e. intentional communication between conspecifics. Therefore, it is important to make the distinction here that the intention of my research was not to study multimodal signalling per se; instead, I used Partan and Marler’s theory of multimodal communication and signalling to provide foundations for the study of the effect of multiple stimuli pertaining to the same type (predator or food) of stimulus on the marmosets.

1.6 Conflicting information

To reiterate, we now know that information is not sent, received or processed in discrete, modal-specific sensory channels. Information provided in one modality may be modulated by other sensory channels, but each perceptual component may not have equal weight in processing importance (Partan and Marler, 2005). This is particularly important when conflicting social signals are presented through different sensory modalities. It has been argued that in some cases there may be a dominance effect by the most ‘persuasive’ sensory cue (e.g. Rock and Victor, 1964; Welch and Warren, 1980). Environmental context may also play a role in the dominance of a particular sensory modality at any given time. Alternatively, cross-modal stimuli, derived from the same event at the same location, produce interactions that may significantly enhance the response of the multisensory neuron that is activated by the most effective of the individual modality-specific stimuli (Wallace and Stein, 2001).

When stimuli occur from different spatial locations, such as would occur from simultaneous but different events, they produce either no multisensory interaction or depress the response of the neuron by an inhibitory effect (Meredith and Stein, 1996). This allows the animal to respond to either of the conflicting stimuli, which may have important implications in certain situations. A study by Skals *et al*. (2005) tested how male moths (*Spodoptera littoralis*) responded when presented with simultaneous, conflicting stimuli: the olfactory cue from a female moth and the auditory cue of a predator (artificial bat echolocation vocalisations). They found that the stimulation of one sensory modality could modulate the flight direction in response to information from another sensory modality. As the amount or quality of sex pheromone from the female moth increased, the male moth tended to decrease response to the auditory cue of the bat. However, if the intensity of the artificial bat cries was increased, simulating closer proximity of the potential predator, the moth responded as though evading the predator. While such behaviour in a natural situation would incur a greater risk of predation, it shows that the moth's response to the sensory conflict is a trade-off dependent on intensity, suggesting that the behavioural thresholds involved in this system are dynamic and context-dependent (Skals *et al*., 2005). This study also shows that testing in the laboratory under unimodal conditions may not produce behavioural thresholds that occur in natural situations (Skals *et al*., 2005).

Despite previous claims that one type of sensory stimulus may be dominant over another (e.g. visual over acoustic, McGurk and MacDonald, 1976; acoustic over olfactory, Agee, 1988), it seems likely that, to respond appropriately to stimuli in different contexts, the sensory modalities should not interact in an organised system. In fact, it is now strongly believed that sensory information is not processed in a passive, hierarchical manner (Small, 2004). Instead, the interaction between modalities during processing and integration is more likely to be fluid, allowing animals to respond differently, and appropriately, to the same stimuli in different situations. Animals may make trade-offs in the decisions they make regarding their daily activities (Lima and Dill, 1989).

1.7 Predation risk versus foraging

Although animals can perform two tasks at once, such as vigilance and foraging, they cannot usually perform both with full attention simultaneously (Dukas, 2002). A prey animal can be faced with predatory cues while foraging and therefore needs to assess whether to continue foraging in the face of a potential threat. The two situations are not just conflicting but extreme opposites, i.e. predatory cues are aversive while food cues are pleasant. There has been some work carried out, using chickens (Rogers *et al*., 2004), showing that when the chickens were presented with a visual food task and a visual cue of a predator simultaneously, they were able to attend to both only when they had fully lateralized brains. Dark-reared chickens developed no hemispheric specialisations and performed poorly in the conflicting stimuli task and also were unable to learn to improve from first performance (Rogers *et al*., 2004). The risk of actual predation needs to be weighed up and appropriate countermeasures taken without overly detracting from other requirements, such as food intake (Brown and Kotler, 2004). As discussed previously, marmosets alter their behaviour in the face of a predation risk by reducing foraging, but they do not stop foraging entirely (Caine, 1998). The state of the prey may affect their response; hungry fish, for example, are less responsive to predators than satiated fish (Gregory, 1993; Magnhagen, 1988). In addition, not all predator cues may indicate an immediate risk of predation, and so circumstances may influence responses instead of constraining foraging behaviour (Lima and Dill, 1989).

In addition, the ability to attend to both stimuli – food and predator – may be constrained by limited attention, i.e. the amount of visual information that is processed at any given time

(Dukas, 1998; Kastner and Ungerleider, 2000; Milinski, 1990). Auditory and olfactory sensory systems may also face the same constraints (Mondor and Zatorre, 1995; Nams, 1997); irrelevant auditory stimuli become ‘background’ or ‘white’ noise (Avison, 1984; Brumm *et al*., 2004). The rate at which the brain processes information is lower than the rate at which information is encountered in the environment (Dukas, 2002) and these processes are likely to be focused on essential stimuli (Pashler, 1998). This allows the animal to focus primarily on a few sounds that may be important at the time and reduce distraction by other auditory cues. It is harder to determine how this system works for olfaction, and few, if any, studies have looked at constraints on olfactory processing, but it is most likely that there are limitations as to how much olfactory information the brain can process at any given time.

1.8 Summary

The study of the recognition of predator cues by primates has focused primarily on a single modal approach. Indeed, most of the literature on this topic is primarily about a visual method of recognition. Yet we know that marmosets have the sensory capabilities of detecting and strongly responding to auditory and olfactory as well as to visual stimuli. It is important to test these responses because the marmosets should respond to these stimuli differently as the information provided within these stimuli may be different, even when of the same type (aversive or pleasant). Whether one modality has a stronger influence in eliciting a response to the combination is also unknown, but is particularly important when an animal is faced with two simultaneous but conflicting stimuli. The research presented in this thesis was concerned with these questions.

Using the theoretical model by Partan and Marler (1999) as a reference point and an existing hypothesis, I aimed to empirically test, not just record (Coss, 2008) how the marmosets respond to each individual component of a signal, and if and how their responses are altered by multiple stimuli presented simultaneously. The method adopted for finding and testing suitable stimuli that are attractive/pleasant and those that are repellent/aversive is presented in Chapter 2. Chapter 3 presents results of establishing robust stimuli in all three modalities signifying different things (food or danger). Chapters 4, 5 and 6 present, in sequence, the results of testing the marmosets' response to 1) individual stimuli from the three modalities, 2) combinations of related stimuli, and 3) combinations of conflicting stimuli. The last two Chapters are an extension of the question of information content and ability to discriminate signals of similar or dissimilar type. The experiment presented in Chapter 7 tested the marmosets' responses to predator vocalisations only and sought to show whether audition alone is capable of arousing specific responses in predator-naïve captive marmosets. Finally, Chapter 8 presents an experiment designed to test whether there are social and cognitive aspects to a specific set of responses (facial expressions) performed by individual marmosets in response to a range of aversive and pleasant stimuli.

CHAPTER TWO

GENERAL METHODS

The methodology presented here broadly details the subjects and housing (Section 2.1), stimuli (Section 2.2), methodology (Section 2.3), behaviour scored (Section 2.4) and statistical analysis (Section 2.5) used in Experiments 1 to 5. Where experiment-specific variation was required, it is included in the methods section of the relevant chapter. The method used for the last experiment (Experiment 6) is described separately (Ch. 8).

2.1 Subjects and housing

The 15 common marmosets in total used in this study (Table 2.1) were housed at the University of New England, Armidale, Australia. Typically 12 marmosets were used in most of the experiments (2, 3, 4 and 5; ten were used in Experiment 1 and eight in Experiment 6), but three other individuals that were used in Experiment 1 had to be replaced, taking the total number of marmosets used in this research to 15. All individuals were captive-born from family lines bred in captivity for several generations. Within this group of subjects there were two family groups – Group 1 had 10 individuals (5 female/5 male) and Group 2 had four individuals (1 female/3 male) and one unrelated individual (female). At the beginning of the research project (February 2008), all 15 marmosets (7 females/8 males) were between the ages of 24 and 161 months. The ages of males and females were not significantly different (two-tailed, Mann-Whitney U-test, $Z = 0.00$, $p = 1.00$).

The marmosets were housed in same-sex groups of 2–3 related individuals across three separate home-rooms (4.5 x 3.0 x 3.5 m) within the housing facility (Fig. 2.1). Three marmosets were housed separately due to social aggression. Each family group or individual was housed in a separate home-cage with a maximum of three groups and/or individuals per room.

Table 2.1. The marmosets used in this study, including sex and age at start of experiments (February 2008) and family associations (0 refers to an individual unrelated to any other marmoset tested). 1a refers to the olfactory trials and 1b refers to the auditory trials in Experiment 1. Individuals with an asterisk (*; 5, 8 and 15) were initially used in experiments but were later replaced.

	Marmoset	Sex	Age (months)	Family group	Experiments
1.	Ness	F	24	1	1b, 2, 3, 4, 5, 6
2.	Bandit	F	36	1	2, 3, 4, 5, 6
3.	Mogwai	F	46	1	1a, 1b, 2, 3, 4, 5, 6
4.	Jade	F	47	2	1a, 1b, 2, 3, 4, 5, 6
5.	Jardine*	F	51	1	1a
6.	Mackybe	F	51	1	1a, 1b, 2, 3, 4, 5,
7.	Ash	F	161	0	1a, 1b, 2, 3, 4, 5
8.	Snowy*	M	24	1	1b
9.	Smokey	M	36	1	1a, 2, 3, 4, 5, 6
10.	Ranger	M	41	1	1a, 2, 3, 4, 5 ,6
11.	Gizmo	M	46	1	1b, 2, 3, 4, 5, 6
12.	Flint	M	47	2	1a, 1b, 5
13.	Inca	M	54	2	1a, 1b, 2, 3, 4, 5
14.	Aziz	M	84	1	1b, 2, 3, 4, 5, 6
15.	Delta*	M	150	2	1a, 2, 3

Home-cages (1.0 x 2.0 x 2.0 m; mean cage space 3.85 m^3 per marmoset) were connected to indoor rooms (4.0 x 4.0 x 3.5 m) and outdoor cages (1.7 x 1.7 x 2.6 m) via wire runways (23 x 23 cm, 220 cm up from the ground) (Fig. 2.1). The cages and indoor rooms were furnished with vertical, horizontal and diagonal climbing structures and play equipment, such as hessian-covered dried *Eucalyptus* branches, dowel, rope, chain and tunnels of varying lengths and widths, and contained at least one nest box with towel bedding material provided. Access to the runways could be controlled manually by slides at various points in the system. Each home-room had a corresponding indoor room and outdoor cage that one marmoset group or individual could access at a time. Access was rotated between home-cages every few days. The outdoor cages were attached to one side of the outer wall of the animal house under a veranda. The veranda was enclosed at each end and along the length of the passage with open-spaced brick walls that allowed light and some weather elements to pass through. The marmosets could view trees,

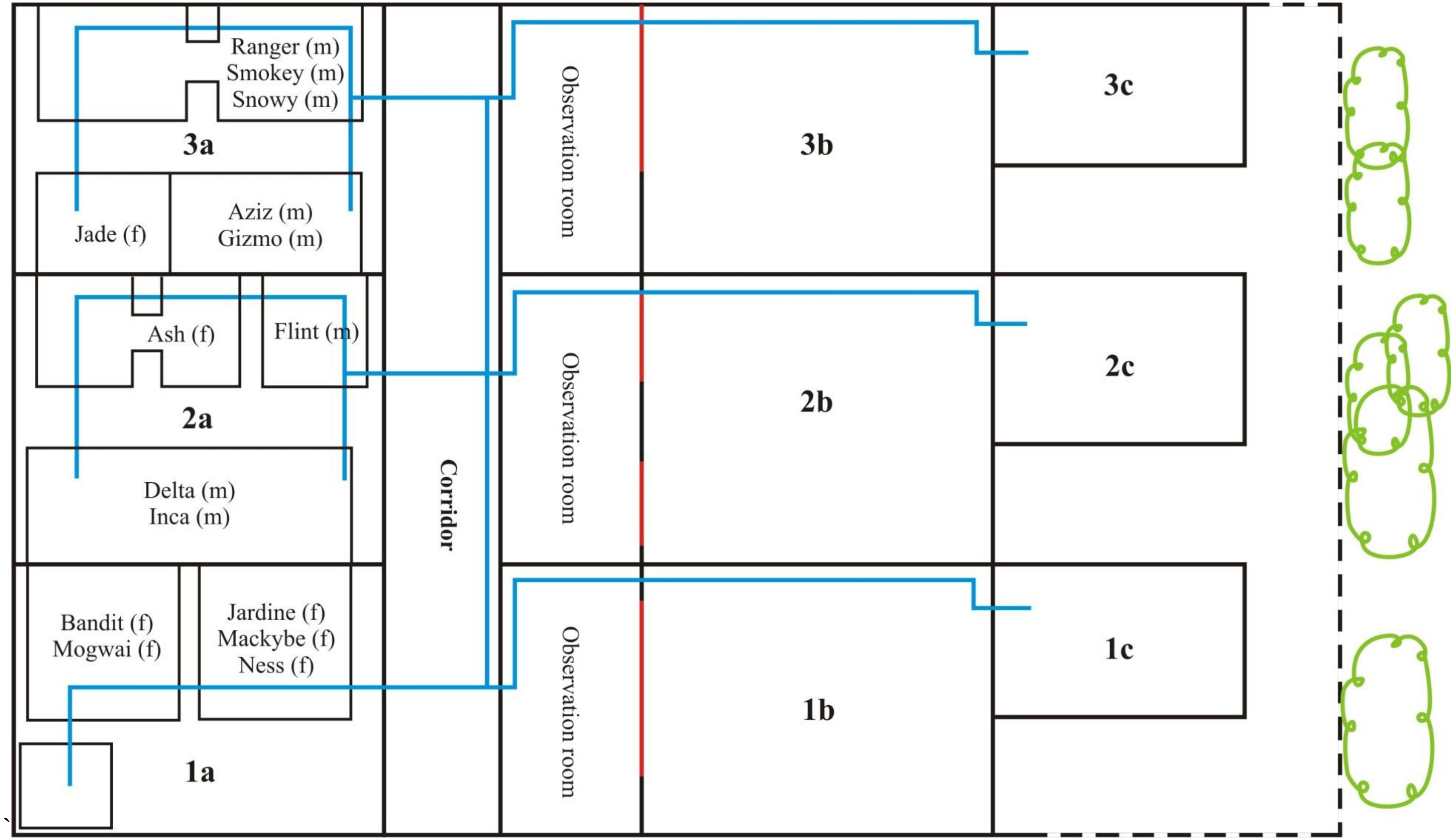


Figure 2.1. Layout of the marmoset housing facility. Home-rooms (1a, 2a, 3a) with cages and occupants, are on the left, the building's corridor divides the home-room from the observation rooms of each indoor room (1b, 2b, 3b). The blue lines indicate the runway network. Access for each group was restricted to corresponding room numbers, i.e. 1a to 1b to 1c but all rooms with same letters were of similar layout and furnishing. During experiments, access to the home and outdoor cages was blocked by runway partitions. The red lines show the locations of the one-way mirrors in observation rooms from which marmosets could be observed in the indoor rooms.

bushes (including small birds, such as sparrows and wrens, in the bushes), cars, people, and possibly a cat used for control of mice in a neighbouring building. They would have also been able to hear sheep, pigs and chickens, but it is unlikely the marmosets would have seen them.

All experiments were conducted in the indoor rooms, which were divided from observation rooms by a one-way mirror to allow the experimenter to observe the marmosets without being seen.

The home-rooms and indoor rooms were temperature-controlled at between 18^{o}C and 30^{o}C with 54.5% ± 1.4% humidity, and had an automatic day–night cycle of 12h : 12h (07:00h–19:00h light period). The outdoor cages received sunlight, and ultraviolet lights (350–390 nm) in the home-rooms were turned on for 30 minutes per day. The home-rooms were also equipped with skylights to allow in natural light. The home-rooms were cleaned three times per week and the indoor rooms were swept once a week. The hessian on the branches was replaced every few months.

The marmosets were provisioned once daily between 12:00h and 14:00h with sufficient food to last for a 24-hour period. The diet varied daily and included meatloaf, polenta cake (Appendix I), a range of fruit and vegetables (including apples, oranges, bananas, corn, beans and sultanas), yoghurt, peanuts, cereal, dog pellets, cheese, brown bread, boiled egg and vitamin supplements. Mealworms and crickets, which were bred and maintained on site, were given to the marmosets as occasional treats or as food rewards during some experiments. Water was provided *ad libitum* from drinking bottles attached to the wire of each cage and in the indoor rooms. The water was changed daily.

2.1.1 Identification of individuals

Although the number of marmosets per cage and room was small, and the cages carried labels of the names of each individual housed within, it was important to be able to recognise each marmoset using its individual features alone. Collars and tags were not used because they were regarded as a potential choking hazard. The experimenter’s ability to identify individuals was as important for testing individuals separately outside their home-cages as it was for the welfare of the marmosets. In case of an escape, for example, the individual had to be returned to its correct cage to avoid social problems.

Sex, distinguishing facial features, tail length, body size, fur colour and behavioural characteristics were used to identify individuals. These traits were distinctive among individuals. The experimenter also regularly participated in the roster system for feeding and caring for the marmosets so that both animals and experimenter were comfortable and familiar with each other from daily interactions; this was considered a precondition for any research involving marmosets or other animals in our laboratory. All marmosets were able to survey the comings and goings in the Animal House by their unrestricted access to the corridor section of the runway (installed above door height) of which the marmosets made extensive use. Positive identification was tested by a long-term carer of the colony who confirmed that correct identification was achieved by this experimenter in all cases (100%) prior to commencement of any trials.

2.2 Stimuli

As responses to pleasant, aversive and neutral stimuli in visual, auditory and olfactory modalities were to be tested, it was important to identify stimuli to which the marmosets might respond consistently and in specific ways, i.e. showing strong aversion, attraction or indifference. The visual stimuli to which the marmosets were known to respond strongly (negatively and positively) were well established in our colony (Clara *et al.*, 2008; Cross and Rogers, 2006; Gordon, 2007; Hook, 2004) and details are described below. However, auditory and olfactory experiments had not been conducted previously, hence this required an initial experiment and details of the method to obtain stimuli in both these modalities are therefore described separately in the following chapter (Ch. 3).

2.2.1 Visual stimuli

The visual stimuli selected are shown in Fig. 2.2.

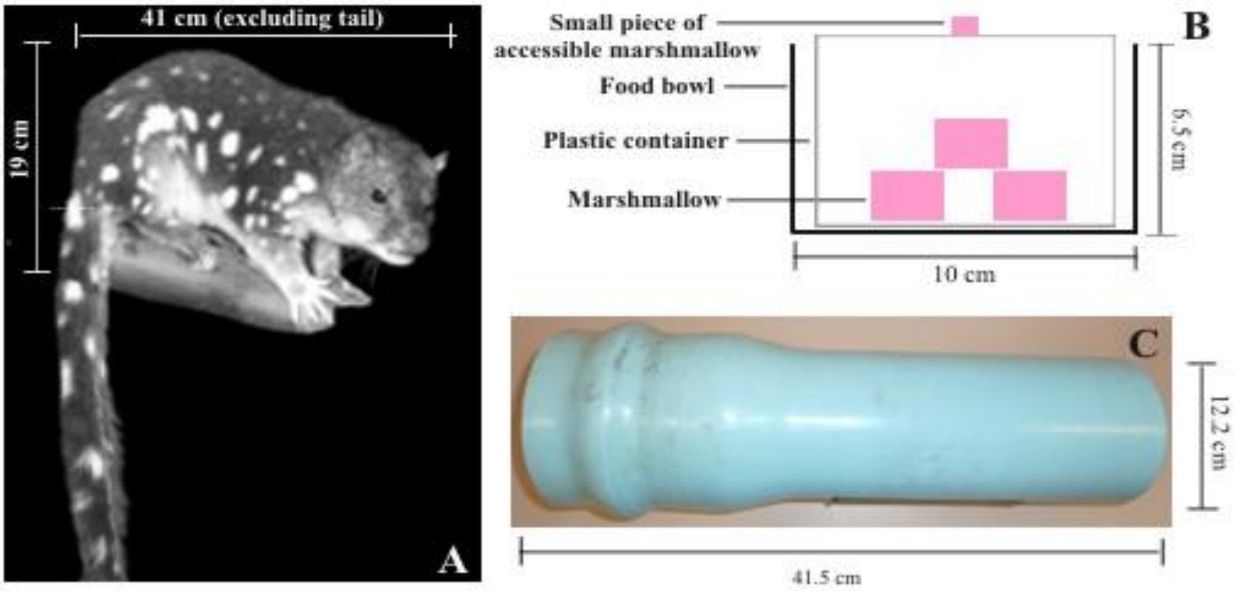


Figure 2.2. Visual stimuli. A – aversive visual stimulus: image of a live quoll (*Dasyurus maculatus*); the measurements refer to the taxidermic specimen used in the experiments, B – pleasant visual stimulus: outer part a white food bowl with a cover, inner part a lidded, clear plastic container on which a small piece of retrievable marshmallow was placed and containing inaccessible but visible additional marshmallow, C – neutral visual stimulus: a piece of PVC tubing used regularly in their housing facility as a climbing structure.

2.2.1.1 Aversive visual stimulus

Previous experiments (Gordon, 2007) involving the same marmosets had shown the effectiveness of a taxidermic specimen of a spotted quoll (*Dasyurus maculatus*) (Fig. 2.2 A) as an aversive visual stimulus. It was found that the quoll's presence elicited the most consistent and most strongly negative response compared to a statue of a cobra, a taxidermic specimen of an eagle, and the frog statue and shoes mentioned previously (Gordon, 2007). All marmosets consistently mobbed the quoll, showing high levels of mobbing vocalisations, piloerection and teeth baring (Gordon, 2007). The mobbing vocalisations produced in response to the quoll in both trials of Experiment 2 were compared to the trials used by Gordon (2007); no statistically significant difference was found over the three tests after a two year gap between Gordon's and my own experiments (repeated measures ANOVA, $F_{(2,22)} = 1.26$, $p = 0.30$). Although the quoll is an Australian carnivorous marsupial that the marmosets would never have seen before, it resembles in type a small feline, similar to the margay (*Leopardus wiedii*), which is thought to be a natural predator of marmosets (Passamani, 1995). The quoll is a relatively small mammal, although it is larger than a marmoset. On average a quoll is 40-60 cm long, excluding the tail, and weighs about 1.3 kg (Strahan, 1995); in contrast, common marmosets are on average just 16 cm long, excluding the tail, and between 250 and 400 g in weight (Rowe, 1996).

2.2.1.2 Pleasant visual stimulus

Pink marshmallow (Coles supermarket brand) was known to be a highly desired food item of the marmosets in our colony and they always retrieved it quickly when it was given to them as a treat. Other studies have also found that marshmallow is a highly preferred food item (e.g. Caldwell *et al*., 2009; Koenig, 1998; McKinley *et al*., 2003). The ingredients in the Coles supermarket brand marshmallow were glucose fructose syrup (from wheat), sugar, dextrose (from wheat), pork gelatine, thickener (1401 from maize), beetroot juice concentrate, elderberry juice concentrate, natural flavourings, potato starch, vegetable fat (palm).

As shown in Figure 2.2 B, this stimulus consisted of a white ceramic food bowl (6.5 cm deep, 10 cm diameter) to which the marmosets were accustomed. A small piece of dried marshmallow (approximately 0.05 g) was placed on top of the lid of the plastic container for the marmosets to access and retrieve. This piece of marshmallow was dried to reduce odour. Inside this bowl was a clean plastic container (6 cm deep, 8.5 cm in diameter) with three large pieces of marshmallow inside. While the three pieces of marshmallow inside the container were not accessible, for health reasons, they improved the visibility of the stimulus from a greater distance and added enticement. The marmosets' ability to approach, touch and consume the small piece of marshmallow provided a basis for comparison with the other two visual stimuli that they could also touch.

2.2.1.3 Neutral visual stimulus

A length (41.5 x 12.2 cm) of PVC tubing (Fig. 2.2 C) used commonly as a climbing structure in the marmosets' enclosures was trialled prior to testing. The marmosets showed no visible or audible signs of interest in the tube and it was therefore used in Experiment 2 as the neutral visual stimulus. The tube was washed before conducting experiments to remove any odours of marmosets.

2.2.2 Olfactory and auditory stimuli

Olfactory and auditory stimuli had to be determined experimentally and the method had to be adapted to suit the modality in each case. An extensive range of stimuli had to be tested before an aversive and pleasant stimulus could be selected for the experiments. Details are provided in Chapters 3 and 4.

2.3 Experimental procedures

All experimental procedures were approved by the University of New England Animal Ethics Committee (AEC 08/028, 08/082, 09/054, 09/101, 09/176) and were in accordance with the *Australian Code of Practice for the Care and Use of Animals for Scientific Purposes edition 7* (National Health and Medical Research Council, 2004). The experiments were conducted between July 2008 and February 2010.

Except for responses to odours in Experiment 1 which were tested in the home-cages (as described in Section 3.2.2.1), all other experiments were conducted in the indoor rooms. This had two advantages. Because of the one-way mirror in the darkened observation room, the experimenter could 1) remain undetected by the marmosets, and 2) marmosets could be isolated visually from conspecifics. Each marmoset was tested individually for several reasons: it was important to record and be able to identify individual vocalisations and to ensure that the behaviour of the marmoset remained as uninfluenced as possible by the actions and responses of conspecifics, and to create optimal conditions for focussed attention on the stimulus being presented. It is also well-known that marmosets may experience stress in isolation (Cross and Rogers, 2004; Kaplan *et al*., 2012; Norcross and Newman, 1999). However, all these marmosets had been accustomed in many years of behavioural experiments to wander over to the playrooms by themselves and they certainly volunteered to do so because the indoor room was designed as an enrichment and playroom area, in which occasionally very special treats could be obtained. It is the latter aspect that made it very easy to get individuals into the indoor room and search for something new. The tests themselves were also of such short duration that conspecifics were able to join them (or the tested individual left) after a short period of time.

Experiments were conducted between 09:00h and 12:00h, prior to feeding. In each case, the marmoset to be tested was separated from its home-cage and encouraged into the indoor room, using small pieces of banana and mealworms if necessary. No marmoset was physically handled or transported to the indoor room. Partitioning slides were used to block access along the route and to contain the marmoset in the indoor room. A small section of the runway at the entrance of the indoor room was accessible by the marmoset throughout the testing period to provide it with an elevated hiding spot should the marmoset require such a feature in response to an aversive stimulus. The marmosets were left to settle for a few minutes before pre-testing observations began. At the completion of the post-testing period the partitioning slide was removed and the marmoset was encouraged back to its home-cage using food rewards when necessary.

2.3.1 Testing period

The period of testing was based on the attention span of marmosets. The period of exposure was limited to between 30 seconds and two minutes, depending on the experiment. Previous studies in our laboratory had shown that interest in stimuli tended to wane after the first minute (Brown *et al.*, 2010). Even if this was not the case, facing predatory stimuli when alone was presumed to be stressful for the marmosets. Moreover, the intention of this research was to determine the immediate behavioural responses to the stimuli and this purpose was well served by a one-minute period of exposure when presenting single stimuli. However, to ensure that the marmosets had time to perceive all stimuli when presented together (Experiments 3 and 4), they were shown for two minutes. However, only the first minute was used for comparisons between the responses to the combination and the stimuli when presented alone (test period only). The pre- and post-testing periods were two minutes. The experimental procedure for the presentation of combinations of stimuli is detailed in Chapters 5 and 6.

2.3.2 Experimental procedure for presenting individual visual stimuli

Method of presentation had to be adapted to the modalities of the stimuli being presented, suitability to the species being tested and appropriateness for the type of housing environment. The method for presenting olfactory, and even auditory, stimuli was especially challenging and is described in detail in Section 3.2.2 (Ch. 3, Experiment 1) and then modified for Experiment 2 (Ch. 4, as described in Section 4.2.2). Each marmoset was tested using only one stimulus per day, except for Experiments 1 and 6 because the time spent isolated in the indoor room and the stimulus exposure time were kept short.

The visual stimuli were placed on a hessian-covered platform (294 x 60 cm, 77 cm from the ground) inside the indoor room (view from above: Fig. 2.3; side view: Fig. 2.4). A two-directional zippered canvas screen, attached between the edge of the door and the doorframe, prevented the marmosets from seeing the head and body of the experimenter during the placement and removal of the stimulus. All the marmosets saw was an arm reaching into the room; this procedure had been trialled to ensure that the appearance of a seemingly disembodied arm was not going to frighten or startle them. This screen reduced interference by and influence of the experimenter while filming the tests so as to reduce the likelihood of the marmosets associating the stimuli with the experimenter. All due care was also taken to ensure that the marmosets never saw the experimenter with the stimuli outside of experiments. This was especially important because all researchers were required to spend time with the marmosets prior to beginning any experiments to encourage trust and develop a comfortable relationship. It was possible that in doing so the impact aversive stimuli had on the marmosets might have been reduced generally because of its association with a positive experience (the researcher). To reduce the likelihood that the impact of the stimuli being presented was lessened I always covered the stimuli before transporting them around the housing facility, and used the screen to

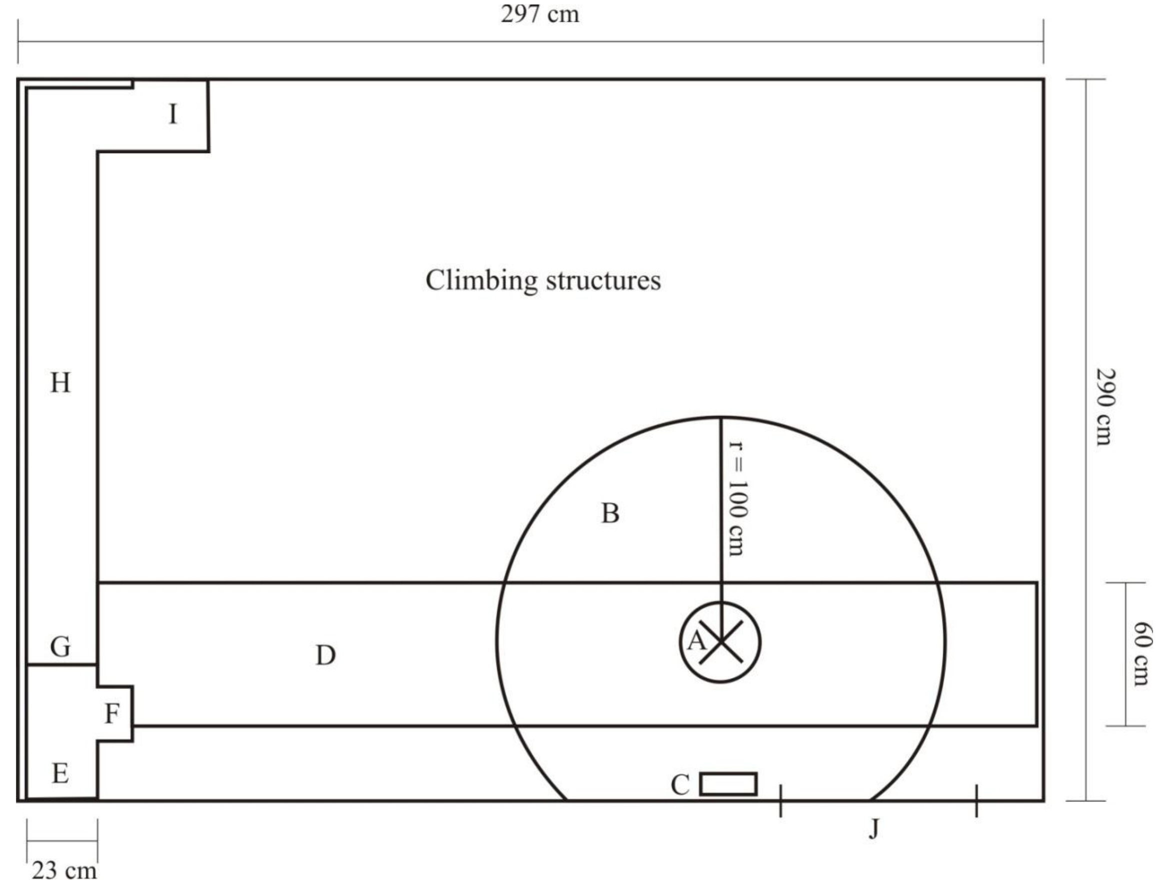


Figure 2.3. View of the indoor room from above. A – visual/olfactory stimulus, B – risk zone, C – speaker for auditory stimuli, D – hessian-covered platform, E – indoor room entry through runway, F – runway entrance with small platform, G – slide blocking passage to rest of runway, H – runway, I – runway exit to outdoor cages, J – screened door to indoor room.

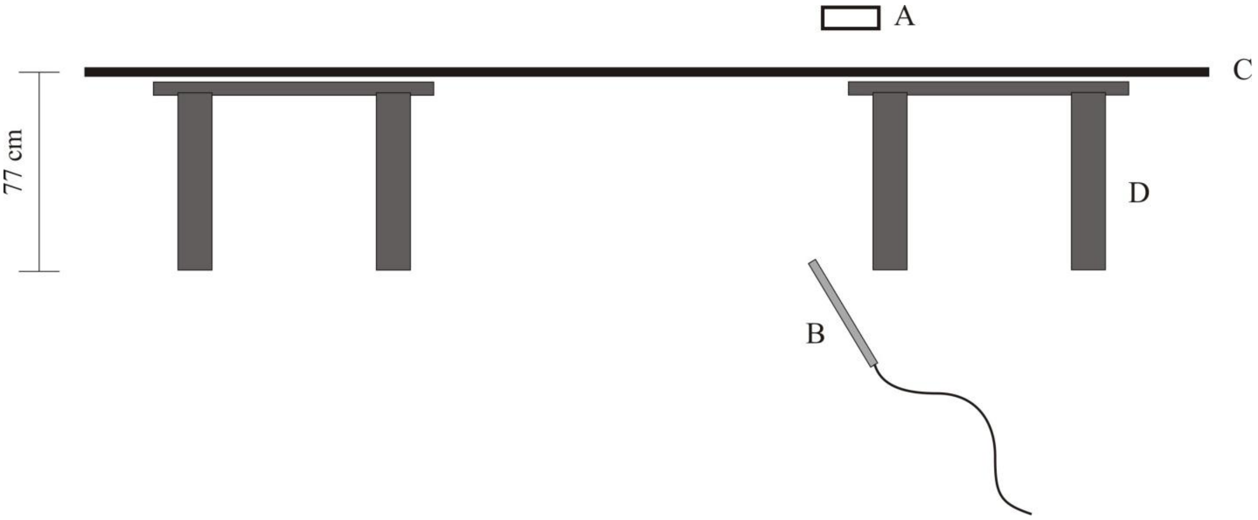


Figure 2.4. Sideview of the experimental set-up. A – speaker for auditory stimuli, B – Sennheiser MKH 418S P48 microphone hidden on the ground, C – hessian-covered platform, D – structural support for platform. Note that the speaker is on a ledge 50 cm behind and 13 cm above the position of the platform. It also marks the horizontal location of the placement of visual and olfactory stimuli.

shield my face and body when placing and removing stimuli in or from the indoor room. The visual stimulus was covered with a cloth prior to being placed in the indoor room. The cloth used was a large piece of cream-coloured calico, also used to tie hessian to the marmosets' climbing branches. Pre-trials showed that the marmosets paid no attention to it. The testing period began with the removal of this cover and ended when the visual stimulus was removed from the room by the experimenter.

The stimuli were tested individually first (Experiment 2) and then in separate experiments, presented in combinations of related stimuli (e.g. aversive visual with aversive auditory) (Experiment 3) and conflicting stimuli (e.g. pleasant visual with aversive visual) (Experiment 4). The methodologies for these experiments are described in detail in Chapters 5 and 6.

2.3.3 Materials used to record behaviour

The marmosets were filmed using two digital Panasonic HD40 video cameras with 40 GB internal memory. These cameras record at 30 frames per second. It was not possible to have a single video camera in a stationary position recording the whole room. One video camera was manually controlled (handheld by the experimenter) and focused on the marmoset for the duration of the experiment in order to film close-ups to capture small and rapid movements, particularly of the face and flanks. The other video footage was focused on the stimulus and immediate vicinity in case the marmoset should approach the stimulus closely. Video footage was downloaded from the cameras to a HP Pavilion dv9000 laptop and then saved to an external hard drive and writable DVDs.

The vocalisations the marmosets made during the experiments were recorded using a digital audio recorder (Marantz solid state recorder PMD670, gain 10; microphone: Sennheiser MKH

418S P48). The microphone was hidden on the floor of the indoor room. The audio recordings were downloaded to the laptop and saved to an external hard drive and DVDs. The files were converted to spectrograms, and the calls identified, using Adobe Audition version 3.0.

2.4 Behaviour scored

Behaviour was scored during the pre-test (2 minutes), test (1 minute) and post-test (2 minutes) periods at intervals of five seconds from the start of each period (pre-test, test, post-test). Responses during pre-tests were scored from the beginning of the video recording. Test period scoring began when the visual stimulus was revealed, and/or when the auditory stimulus commenced playing, and/or when the cardboard cover was removed by the marmoset from the bowl containing the olfactory stimulus and the lid of the container was sniffed. Post-test scoring began after the removal of the stimulus or stimuli from the indoor room and the video camera was again trained on the marmoset. A number of the behavioural responses scored were known to be related to caution or fear (or risk-taking and boldness). These included distance from the stimulus and latency to respond/approach. Other responses which were also scored, are described as follows.

2.4.1 Distance/activity

Distance from the animal to the stimulus is a commonly scored behaviour in predator recognition studies (e.g. Brown and Godin, 1999). This behaviour has been associated with risk-taking and cautiousness and provides an easily measurable distinction between repelling and attracting stimuli. Distance (cm) was measured as the distance of the marmoset from the visual and olfactory stimuli on the platform. These scores were taken at interval samples every five seconds using the time counter on the video footage: 13 data points for a 1-minute testing period (i.e. individually presented stimuli) and 25 data points for a 2-minute testing period (i.e. combined stimuli presentations). The mean of these data points was then taken to get a ‘mean distance from the stimulus’. Distance closest to the visual stimuli (nearest approach) was also recorded.

All olfactory distance measures began at 0 cm. This was because the testing period began only when the marmoset was positioned at the stimulus and sniffed. Due to the 0 cm starting point, testing-period scores of distance were not statistically compared to the pre- and post-test periods because the data were automatically skewed to closer mean distances.

The auditory measure was purposely not considered and analysed in terms of distances. Although the speaker (at 90 cm height and 50 cm horizontal distance from the table, see Fig. 2.4, above) potentially offered a concrete local point of identification, the sound was reflected from the walls in all directions and a measure of distance to the stimulus was not considered accurate. Moreover, in pre-trials the marmosets showed no apparent behavioural indication that they had identified the speaker as the origin of the sound. Therefore, distance measurements were not taken for auditory stimuli. Instead, the indoor rooms were divided into virtual sections: three sections vertically, three sections horizontally, and back and front sections. The marmosets’ movements and locations between sections were recorded at intervals of five seconds. The number of movements between (virtual) room sections was called ‘activity’ and was also recorded in response to the visual and olfactory stimuli.

2.4.2 Latency to approach/move

Predator inspection and mobbing studies have commonly used latency to approach to measure the level of risk perceived from a stimulus (e.g. Brown and Godin, 1999; Brown and Magnavacca, 2003). Latency to approach was scored in this study as the time taken (to 2 milliseconds) by the marmoset to start moving towards the visual stimulus. As scoring began when the marmoset was already next to the olfactory stimulus, latency to approach could not be scored for this modality. For the auditory stimulus this was also the case. As said before, the marmosets did not appear to identify the speaker as the origin of the stimulus; instead, latency to move (in any direction) was recorded.

2.4.3 Vocal behaviour

The number and types of vocalisations produced in the presence of stimuli are well-documented behavioural responses to different types of stimuli in primates and other species (e.g. Gordon and Rogers, 2010; Hayes and Snowdon, 1990). Marmosets have a relatively large vocal repertoire and are known to use vocalisations when mobbing predators (Bezerra and Souto, 2008; Campbell and Snowdon, 2009; Clara *et al.*, 2008; Cross and Rogers, 2006) and to contact conspecifics when isolated or in the presence of food (Chen *et al.*, 2009; Vitale *et al.*, 2003). Results of other projects conducted in our laboratory (Stewart, 2009) have shown that the call types produced by the marmosets are very varied and call combinations are not necessarily stereotyped. It was therefore important to be able to compare whether certain stimuli elicited more call types and different combinations of vocalisations than others. The calls noted were identified using published studies (Bezerra and Souto, 2008; Epple, 1968; Vitale *et al.*, 2003) that have described the vocalisations of common marmosets. In some cases, individual differences were found in the structure of certain calls. In these situations, the context and surrounding vocalisations were considered in trying to identify the calls. Previously undescribed vocalisations were also scored. These were noted and included in the total number of vocalisations produced, but could not be analysed further. All calls were downloaded to the software sound analysis program Adobe Audition version 3.0 and then scored from the spectrograms of the audio recordings. Spectrograms were produced in standard speed, wave format, standard sampling rate of 44100 Hz and 16-bit signed encoding.

2.4.3.1 Contact calls

Two types of contact calls have been described in the vocal repertoire of common marmosets (Bezerra and Souto, 2008; Epple, 1968): the long-distance contact call, or ‘phee’ (Fig. 2.5), and the short-distance contact call, or ‘twitter’ (Fig. 2.5). Phee calls may occur as single or multiple syllables (as shown in Fig. 2.5B) ranging in frequency between 7.24 and 10.06 kHz (Bezerra and Souto, 2008). Average length and number of syllables appears to differ between individuals and may be influenced by sex, age and social standing (Chen *et al*., 2009). Phees with multiple syllables were counted as one call when there was no more than a one-second gap between syllables. Twitters vary between 5.49 and 13.08 kHz and always had multiple syllables (Bezerra and Souto, 2008; as shown in Fig. 2.5A). In addition, they are typically shorter and have a lower intensity than phee calls (Bezerra and Souto, 2008). A single twitter was scored at the end of the vocalisation; multiple twitters produced within one second of each other were never observed. When twitters were directly followed by a phee without a pause in the call (not described in the literature), this was scored as a single vocalisation and dubbed a ‘twitterphee’.

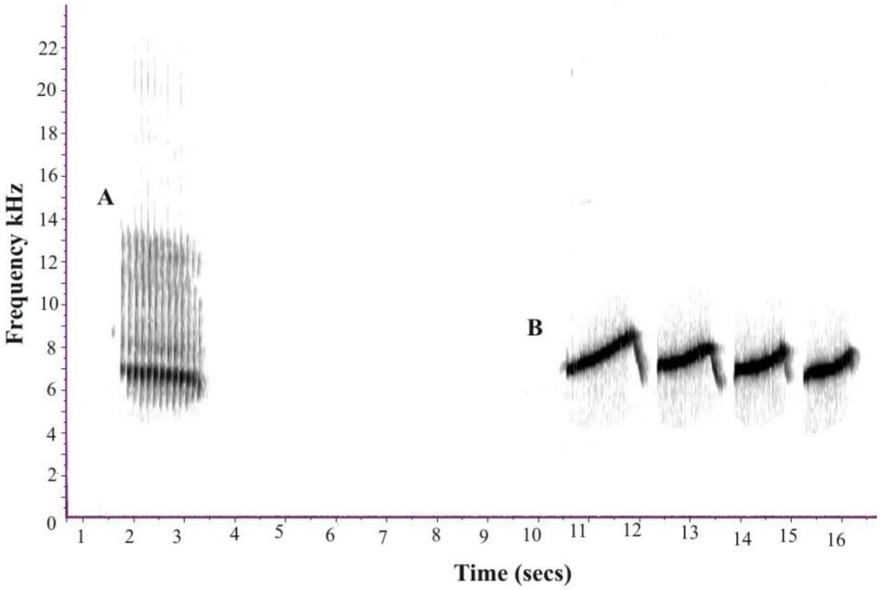


Figure 2.5. Spectrogram of contact calls: A - ‘twitter’ call (short-distance contact call), B - ‘phee’ call (long-distance contact call). All spectrograms presented in this thesis were created using Raven: Interactive Sound Analysis Software, version Pro 1.3.

2.4.3.2 Mobbing/alarm calls

Mobbing/alarm vocalisations have been described in the literature (Bezerra and Souto, 2008; Clara *et al*., 2008; Epple, 1968) and have been identified as ‘crackle’ (also as ‘egg’, Epple, 1968), ‘tsik’, ‘ock’ and ‘alarm 2’ (also as ‘warning call’, Epple, 1968) (Fig. 2.6).

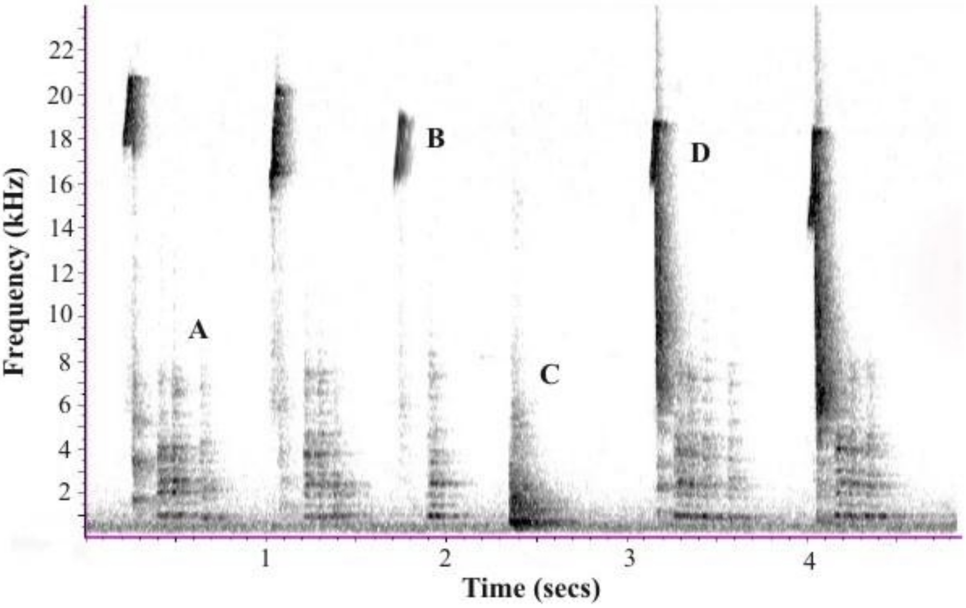


Figure 2.6. Spectrogram of mobbing calls: A – crackle, B – alarm 2 (also known as ‘warning call’; with crackle), C – ock, D – tsik (with crackle).

The crackle vocalisation is often observed in close temporal proximity (less than one second) to the tsik and the alarm 2 (as shown in Fig. 2.6); in such cases these were counted as one call (e.g. the tsik-crackle). Ock calls were never paired directly with other vocalisations, although they occurred during mobbing with other tsiks, crackles and alarm 2 calls made before and after. They were infrequent. They have not been described as a strong-response mobbing vocalisation. Tsiks are a high-intensity mobbing vocalisation and are the main call given to aversive stimuli (Bezerra and Souto, 2008; Clara *et al*., 2008; Epple, 1968). Tsik calls produced by the marmosets in our colony typically had a frequency range of 4 to 18 kHz, and were produced singularly and in quick succession. Each individual tsik was counted. Crackles, either alone or paired, suggest the intensity of the mobbing is lower (Epple, 1968); they have a frequency range of 0.82 to 9.79 kHz and occur frequently.

2.4.3.3 Food-related calls

One food call was described by Vitale *et al.* (2003; Fig. 2.7A), and there are several others that are believed to be either food calls or food-related. The first is the ‘very brief whistle’ (Bezerra and Souto, 2008), which the authors scored only after the marmosets had discovered a large amount of food. The alarm 2 and the very brief whistle are very similar in appearance on a spectrogram and there is some overlap in the frequency ranges of these two vocalisations; however, Bezerra and Souto (2008) describe the very brief whistle as being higher in frequency. During my research, the crackle vocalisation was observed to sometimes directly follow the very brief whistle, although Bezerra and Souto (2008) made no mention of this occurring in their study. Other suspected food-related calls (Stewart, 2009) are shown in Fig. 2.7 C and D). Note that the phee call in Figure 2.7 (B) has been included to show the structural and frequency difference between phee calls and call C that Stewart found in conjunction with other food calls but which, by itself, seemed to have no special reference to food (Stewart, 2009). These vocalisations (as described by Bezerra and Souto, 2008, Stewart, 2009 and Vitale *et al*., 2003) were called ‘food-related calls’ as opposed to ‘food calls’ for the purpose of this study.

2.4.3.4 Latency to vocalise

Latency to commence vocalising was recorded to two milliseconds from the start of the testing period. For visual stimuli, this was scored as the time until the first vocalisation produced when the marmoset was looking at or had looked at the stimulus. Direction of eye gaze could be determined from the video footage; the time frame of first exposure to when the marmoset looked at the stimulus was then matched to the spectrograms produced using the software program

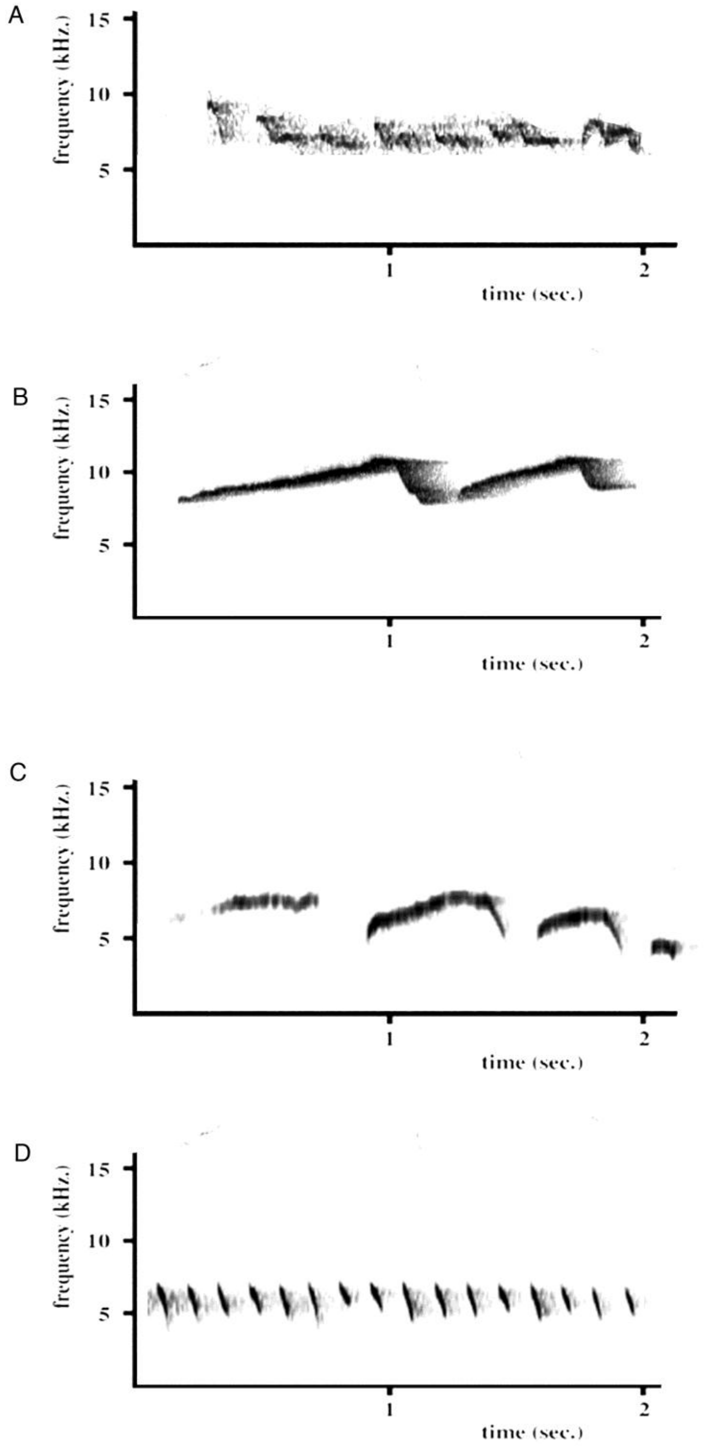


Figure 2.7. Spectrograms of food-related calls produced by the marmosets. A – the food call described by Vitale *et al*. (2003) given particularly to live food. B – phee call (included to compare with C). C – unidentified call often given in conjunction with D (Stewart, 2009). D – chirp, given typically to fruit (Stewart, 2009).

Adobe Audition version 3.0. A feature of this program allowed for an accurate computer-based measurement (to two milliseconds) of the time lapsed between the start point of the trial (the marmoset seeing the stimulus, sniffing the odour or the start of the sound) to the beginning of the first vocalisation produced by the marmoset. Using the video recording in conjunction with the audio recording ensured that the latency to vocalise could be tied specifically with viewing of the stimulus. Latency to vocalise in response to the olfactory and auditory stimuli was scored from first exposure, i.e. after the marmoset had sniffed the bowl or when the sound was played.

2.4.4 Vigilance behaviour

An important anti-predator behaviour in common marmosets, as well as in other prey species, is vigilance (Barros *et al*., 2008). Vigilance was scored as looking up or looking down, either with a stationary head position or moving the head from side to side. Vigilance direction was typically scored from head movements (i.e. head tiled back or down), but direction of eye gaze was also used when possible. While filming the marmosets, it was sometimes possible to zoom in while the marmosets were stationary (resting) and record frame-filling close ups of the faces to reveal eye movements and movements of the facial features. This made it possible to use only eye gaze for direction of vigilance. In those instances, eye movement up or down was clearly visible from viewing the video playback. The direction of the marmoset's eye gaze always corresponded with the direction of the head movement, i.e. up or down. However, the marmosets sometimes directed their eyes up or down without moving their head from the normal position, highlighting the importance of using eye movements when scoring vigilance. As this was not always the case and not always possible to determine (e.g. when the marmoset's back was turned towards the camera), head movements were predominantly used for determining vigilance direction. Looking at the visual stimuli was also scored.

2.4.5 Facial expressions

Researchers have become increasingly interested in facial expressions in great apes (e.g. chimpanzees, *Pan troglodytes*, Parr and Waller, 2006), Old World monkeys (e.g. rhesus macaques, *Macaca mulatta*, Burrows *et al*., 2006, Parr and Heintz, 2009; baboons, *Papio ursinus*, Cheney and Seyfarth, 2007; vervet monkeys, *Chlorocebus pygerythrus*, Gouzoules and Gouzoules, 1987) and, albeit to a lesser degree, New World monkeys (e.g. white-faced capuchins, *Cebus capucinus*, Perry, 1997). Empirical studies testing facial expressions in primates have typically focused on the responses to social stimuli.

Common marmosets are thought to have a very limited range of facial movements in comparison to the other primates so far studied (Burrows, 2008). Despite this, 23 variations of eyes, mouth and ears (Table 2.2) have been described – one reference to the use of the tongue in relation to a facial expression has also been made (Epple, 1967; Hook-Costigan and Rogers, 1998; Stevenson and Poole, 1976; van Hooff, 1967). A neutral position was considered to be a ‘relaxed face’ (as described by Stevenson and Poole, 1976), without movement of any facial features from the typical position, as shown in Figure 2.8.

Figure 2.8. Relaxed (or neutral) face of a common marmoset. Note that the ear tufts are neither perked nor back, the teeth are not exposed and the lips are not tightly compressed. The eyes are neither narrowed nor widened

Table 2.2. Facial expressions of common marmosets described in the literature.

Facial Expression	Description	Literature
Relaxed face	No movement of facial features.	Stevenson and Pool, 1976
Lip smacking	A sexual behaviour with smacking of the lips.	Epple, 1967; Stevenson and Pool, 1976
Tongue in/out	Made by adults in sexual situations, and also by juveniles towards adult marmosets or familiar humans.	Epple, 1967; Stevenson and Pool, 1976
Stare (with or without head cock)	Visual fixation at objects or marmosets.	Stevenson and Pool, 1976
Slit stare	Eyes narrowed to horizontal slits; can occur in aggressive situations, but also play.	Stevenson and Pool, 1976
Frown	Lowered brows. Can often precede an attack.	Stevenson and Pool, 1976
Open mouth	Teeth visible but lips not retracted. Usually seen in play situations.	Stevenson and Pool, 1976
Partial open mouth	Medial portion of the lips parted; teeth not bared. May also involve staring at strange objects.	Stevenson and Pool, 1976
Partial open mouth slit stare	As above with eyes narrowed to slits.	Stevenson and Pool, 1976
Pout		Stevenson and Pool, 1976
Bared teeth gecker face	Teeth visible, lips retracted, often accompanied by vocalisations.	Stevenson and Pool, 1976; van Hooff, 1967
Bared teeth gecker slit stare	As previous, with eyes narrowed to horizontal slits.	Stevenson and Pool, 1976
Grin	Lips retracted.	Stevenson and Pool, 1976; van Hooff, 1967
Bared teeth	Teeth visible (no mention of upper, lower or both), no vocalisation. Often seen in aggressive encounters and may be accompanied by 'tufts flatten' and 'slit stare'.	Stevenson and Pool, 1976; van Hooff, 1967
Bared teeth scream	Teeth visible, gums may show. Scream vocalisation. Considered a 'high intensity' expression.	Stevenson and Pool, 1976; van Hooff, 1967
Bared teeth scream with tufts flattened	As previous, with ear tufts flattened.	Stevenson and Pool, 1976
Tufts flick stare	Ear movements back and forth with visual fixation.	Stevenson and Pool, 1976
Tufts flick slit stare	Ear movements back and forth with narrowed eyes. Typically given in response to approach by strange marmoset or human.	Stevenson and Pool, 1976
Tufts flatten	Ear position back. Seen when approaching strange object or marmoset or in response to an aggressive marmoset.	Stevenson and Pool, 1976
Tufts flatten slit stare	As above, with eyes narrowed to horizontal slits.	Stevenson and Pool, 1976
Tufts erect stare	Ear position up with visual fixation. Precedes an attack.	Stevenson and Pool, 1976
Tufts erect frown	Ear position up with lowered brows.	Stevenson and Pool, 1976
Fear expression	Lips are drawn laterally with only the lower teeth bared. May be the same as 'bared teeth'.	Hook-Costigan and Rogers, 1998

However, it became apparent during the course of this research that the marmosets, although tested individually, showed facial expressions in response to the visual, olfactory and auditory stimuli. The facial expressions produced by the marmosets during the presentation of the stimuli were recorded. An experiment specifically designed around the discovery of facial expressions is described later (Ch. 8). Facial expressions included changes to positions of the mouth, eyes and ears from a neutral position.

2.5 Statistical analysis

Statistical analyses were performed using SPSS (SPSS Inc. Release 17.0.0). Normality (Shapiro-Wilk) and equal variance (Levene's test) were assessed. For data with non-normal distribution and/or unequal variance, square-root or log transformations were attempted. If the transformation was unsuccessful in normalising the data, non-parametric tests were conducted. Trials were compared using t-tests for normal data and Wilcoxon signed-rank tests for non-normal data. Pre-test, test and post-test periods within and between stimuli were first analysed for heterogeneity using a repeated measures ANOVA for parametric data and Friedman's test for non-parametric data. *Post hoc* tests were applied if significant heterogeneity ($p \leq 0.05$) was found (Bonferroni pairwise comparisons for parametric data and Wilcoxon signed-rank tests for non-parametric data). As the pre- and post-test periods of the trials of the individually presented stimuli were conducted for two minutes but the test period was only one minute, the first and second minute of were compared; no differences were ever found so the pre- and post-test periods were divided by two in order to be comparable to the test period.

2.6 Inter-rater reliability

One independent observer scored and collected data in addition to the experimenter to ensure that observations of behaviour were consistent and unbiased by the experimenter. An inter-rater reliability analysis was conducted using correlations. A member of our laboratory, trained in scoring behaviour in avian species, but condition blind to my research, scored from video footage of nine trials using three different stimuli (aversive visual, neutral olfactory and pleasant auditory): activity, latency to approach (visual stimulus), latency to move (auditory stimulus) and looking downward (test periods only). As latency to approach and move could only be scored for the visual and auditory stimulus, respectively, nine trials were used for each. Vocalisations and latency to vocalise were not tested as these scores were taken directly from the spectrograms and could not be misinterpreted. Distance from stimulus was also not used as a measure to test inter-rater reliability as each indoor room had been measured in relation to the position of the visual and olfactory stimuli to a minimum of 20 points around the room and it was not considered to be a variable of contention. The inter-rater reliability between the author of the thesis and the independent rater was found to be: activity, Pearson’s $r(7) = 0.95$, $p = 0.000$; latency to approach, Pearson’s $r(7) = 0.86$, $p = 0.002$; latency to move, Pearson’s $r(7) = 0.90$, $p = 0.001$; looking downward, Pearson’s $r(7) = 0.85$, $p = 0.002$.

2.7 Welfare of Marmosets

The care and welfare of the marmosets was a priority throughout this research and within our laboratory. No marmoset was tested more than once in any given day and each marmoset had at least one day between trials. Experiments were also alternated so that any one marmoset was not presented with only aversive stimuli on consecutive days. Although the marmosets were tested individually, the trials were kept short to reduce separation stress and anxiety. If a marmoset became particularly agitated during testing it was policy to stop the test immediately and allow the marmoset access back to its home-room and cage-mates. However, this did not occur. As mentioned previously the marmosets were accustomed to being tested individually and could maintain auditory contact with conspecifics during the test. No marmoset was forced into the indoor room for testing but came voluntarily, and were often given a small food reward (e.g. mealworm) for doing so.

Furthermore, as mentioned before, I also fed the marmosets at least twice weekly and spent time interacting and playing with them. Caretaker interaction with captive common marmosets has been shown to have a positive impact and improve the welfare of the marmosets (Manciocco *et al*., 2009; Vitale *et al*., 2007). Although the marmosets could not see me during experiments, they did before and after each test, so it was important that they did not just associate me with experiments. All Australian welfare standards were met (Australian Government, National Health and Medical Research Council, 2004).

CHAPTER THREE

EXPERIMENT 1: TESTING OF OLFACTORY AND AUDITORY STIMULI

3.1 Introduction

There is growing evidence to suggest that olfactory and auditory cues are important sources of information for primates and are actively used in detecting predators (e.g. Macedonia and Yount, 1991; Searcy and Caine, 2003; Sündermann *et al*., 2008), finding food (e.g. Dominy *et al*., 2001; Laska and Seibt, 2002) and seeking out potential mates (e.g. Heymann, 1998; Smith and Abbott, 1998). However, diurnal primates have long been considered to be visually orientated (Barton, 2006; Dominy *et al.*, 2001; Farbman, 1992; King and Fobes, 1974; Rouquier *et al*., 2000; Walker and Jennings, 1991). Indeed, the majority of predator recognition studies have focused on visual perception. Olfaction in primates has received far less scientific attention, while our knowledge of these senses in other animal groups (Ache and Young, 2005), and even in humans, is extensive (Heymann, 2006). Studies on audition in primates have most recently stemmed from an interest in cognition (Castellano *et al*., 2004; Gamba and Giacomo, 2005, 2010) and, specifically, several in music perception (McDermott and Hauser, 2007; Remedios *et al*., 2009; Snowdon and Teie, 2010; Wright *et al*., 2000), but studies on the role of audition in predator recognition and even food detection are still relatively scarce.

Most reports of olfactory-guided foraging in primates are restricted to nocturnal species, particularly prosimians, and are largely anecdotal (Dominy *et al*., 2001). However, it is now known that spider monkeys (*Ateles geoffroyi*), squirrel monkeys (*Saimiri sciureus*) and pigtailed macaques (*Macaca nemestrina*) are extremely sensitive to fruit-based odours (Dominy, 2004; Hübener and Laska, 2001; Laska *et al*., 2000, 2007; Siemers *et al*., 2007). Indeed, the squirrel monkey, a New World primate, has demonstrated a sense of smell in response to some odours, particularly fruit-based odours, that equals or excels that found in rats or dogs, species considered to be macrosmatic (having a keen sense of smell) (Hudson *et al*., 1992; Laska and Alicke, 1996; Laska and Freyer, 1997; Laska and Hudson, 1993; Laska *et al*., 2000, 2007). These studies tested a variety of odours, and their results guided the selection of food-based odours administered to the marmosets in my experiment.

Food-based auditory cues are known to be used by primates to detect food in two ways: directly and indirectly (Dominy *et al*., 2001). Direct cues are the sounds produced by or due to the presence of food, while indirect cues are those produced by foraging conspecifics or other species, which aid in determining the location of the food. For example, nocturnal primates, such as the aye-aye (*Daubentonia madagascariensis*, Erickson *et al.*, 1998), the tarsier (*Tarsius* spp., MacKinnon and MacKinnon, 1980; Niemitz, 1979) and the galago (*Galago alleni,* Charles-Dominique, 1977), use direct auditory cues of insects to determine the presence and location of potential prey. These cues include insect vocalisations, the sound of flapping wings of aerial insects, and the sound made by larvae and burrowing insects when aye-ayes tap tree trunks (Erickson *et al*., 1998). It is thought chimpanzees may use direct auditory cues to detect prey when hunting (Milton, 2000), but otherwise there seem to be few, if any, known cases of the sounds of prey contributing directly to capture by diurnal primates (Dominy *et al*., 2001). The sound made by falling fruit is considered a direct cue that can be utilised to determine the location of fruiting trees (Dominy *et al*., 2001).

Indirect auditory cues of prey, such as the food-related calls made by conspecifics or even other species, have been observed to be used by diurnal primates, including red-tailed monkeys, blue monkeys, mangabeys and siamangs (Dominy *et al*., 2001; Hauser and Wrangham, 1990; Olupot *et al.*, 1998). Marmosets do produce food and food-related calls (Bezerra and Souto, 2008; Stewart, 2009; Vitale *et al*., 2003) and therefore it was possible to test this type of indirect auditory food cue. Ultimately, however, it is unknown whether marmosets use direct and/or indirect auditory cues to locate food, or whether one is more important than the other, so it was important to test both types of cues.

The aim of the experiment presented in this chapter was to establish behavioural responses to a variety of predator- and food-based olfactory and auditory stimuli, and to determine the most aversive, most pleasant and a neutral stimulus from each modality for further testing. The visual stimuli by which the marmosets had been consistently repelled or attracted had already been experimentally established in our laboratory (studies include Clara *et al*., 2008; Cross and Rogers, 2006; Gordon, 2007). These were a taxidermic specimen of a quoll (as the most aversive), marshmallow (as the consistently most attractive) and a piece of PVC tubing (neutral stimulus). The visual stimuli were presented individually first (in Experiment 2) and in combination with the stimuli selected from the two other modalities presented in this chapter (Experiments 3 and 4). It was also important to establish to what extent the marmosets' response could be observed and measured.

3.2 Materials and methods

Ten marmosets (5 females : 5 males, aged 36 to 161 months) were tested for their response to potentially aversive, pleasant and neutral olfactory (Experiment 1a in Table 2.1) and auditory (Experiment 1b in Table 2.1) stimuli. Only ten marmosets were used as this was an initial experiment to gather information on responses and determine the stimuli for further and more extensive testing. Therefore not as many subjects were required for the purpose of this experiment as was used in later experiments.

3.2.1 Stimuli

3.2.1.1 Olfactory stimuli

The marmosets were presented with 22 odours (Table 3.1), including the faeces and urine of carnivorous animals (the dog was fed a strict meat-only diet for one week prior to collection of the faeces and urine samples) and herbivorous animals (including a dog fed a strict vegetable-only diet for one week prior to faeces collection), and food-based scents. Herbivorous animal faeces were tested as a control for the faeces of the carnivorous animals, to determine whether faeces in general were aversive or whether the process of meat digestion produced an odour that specifically influenced the behaviour of the marmosets. The faeces and urine were collected from privately owned, disease-free animals. The vectors used to present the odours – a cotton ball inside a tea infuser, the tea infuser alone and the distilled water – were also tested as controls (as shown in Table 3.1) to ensure the marmosets did not respond positively or negatively to the natural odour or appearance of these items.

The odours were diluted with distilled water at different dilution ratios, as described in Table 3.1, so that all scents were just detectable by the human nose. Ten human subjects were used to establish stimuli intensities of odours and then the odours were reduced to strengths considered comparable. This was necessary because equal dilutions of all solutions produced some very faint and some very pungent odours and this could have led to discrimination based on intensity rather than type.

3.2.1.2 Auditory stimuli

There was already some indication in the literature as to what sounds might be potentially effective, at least as far as predatory cues are concerned (e.g. Arnold and Zuberbühler, 2006;

Table 3.1. Olfactory and auditory stimuli. The odours and sounds tested, including the dilution factors of the odours and the length and sources of the auditory stimuli. Multiple lengths for any one stimulus identify multiple clips spliced together to make a natural-sounding vocalisation.
(MLNS = Macaulay Library of Natural Sounds).

Olfactory stimuli	**Dilution**	**Auditory stimuli**	**Source**
Dog (*Canis lupus familiaris*) faeces (meat diet)	1:10	Leopard growl (14 secs, 10 secs, 6 secs)	junglewalk.com and
Cat (*Felis catus*) faeces	1:10		grsites.com/archive/sounds/
Snake (python sps.) faeces	1:10	Peregrine falcon call (*Falco peregrinus*) (30 secs)	junglewalk.com
Tawny frogmouth (*Podargus strigoides*) faeces	1:10	Red-shouldered hawk whistle (*Buteo linetus*) (22 secs)	MLNS #4303
Dog (*Canis lupus familiaris*) urine (meat diet)	1:10	Red-tailed hawk whistle (*Buteo jamaicensis*) (20 secs)	MLNS #105673/105680
Cat (*Felis catus*) urine	1:10	Harpy eagle scream (*Harpia harpyja*) (13 secs)	xeno-canto.org
Dog (*Canis lupus familiaris*) faeces (vegetarian diet)	1:100	Snake hiss (6 secs, 2 secs, 1 secs)	partnersinrhyme.com, soundjax.com
Rabbit (*Oryctolagus cuniculus*) faeces	1:10		and audiosparx.com
Apple juice, Just Juice, 99%	1:10	Snake rattle (30 secs)	MLNS #107975
Iso-amyl acetate (banana), Aldrich Chemical Co., 98%	1:10000	Food-related calls of a common marmoset (30 secs)	Personal recording
Orange essence, Queen Fine Foods	1:100	Marshmallow bag rustling (30 secs)	Personal recording
Almond essence, Queen Fine Foods	1:100	Cricket chirps (30 secs)	Personal recording
Vanilla essence, Queen Fine Foods	1:100	Voice of familiar human (30 secs)	Personal recording
Marshmallow, Coles supermarket brand	1:10	Radiator noise increasing in volume (30 secs)	Personal recording
Orange juice, Just Juice, 99%	1:10	Background noise of animal housing (30 secs)	Personal recording
Smooth peanut butter, Kraft, 91%	1:10		
Australian honey, Woolworths supermarket brand	1:10		
Tree exudate (gum arabic)	1:10		
Distilled water, Glendale	0:00		
Clove oil, Gold Crest, 100%	1:10000		
Tea infuser with cotton ball	-		
Tea infuser	-		

Searcy and Caine, 2003). Hence, not as many auditory stimuli were tested as was necessary for the olfactory trials.

The marmosets were presented with 13 auditory stimuli, consisting of predator vocalisations (a feline, birds of prey and snakes), food-based (including the marmosets' own food-related calls) and potentially neutral sounds, as shown in Table 3.1. The 30-second sound clips were recorded personally or sourced online. Some sounds were created from multiple clips of varying lengths (Table 3.1); these had been lengthened and/or spliced together to create natural sounding vocalisations using Goldwave version 5.25. Using multiple clips provided variation within the sounds that may not have been present from a single clip and eradicated bias that may have occurred from the repetition of short clips extended to 30 seconds. The sounds not sourced online were recorded using a Sennheiser MKH 418S P48 microphone attached to a Marantz solid state recorder PMD670, gain 10 digital audio recorder. All sounds were cleaned of excessive background and/or other noise not related to the stimulus being tested using Raven: Interactive Sound Analysis Software, Pro version 1.3. The marmoset food-related call used included the call described by Vitale *et al*. (2003) and the suspected food-related calls from Stewart (2009). It was recorded from a single marmoset in our colony when presented with its daily food. Only the vocalisations from one marmoset were recorded as she produced these calls readily and consistently. Furthermore, the marmosets had auditory contact with conspecifics in different home-rooms and therefore the vocalisations of any marmoset in the colony would not be considered unfamiliar. Crickets were tested as a stimulus as the marmosets in our colony were occasionally given live crickets as a protein supplement in their diet and also during experiments (Gordon and Rogers, 2010). The radiator noise was a recording of a hot-water radiator from an office, which was altered to increase in intensity as though getting closer ('looming' stimulus). There were no hot-water radiators in the marmoset housing facility so they would not have heard this sound before. The background noise of the marmoset housing facility did not include human or marmoset vocalisations or other loud noises, but mostly consisted of the heating/cooling unit.

3.2.2 Experimental procedure

3.2.2.1 Olfactory stimuli

Studies testing the response of animals to odours have used a variety of methods, including faeces placed next to or under a feeding bowl (e.g. Blumstein *et al*., 2002*b*; Sündermann *et al*., 2008), urine or other secretions on a branch (e.g. Caine and Weldon, 1989; Morgan and Woolhouse, 1997; Swihart, 1991; Woolhouse and Morgan, 1995), and a spray of the odour into the air of the testing room (e.g. Courtney *et al*., 1968; Ueno, 1994). There were five main problems associated with the presentation of the odours. Firstly, as these were captive marmosets that were easily susceptible to disease, allowing them direct contact with faeces was not considered advisable. Using a spray was inadvisable because odour molecules can spread and linger, and brought the marmosets in contact with faecal matter, albeit in smaller doses; this would have also contaminated the room for the post-test period and later trials. Secondly, the marshmallow odour was so favourable that the marmosets tried to lick the solution so access had to be limited. Thirdly, the odour had to be removed after the end of the testing. The fourth problem was that interference and influence by the experimenter had to be avoided (as in all experiments). Finally, the method had to be compatible with that of presenting the visual and auditory stimuli so that they could be presented together for the combined stimuli trials (see Ch. 5 for more detail). A sustainable method was one that would stop the marmosets from accessing the odour solution directly while still allowing the odour molecules to be detected and examined.

Initially, a cotton bud dipped in the odour solution was used to present the scent to the marmosets. However, when the bud was held up to the cage wire, the marmosets would attempt to grasp and chew on it. Therefore a vector needed to be found that allowed the solution to be detected while also restricting access (i.e. the odour needed to be presented outside the cage). Moreover, the presentation vector had to be something that could be hung on the outside wire of the cage and that could contain an absorbent material that could be soaked in the odour solution. A tea infuser proved to be ideal because it could house a cotton ball soaked in the odour solution (with any excess liquid squeezed out; Fig. 3.1). The tea infuser allowed the odour to escape while reducing the marmosets' access to the solution. To my knowledge, this methodology has not been used previously in an olfactory study.

Figure 3.1. Method of presenting olfactory stimuli: a tea infuser (opened) with a cotton ball inside.

The faeces were kept frozen, and the urine, juices, marshmallow, tree exudate and iso-amyl acetate were refrigerated, and not kept for more than a month. They were warmed to room temperature prior to making up the solution; fresh solutions were made up each testing day. Inside the tea infuser was placed a cotton ball soaked in the solution being tested (with the excess liquid squeezed out so that the cotton ball was damp, but not dripping). Only one tea infuser per odour was used to avoid any contamination between stimuli. The tea infusers were hung one at a time on the outside of the marmosets' wire home-cages. This allowed the marmosets to sniff at the tea infuser and use their claws to steady it, without being able to carry it away or come in direct contact with the cotton ball. The odours were presented to individual marmosets in random order for 30 seconds (other marmosets were blocked from accessing the home-cage so that only one marmoset was tested at a time). There was a two-minute gap between stimulus presentations. The marmosets very occasionally (< 5% of all odour presentations) needed to be encouraged to approach the tea infuser using a mealworm, which is odourless at least to humans, but for the most part they were curious enough to sniff the tea infuser voluntarily. The trials were filmed using a digital Panasonic HD40 video camera with 40 GB internal memory, on a tripod.

3.2.2.2 Auditory stimuli

The marmosets were encouraged individually into the playroom as per the procedure described in Chapter 2. The trials were conducted in the indoor rooms so that the stimuli affected only the marmoset being tested and did not influence the other marmosets in the colony prior to their being tested.

The sounds were played through a Logitech speaker (Z-5, USB digital) placed in the indoor room, connected to a PC laptop (HP Pavilion dv9000) or iPod in the observation room, at 60 dB_{SPL} for 30 seconds, in random order. A decibel reader was used to determine the decibels at 1 metre from the speaker. All decibel levels (dB) reported in this thesis refer to sound pressure levels (SPL). There was a two-minute break between each stimulus presentation.

3.2.3 Behaviour scored

3.2.3.1 Olfactory stimuli

The behaviour of the marmosets was recorded from the video footage. The length of time a marmoset spent in close proximity of an odour stimulus was recorded (in seconds to two decimal places). Marmosets were considered to be in close proximity to the odour while sniffing or licking the tea infuser, i.e. nose within approximately 2 cm of the tea infuser. The length of time spent at the tea infuser was also scored and analysed separately. Distance-increasing behaviour, such as pulling back, retreating, and avoidance, were given negative scores (-1 or -2; Table 3.2); additionally, mobbing/alarm vocalisations were also given a negative score as these are well-established behavioural indications of perception of an aversive stimulus. On the other hand, distance-decreasing behaviour, such as investigation and lingering around a stimulus, and food-related calls were scored as positives (+1 or +2; Table 3.2) as these tend to be indicative of behaviour towards pleasant stimuli. A general reactivity index was established (Table 3.2).

Although such indices are arbitrary in some ways, there seemed enough clear differences in behaviour to warrant two grades of negative scores and two grades of positive scores. For instance, pulling away sharply from the tea infuser after sniffing was considered a stronger negative response than simply moving away without any urgency, and licking the tea infuser repeatedly was considered a stronger positive response than just sniffing it a second or third time.

Additional behaviour noted included facial expressions and tongue movements. These responses were compared to facial expressions described in the literature for common marmosets (Stevenson and Poole, 1976; also Table 2.2 in Ch. 2) and primates generally (e.g. Parr and Heintz, 2009; Parr and Waller, 2006), including humans (Ekman and Friesen, 1969). To clarify

Table 3.2. Reactivity index scoring system for responses to olfactory stimuli. Behavioural responses and scores, negative on the left and positive and neutral on the right.

	Behaviour	Score	Behaviour	Score
Distance	Moving away	-1	Number of sniffs after the initial sniff	+1
	Pull back	-2	Licking the tea infuser	+2
Facial expressions and head movements	Eye squint	-1	Eyelid flutter	+1
	Smacking lips together	-1	Licking of lips	+1
	Mouth open wide (no audible sound)	-1	Neutral mouth	0
	Teeth baring	-2		
	Face scrunch	-2	Neutral face	0
	Head shake	-2	No head movement	0
Vocalisations	Tsik or crackle	-2	Food-related call	+2

two of the facial expressions listed in Table 3.2, ‘smacking of lips together’ was scored as the mouth opening and closing several times, no teeth bared, and occasionally small movements of the tongue within the mouth, while ‘licking of lips’ was scored as repeated movements of the tongue in and out of the mouth. Smacking of lips together was different to the ‘lip smacking’ described by Epple (1967) and Stevenson and Poole (1976) (as described in Table 2.2). Other expressions recorded are noted in Table 3.2. Movements involving the head, such as shaking, were also included as a behavioural response (Table 3.2).

Indications of attraction to the odours also included the number of sniffs. One sniff constituted the beginning of the test (i.e. detection) and therefore scored zero. Subsequent sniffs scored +1 each as they indicated a curiosity about the stimulus and no apparent immediate aversion. Preliminary trials had shown that, regardless of the type of odour presented, the marmosets pressed their nose against or very close to the tea infuser and sniffed. Sniffing was evident by the slight flare of the nostrils and expansion of the ribs from the intake of air.

Each behavioural response (other than time spent at the tea infuser) was allocated a score (-2 to +2) and these were then added together for that stimulus for each marmoset to produce a reactivity score for that stimulus. Additionally, as common marmosets had not been tested for their response to olfactory stimuli in any project in our laboratory, any other behavioural responses observed but not already included in the score sheet were noted as well. By choosing as many as 22 stimuli for testing across a wide range of predator- and food-based olfactory substances, it was hoped that the most aversive and the most pleasant odours could be established.

3.2.3.2 Auditory stimuli

As per the trials of olfactory stimuli, the behaviour of the marmosets in response to the auditory stimuli was recorded from the video footage and analysed using the reactivity scores, as shown in Table 3.3. Behavioural responses were classified by degree of repellence (or fear) or attraction, and scored according to the strength of the behaviour. Trembling, freezing and fleeing were considered strong fear responses and have been noted in other studies on primate species (Nelson *et al.,* 2003). Mobbing and other alarm calls were also classified as a negative response, as these vocalisations are used in response to predators and fearful situations (Bezerra and Souto, 2008).

Lip licking, food-related calls and increased activity around the room were considered to be responses to pleasant sounds, indicative of curiosity and interest. Increased activity, such as locomotion, was classified as behaviour elicited by attractive stimuli: studies on auditory predator recognition in primates have found that activity is generally reduced when presented with a fearful stimulus (Abramsky *et al*., 1996; Dielenberg *et al*., 2001; Gall and Brodie, Jr., 2009). These behavioural responses and their scores are presented in Table 3.3.

Head cocking and parallax movements were initially included in the score sheet because they are known to be exhibited in response to visual stimuli to assess and improve depth perception of the object, and occur in response to both aversive and pleasant stimuli (Bezerra *et al*., 2009; Kaplan and Rogers, 2006). This category of behavioural response was disregarded as no observations of these responses were made (also for the olfactory trials).

Facial expressions were included in the behavioural reactivity index score (Table 3.3). More expressions occurred in response to aversive sounds than to pleasant sounds; this was also the

Table 3.3. Reactivity index scoring system for responses to auditory stimuli. Behavioural responses and scores, negative on the left and positive and neutral on the right.

	Behaviour	**Score**	**Behaviour**	**Score**
Movement	Crouching	-1	Sitting up	+2
	Pull back sharply	-1	Leaning forward	+1
	Head flicker side to side	-1	Scratching	+1
	Stationary	-1	Increased activity	+2
	Fleeing	-1	Scent marking	+1
	Hiding/use of runway	-2	Marmoset in an exposed position	+1
	Freezing	-2		
	Trembling	-2		
Facial expressions	Tight face	-1	Relaxed face	0
	Eyes wide	-1	Neutral eye position	0
	Eyes slitted (narrowed)	-1		
	Ears back (flattened)	-1	Ears up (perked)	+1
	Smacking lips together	-1	Licking of lips	+1
	Mouth open (no audible sound)	-2	Neutral mouth position	0
	Compressed lips	-1		
	Teeth baring	-2		
Body displays	Piloerection	-2	Relaxed posture	0
	Sharp body jerks	-1		
	Stiff tail	-1		
Vocalisations	Mobbing/alarm calls	-2	Marmoset food-related calls	+2
	Silent	-1	Contact calls	+1

case for olfactory stimuli. There were also more body movements scored than there were in response to any of the olfactory stimuli. Crouching and piloerection were considered to be responses to aversive stimuli as they are often evident in fearful situations (Stevenson and Poole, 1976). Scent marking, however, was considered to be a positive behaviour as it was typically only performed when the marmosets showed no other behaviour to indicate concern towards the stimulus being presented. This behaviour was not observed in response to the olfactory stimuli.

3.2.4 Statistical analysis

The reactivity index gave an indication of the direction (negative or positive) and strength (highly or weakly negative/positive) of the response. Individual responses were also considered to ensure that the stimuli selected for further testing were reliably aversive or pleasant – that is, no marmoset showed a strong opposite reaction to the general trend observed. For example, if one or more marmosets had a strong positive reaction to any of the stimuli that otherwise scored negative values and had a strong negative mean, the stimulus was disregarded as it was not consistently aversive for the group, making it a poor choice for an aversive stimulus. If two or more strongly negative or strongly positive stimuli were too close in score to separate by eye, statistical analysis was used to attempt to separate them in order to select a stimulus for further testing. Two-tailed t-tests or repeated measure ANOVAs were used for normal data (two or more stimuli, respectively) and Wilcoxon signed-rank tests or Friedman’s test (two or more stimuli, respectively) were used for non-parametric data.

3.3 Results

3.3.1 Olfactory

Mean times spent in proximity to the odours (< 2 cm) (mean in seconds ± standard error) are shown in Figure 3.2, from least to most time spent. Marmosets spent a mean of 1.53 seconds (± 0.24 sem) in close proximity to the faecal odours belonging to potential predators and a mean of 8.21 seconds (± 1.76 secs) in close proximity to the food-based odours (significant difference: Wilcoxon signed-rank test, $Z = -2.80$, $p = 0.01$). When the stimuli were considered individually, the response to the marshmallow odour was clearly the strongest, as the marmosets were in close proximity to the tea infuser for a mean of 21.69 seconds (± 3.33). At the other end of the scale, there were three stimuli for which the marmosets spent less time at the tea infuser than the mean of all the predatory stimuli combined; these were the faecal odours of the cat (0.75 ± 0.16 secs), snake (1.00 ± 0.19 secs) and tawny frogmouth (1.36 ± 0.25 secs). There was no significant difference between these three stimuli for time spent at the tea infuser (Friedman's test, $X^2 = 1.40$, $p = 0.50$).

The results of the reactivity index (combined negative and positive scores) are shown in Figure 3.3. The stimuli presented in Figure 3.3 are sorted into the order shown in Figure 3.2. This was to determine if the results of time spent in proximity to the odour were comparable to the other behavioural responses exhibited. The responses to the faecal odours of the four carnivorous animals (cat, snake, tawny frogmouth and dog on a meat diet) were not significantly different (Friedman's test, $X^2 = 3.73$, $p = 0.29$), but typically scored negative values (Fig. 3.3). Orange juice, honey, tree exudate, peanut butter, apple juice and marshmallow odours elicited the strongest positive responses (Fig. 3.3) and were statistically compared using their reactivity index scores. There was no significant difference between the responses to these stimuli (Friedman's test, $X^2 = 7.74$, $p = 0.17$).

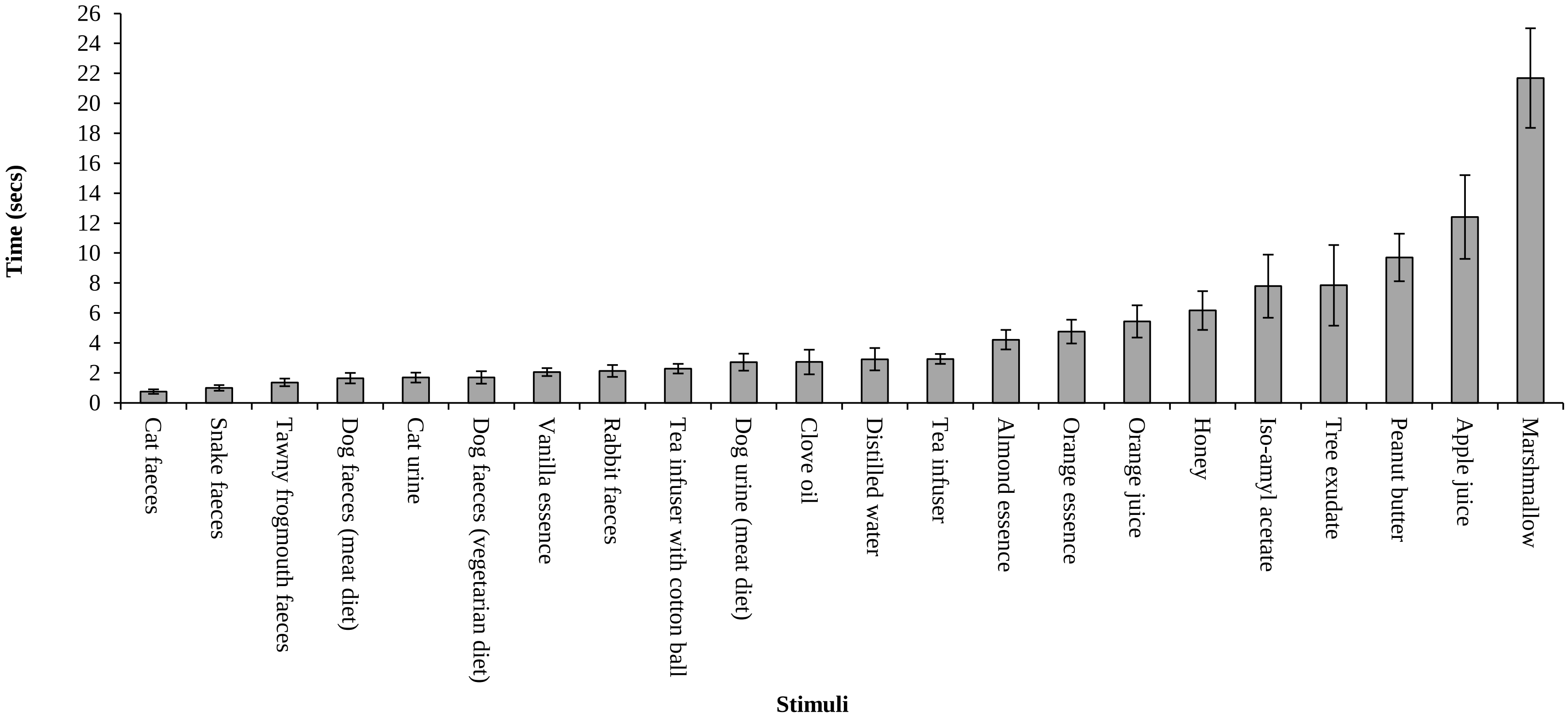


Figure 3.2. Time (seconds) spent in close proximity (nose < 2 cm) to the odours (means ± sem). Note that the marmosets clearly showed a preference for the marshmallow odour, but showed little differentiation between faecal odours.

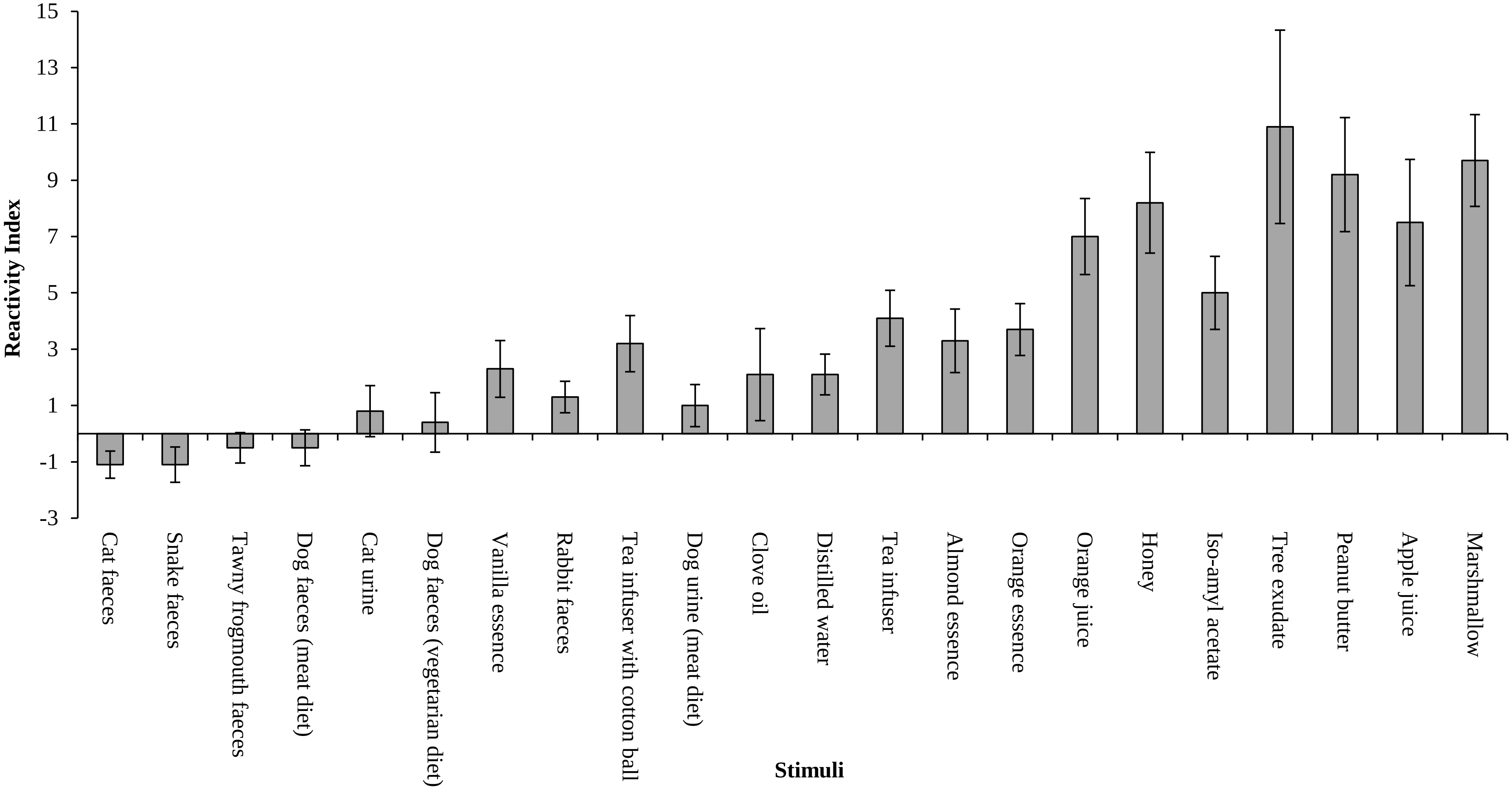


Figure 3.3. Reactivity index scores for the olfactory stimuli (means ± sem). Scores are in order of the mean time spent in proximity to the tea infuser, as shown in Figure 3.2.

The three control stimuli (distilled water, tea infuser with cotton ball and tea infuser alone) elicited similar responses, as shown in Figures 3.2 and 3.3. Their mean reactivity index scores were not significantly different from each other (repeated measures ANOVA, $F_{(2,18)} = 1.48$, $p = 0.25$). There was also no significant difference in the mean time (seconds) spent in proximity (nose < 2 cm) to the odours (Friedman's test, $X^2 = 0.60$, $p = 0.74$).

3.3.2 Auditory

The results of the mean reactivity index scores are shown in Figure 3.4. Facial expressions were found to be strong indicators of aversion or attraction towards the auditory stimuli.

The marmosets showed the strongest aversion to the leopard growl and red-shouldered hawk whistle (reactivity indexes = -8.0 ± 2.41 and -7.1 ± 1.55, respectively) (Fig. 3.4). There was no significant difference in response to these two stimuli (Wilcoxon signed-rank test, $Z = -0.87$, $p = 0.38$).

On hearing these vocalisations, the marmosets trembled, 'froze', hid and flattened their ear tufts. They sought higher branches and typically look down more than up in response to the leopard. In response to the red-shouldered hawk call the marmosets did not move or look in any particular direction.

There was no significant difference in mean reactivity scores between the responses to the marmoset food-related call, the rustling of the marshmallow bag, the crickets and the familiar human voice (Friedman's test, $X^2 = 1.55$, $p = 0.67$). However, negative reactions were more common in response to the marshmallow bag (negative scores-only RI = -3.6 ± 1.25), cricket

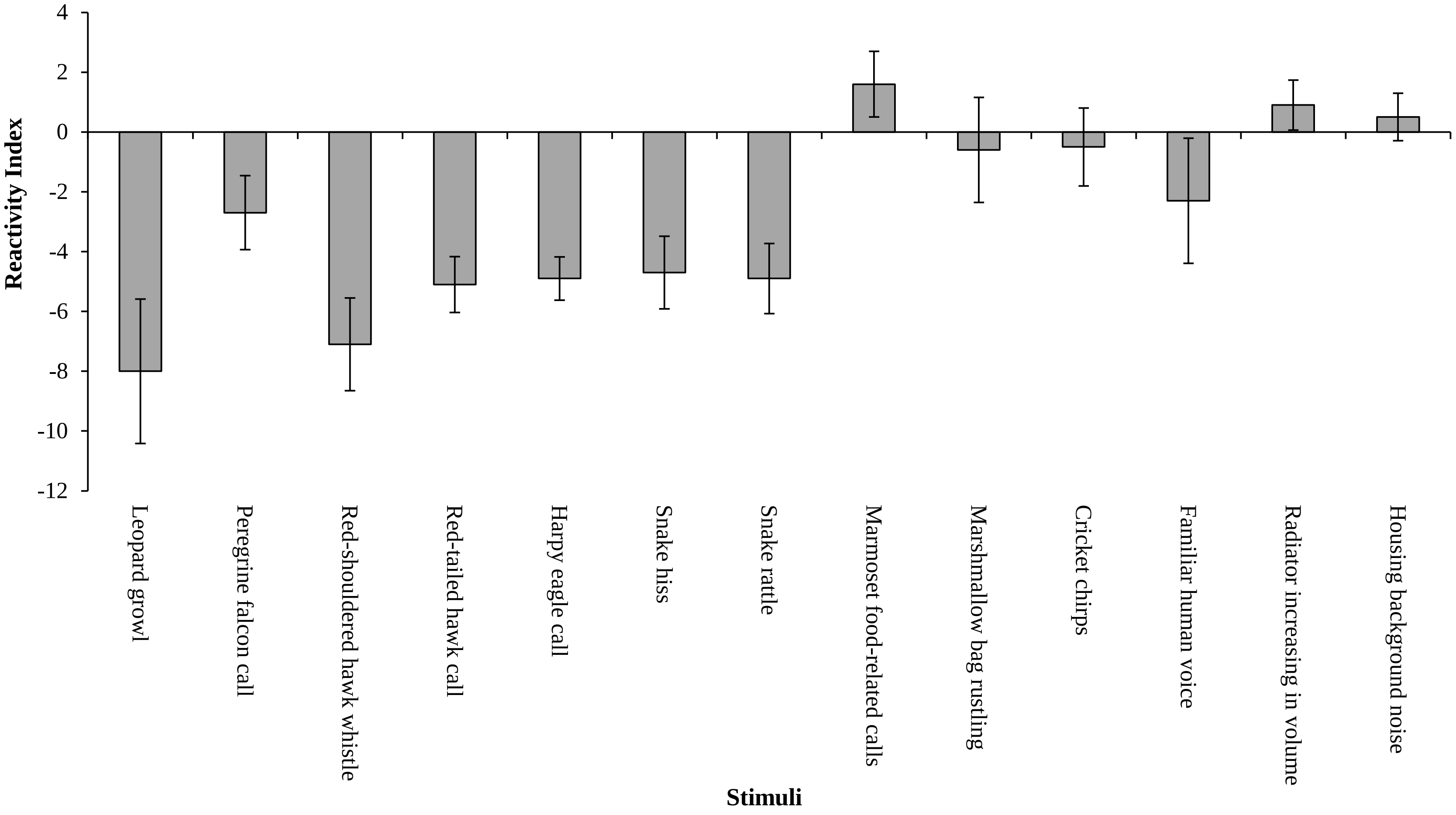


Figure 3.4. Reactivity index scores for the auditory stimuli (means ± sem). Scores are in order from most strongly negative to most strongly positive. The leopard and red-shouldered hawk vocalisations elicited strongly negative reactions while there was no identifiably strong positive response to any stimulus.

chirps (negative scores-only RI = -2.9 ± 0.80) and human voice (negative scores-only RI = -4.4 ± 1.89) than to the food-related calls (negative scores-only RI = -1.4 ± 0.96) (heterogeneity: Friedman’s test, $X^2 = 13.72$, $p = 0.003$; food-related calls versus cricket chirps, $Z = -2.53$, $p = 0.01$, food-related calls versus familiar human voice, $Z = -2.55$, $p = 0.01$, food-related calls versus marshmallow bag, $Z = -2.81$, $p = 0.01$, cricket chirps versus familiar human voice, $Z = -0.65$, $p = 0.51$, cricket chirps versus marshmallow bag, $Z = -0.61$, $p = 0.54$, familiar human voice versus marshmallow bag, $Z = -0.67$, $p = 0.50$).

The response to the background noise of the marmoset housing facility had a weak reactivity index (0.50 ± 0.79) (Fig. 3.3). Mean reactivity to this stimulus was not significantly different from that of the sounds of the radiator (0.9 ± 0.84) (two-tailed t-test, $t = 0.32$, $p = 0.75$).

3.4 Discussion

Responses varied with modality and were affected by the type (predator- or food-based) of stimulus. Predator vocalisations elicited freezing and trembling responses, whereas predator odours elicited avoidance, pulling back and facial expressions. These expressions involved scrunching of the face, tightening of the mouth, lowering of the brow and narrowing of the eyes, similar to that described as ‘disgust’ in humans (Ekman and Friesen, 1969). There were also differences in the behavioural response to the various predator odours. For example, the marmosets often responded to the odour of cat faeces with lip smacking (different from the lip smacking described by Epple, 1967, and Stevenson and Poole, 1976). This behaviour was only observed once in response to snake faeces. Instead, response to the odour of snake faeces was characterised by rapid eye squinting (eyes opening and closing tightly and repeatedly in quick succession).

The results of the trials testing responses to olfactory stimuli showed that the marmosets distinguished between food-based and predator-based odours. Only the dog (meat diet) urine produced unexpected results, with some marmosets remaining in proximity to the odour for longer than other predator-based odours and sniffing it repeatedly. Of the two faeces of herbivorous animals, the dog (vegetarian diet) odour elicited mostly responses indicating aversion, whereas the faeces of a truly herbivorous animal, the rabbit, appeared to be neither pleasant nor aversive (i.e. neutral). Previous studies have suggested that the odour to which prey animals respond in the urine and faeces of predators is due to the sulphuric metabolites from meat digestion (Nolte *et al*., 1994). Therefore, regardless of their lack of experience, the marmosets were not expected to respond strongly, particularly in an aversive manner, to these two odours. It is unknown why the marmosets were somewhat repelled by the faeces of a dog on a vegetarian diet. Nolte and colleagues (1994) also used an omnivorous animal, the coyote (*Canis latrans*), to test why prey animals respond to the faeces of predators regardless of experience. Their study found that mountain beavers (*Aplodontia rufa*), house mice (*Mus musculus*) and guinea pigs (*Cavia porcellus*) were less likely to react to coyote’s urine when it had been fed a diet of cantaloupe. It is possible that the dog on the vegetarian diet in my study had not been on this food regime for long enough at the time of faecal collection, although it was the same length of time that Nolte *et al*. (1994) had used (one week).

The marmosets showed a clear preference for the marshmallow odour over any of the other odours presented, remaining in proximity to this scent for the longest period of time. This finding corresponded to the marmosets’ liking of marshmallow treats. Similar observations have been reported in other marmoset colonies, and marshmallow has been used as a food reward in some studies (e.g. Caldwell *et al*., 2009; McKinley *et al*., 2003). However, the results of the reactivity index (Fig. 3.3) did not show such a clear preference. Food-based odours, such as orange juice, honey, tree exudate, apple juice, marshmallow and peanut butter, received nearly equal and strongly positive responses in the overall reactivity index. Still, the marmosets receive oranges, apples and peanuts regularly in their diet and it was therefore thought that after multiple testings they might become rapidly uninterested in these odours. Furthermore, several marmosets showed some aversion and disinterest in the honey and apple juice odours. That is, although the general result was that these odours elicited positive responses, the response of some individuals did not follow this pattern. Additionally, the results of the proximity scores showed that the marmosets spent relatively little time at the tea infuser in response to the honey and orange juice odours. For the reasons discussed above, and despite the generally positive response to these stimuli, honey, apple juice, orange juice and peanut butter were disregarded as options for further testing.

An attempt to give the marmosets gum arabic (tree exudate) as a dietary supplement was made several years prior to this experiment, because marmosets are gum feeders in the wild (Clarke, 1994; Ferrari, 1993; Stevenson and Poole, 1976; Stevenson and Rylands, 1988). However, at the time, the marmosets showed no inclination to consume the exudate and it was discontinued. It may be that the strong positive reaction to this odour in my experiment was due to curiosity, especially the younger marmosets, for whom this was a relatively novel food. Indeed, the strongly positive scores were predominantly derived from the number of sniffing events.

3.4.1 Selection of stimuli for further testing

As the other food-based odours (not discussed above) elicited either mixed responses or the marmosets spent relatively little time in proximity to them, the marshmallow odour was selected as the pleasant olfactory stimulus to be used in subsequent experiments. The marmosets showed no signs of aversion to this stimulus. Furthermore, marshmallow had been used only very occasionally as a treat in this colony, and it was thought that the marmosets would not habituate or show a reduction in interest towards this odour.

The marmosets responded similarly to the odours of cat, snake and tawny frogmouth faeces in terms of time spent in proximity and mean reactivity scores. The faeces of the dog on the meat diet elicited general aversion, but some marmosets responded to this odour with behaviour considered to be positive. Thus, it was disregarded for further testing. It was not possible to distinguish clearly enough between responses to the odours of cat, snake and tawny frogmouth faeces to select one as the aversive olfactory stimulus for further testing. On the basis of these results, and because these three stimuli elicited equally negative responses, one odour was selected arbitrarily because it fitted in well with the selection of the aversive visual and auditory stimuli. The odour of the cat faeces was ultimately chosen because of the findings of the trials of the auditory stimuli (as discussed below) and the already-selected aversive visual stimulus (a taxidermic specimen of a quoll, which has a similar appearance to feline predators).

It is also important to point out that the response of the marmosets to the faecal odours of any of the carnivorous species tested could not necessarily be classified as a response to a predator odour. The marmosets may have been repelled by the unpleasantness of these odours, but showed no fear responses. However, two marmosets gave a single tsik call, a known mobbing call (Bezerra and Souto, 2008), in response to the odour of carnivorous dog faeces and urine. As the response of marmosets to olfactory stimuli has not been previously tested, it cannot be determined whether wild marmosets would vocalise in response to predator-based or other odours. In general, the marmosets did not vocalise in response to the odours presented.

The ‘neutral’ odour was selected even though the marmosets showed some curiosity to the tea infuser on its own by remaining in close proximity to it for longer than expected. This may have been due to previous experience and perhaps to an expectation of a particular odour, or because it was a shiny object. It was nevertheless chosen for further testing because the wide range of positive and negative responses recorded in relation to food- or predator-based stimuli were absent.

The marmosets in our colony are captive-bred and predator-naive and yet they displayed strong fear responses to some of the auditory stimuli presented. The response of some marmosets to the calls presented included freezing, trembling and hiding. One marmoset, in response to the snake hiss, clung to the underside of a branch and remained there after the sound ended. Due to these strongly differentiated responses, a separate experiment (Experiment 5) was conducted (Ch. 7). Suffice it to say here that the sounds of predators evoked strong fear responses in the absence of any other known or concomitant fear-inducing stimuli. The leopard growl produced one of the strongest negative responses and was selected as the aversive auditory stimulus for testing individually and in related and conflicting combinations (Experiments 2 to 4). Hence, all the aversive stimuli selected for further testing derived from terrestrial mammals and predators (taxidermic specimen of a quoll, odour of cat faeces, leopard growl). All had shown the potential to be regarded as threatening, or at the very least aversive, and therefore could be used to test the threat-sensitivity hypothesis (Helfman, 1989) and responses to multimodal presentations, as suggested by Partan and Marler (1999).

The food-related calls of the common marmoset were selected for further testing as the pleasant auditory stimulus because the marmosets remained alert during its presentation, sitting up, moving and looking around. A longer excerpt (one min) was selected from the same recording and included the 30-second selection used in this experiment and is described in Section 4.2.1.2 (Ch. 4). In addition, this stimulus elicited the weakest negative response compared to any of the other potentially pleasant sounds.

Neither the sounds of the radiator nor those of the background noise of the animal housing elicited strongly negative or positive responses. However, the marmosets would have been more accustomed to the background noise and the intensity level of this stimulus did not change, as it did in the sound of the radiator. The background noise, therefore, was selected as the neutral auditory stimulus. As mentioned previously, this sound consisted mostly of the heating/cooling unit in the marmoset housing and did not include any loud sounds or vocalisations from marmosets or humans.

Certainly this experiment, concerned with non-visual stimuli (olfactory and auditory), highlighted the problems in trying to measure behavioural responses accurately. This was as true in terms of devising reliable methods as it was in interpreting the results. Behaviour indicating aversion and repulsion was typically strong and easily detected. However, as shown in Tables 3.2 and 3.3, there were stronger behavioural responses indicating aversion than attraction. This was especially evident in the responses to the auditory stimuli (Table 3.3). The marmosets seemed to show interest in a sound by increased activity and by the absence of any measurable behavioural responses, such as freezing or trembling, indicating aversion. Responses to pleasant visual stimuli, by contrast, are easier to measure and more evident, because the animals have something to orientate towards. This difference in response to different modalities showed a need for careful consideration when comparing the results of stimuli throughout this thesis.

3.4.2 Summary

The findings based on the marmosets' responses formed the basis of selection of the most aversive stimulus, as well as the most pleasant, in each modality. To reiterate, these were, in the aversive range, a taxidermic specimen of a quoll, odour of cat faeces and leopard growls, and in the pleasant range, marshmallow, marshmallow odour and marmoset food-related call. Neutral stimuli were a PVC tube (visual stimulus), an empty tea infuser (olfactory stimulus), and background noise of the marmosets' housing facility (auditory stimulus). The marmosets were known to respond to the quoll with mobbing behaviour and the marshmallow with attraction and eagerness to retrieve this food. The experiment presented in this chapter found that the marmosets responded to the odour of cat faeces with avoidance and possible 'disgust' facial expressions and the marshmallow odour with licking of the tea infuser and remaining near the stimulus for an extended period of time. They responded to the leopard growl with freezing, trembling and hiding, and also fell silent during the presentation of this sound; the marmoset food-related calls, on the other hand, elicited arousal and increased activity. The stimuli had to be tested in more controlled settings to determine if the responses remained consistent over time and if a set suite of behavioural responses scored for all stimuli could provide a means for comparisons to be made. The results of this experiment are presented in the following chapter.

CHAPTER FOUR

EXPERIMENT 2: TESTING INDIVIDUAL VISUAL, OLFACTORY AND AUDITORY STIMULI

4.1 Introduction

The last experiment (Experiment 1, Ch. 3) was designed to test the responses of marmosets to a wide range of stimuli. Once the strongest responses had been established, it was now important to test all nine selected stimuli multiple times to ensure that the marmosets’ reactions were consistently strong and measureable across a longer period of presentation. The controlled setting also made it possible to determine whether the stimuli altered pre-test behaviour and continued to affect behaviour after removal (post-test behaviour). The aim was to gather a set of data that would enable cross-modal comparisons and, later, multimodal experiments, discussed in Chapters 5 and 6. It was predicted that the behaviour of the marmosets would be affected by both the type (aversive or pleasant) and modality (visual, olfactory or auditory) of the stimulus presented, and that the visual stimuli would elicit the strongest reactions as argued in the primate literature.

The best-studied aversive responses are associated with potential predators (e.g. Arnold *et al*., 2008; Caine and Weldon, 1989; Caro, 2005; Lima and Dill, 1989; Searcy and Caine, 2003), and for prey animals it is obviously useful to remember cues that could enhance their chances of survival. A visual cue of a predator may represent an immediate potential threat (especially in close proximity), which requires a strong and immediate anti-predator response, whereas an olfactory cue may suggest that a predator has been in the area but there may be no need for immediate alarm (Kubovy and Schutz, 2010; Mattiessen, 2010; Nudds, 2010). Identification of the sound is important, because it may stem from a potential food item, mate, competitor or predator, i.e. be rewarding or life-threatening. It was predicted that the marmosets would show strong anti-predator behaviour on presentation of the taxidermic specimen of a quoll but show only low-level fear responses, such as avoidance, to the odour of cat faeces. It was also predicted that the leopard growl would elicit the strongest fear response. Its physical properties consisted of low-frequency, disembodied and entirely unfamiliar sounds that gave the marmosets no opportunity to display anti-predator behaviour, such as mobbing, known to reduce stress hormone levels (Clara *et al.*, 2008; Cross and Rogers, 2006).

4.1.1 Vision

The relative importance of the visual, auditory and olfactory senses in primates is still largely being debated. According to some researchers (e.g. Ache, 1991), olfaction functions as the main source of sensory information from the environment for most animals. However, for every publication on olfaction in primates in the last ten years there are approximately 115 publications on vision (Colquhoun, 2011).

All primates are said to have a highly developed visual system (Lythgoe, 1979; Martin, 1990). The eye of nocturnal primates is designed to increase visual sensitivity, while the eye of diurnal primates maximises visual acuity (Kirk, 2004). The eyes of diurnal primates are large compared to most other mammals; they also scale allometrically with body size (Ross, 2000). The axial length in the eye of common marmosets is 10.9 mm, with posterior nodal distance 7.63 mm (Osorio *et al.*, 2005), and peak cone density is $190/10^3$ mm^2 (Franco *et al.*, 2000). This cone density is similar to that found in humans and one reason why the eye of the common marmoset is considered to be a scaled-down version of the human eye (Troilo *et al.*, 1993) and is used in medical research. Common marmosets, as well as other New World monkeys, exhibit a polymorphism of cone pigments so that males are dichromatic and females are either dichromatic or trichomatic (Jacobs, 1998; Travis *et al*., 1988), as said before (Ch. 1, Section 1.2). While the anatomy and physiology of the marmoset eye has been extensively studied, the visual behaviour of marmosets has received relatively little attention, although some studies have shown that marmosets can perform visually demanding discrimination tasks (Tovée *et al*., 1992).

4.1.2 Olfaction

Primates have been typically regarded as microsmatic in their olfactory sensitivities, i.e. having a poor sense of smell (Heymann, 2006; Laska *et* al., 2000), a belief has that may have led to an under-estimation of the possible efficiency of their olfactory system. Diurnal primates are thought to have an even poorer olfactory system than nocturnal primates, yet the vomeronasal organ, connected with both the oral and nasal cavities in diurnal Callitrichids, is well developed and considered to constitute an additional, and probably independent, chemosensory system (Epple, 1986). That primates have smaller morphological sizes of olfactory structures compared to most other mammals (Baron *et al*., 1983), particularly in the brain (Martin, 1990), has been considered proof that olfaction is of minor importance in primates (Heymann, 2006). However, whether these smaller peripheral and central olfactory structures indicate a reduction in functional olfactory sensitivities is of current debate. In marmosets, olfaction would seem to be important as scent marking can be used to set territory boundaries (Gosling and Roberts, 2001), communicate between and within groups (Lazaro-Perea *et al*., 1999) and identify females (Smith *et al*., 2001). The role of olfaction in prosimians and New World monkeys is widely acknowledged to be of great importance, with most of the species studied in these groups possessing specialised scent-producing skin glands and displaying scent-marking behaviour (Epple *et al*., 1993).

In some primate species olfaction plays a role in territorial defence (Mertl-Millhollen, 1986), communication of reproductive status (Smith and Abbott, 1998), rank (Kappeler, 1998), and identification of sexual partners (Heymann, 1998) as well as of group members (Epple *et al*., 1993). Olfactory discrimination and sensitivity have been studied in the squirrel monkey (*Saimiri sciureus*), a New World primate, and the studies have shown that it demonstrates a strong sense of smell (Hudson *et al*., 1992; Laska and Alicke, 1996; Laska and Freyer, 1997; Laska and Hudson, 1993; Laska *et al*., 2000, 2007). In response to some odours, particularly fruit-based odours, the olfactory sensitivity of squirrel monkeys equalled or excelled that found in rats or dogs – species that are considered to be macrosmatic, or having a keen sense of smell (Laska *et al*., 2000).

Hence there is a growing wealth of knowledge of the importance of olfaction in primate sensory systems, although the use of olfaction in food and predator detection, as examined in this thesis, has been less well studied. The results of the olfactory trials in Experiment 1 presented in the previous chapter showed that the marshmallow odour was highly preferred, and we know that the marmosets are extremely eager to receive marshmallow treats, which have been used as rewards both in our laboratory and in others (e.g. Kemp and Kaplan, 2011). However, whether the sight of marshmallow is still as attractive without an accompanying odour, or vice versa, needs to be tested. Furthermore, by testing the two sensory cues separately, it will be possible to determine whether the marmosets respond more strongly to one modality than the other.

4.1.3 Audition

Common marmosets and other primates are known to use vocalisations as contact calls to maintain group cohesion, communicate territory boundaries with other groups or individuals, provide social communication between individuals of long-ranging species, locate group members or potential sexual partners, announce food discoveries, and warn of predators and predatory risk (Brown *et al*., 1992; Coss *et al*., 2007; Epple, 1968; Moody and Menzel, 1976). Indeed, even small variations in these calls can alter the response of the recipient, suggesting that the perception of such sounds is fine-tuned (Gamba and Giacoma, 2005, 2010). It stands to reason, therefore, that this perception sensitivity could be used for other auditory stimuli (Kaplan, 2009). Some primate species, particularly nocturnal primates, are known to use sound to detect food items, such as insects (Blumstein *et al*., 2008; Goerlitz and Siemers, 2007; Piep *et al*., 2008; Siemers *et al*., 2007). Auditory cues can also be used to detect predators.

Raptors produce high-frequency calls, typically ranging between 7 and 10 kHz (Jurisevic, 1998), while feline predators have low-frequency vocalisations, correlating with the advertisement of size and power (Peters and Tonkin-Leyhausen, 1999). These strong frequency differences between raptors and felines may help identify the danger as coming either from above (aerial attack) or from the ground (terrestrial predator).

4.2 Materials and methods

Twelve marmosets (6 female/6 male, aged 24 to 197 months) were tested individually in all three sensory modalities.

4.2.1 Stimuli

A list of the stimuli selected for further experimentation (Experiments 2 to 4) is shown in Table 4.1.

Table 4.1. Stimuli to be tested in three modalities: the nine stimuli used in this experiment from the visual, olfactory and auditory modalities.

	Visual	Olfactory	Auditory
Aversive	Taxidermic specimen of a quoll	Odour of cat faeces	Leopard growl
Pleasant	Marshmallow	Marshmallow odour	Marmoset food-related calls
Neutral	PVC tubing	Odour of tea infuser	Housing background noise

The aversive and pleasant stimuli were selected based on the strength of the marmosets' response, as described above. At least for the marmosets in our colony, these stimuli were identified as the most aversive or pleasant stimuli (and neutral).

4.2.1.1 Olfactory stimuli

The cat faeces (from a privately-owned animal) and marshmallow (Coles supermarket brand, pink) were diluted in distilled water at a ratio of 1:10 and presented as liquids using the methodology described below (Section 4.2.2.2).

4.2.1.2 Auditory stimuli

Audio clips included personal recordings and clips sourced from the internet as described below and presented in Figure 4.1.

<u>4.2.1.2.1 Food-related calls</u>: Marmosets were presented with a wide range of food items at feeding time and the vocal responses were recorded using a Marantz solid state digital recorder PMD670 and a gain 10 Sennheiser MKH 418S P48 microphone. In all, 5 minutes of intense food calling were obtained from which 60 seconds were used as playback, cleaned only of background sounds (Fig. 4.1 A). Instead of cutting and pasting a series of identical food-related

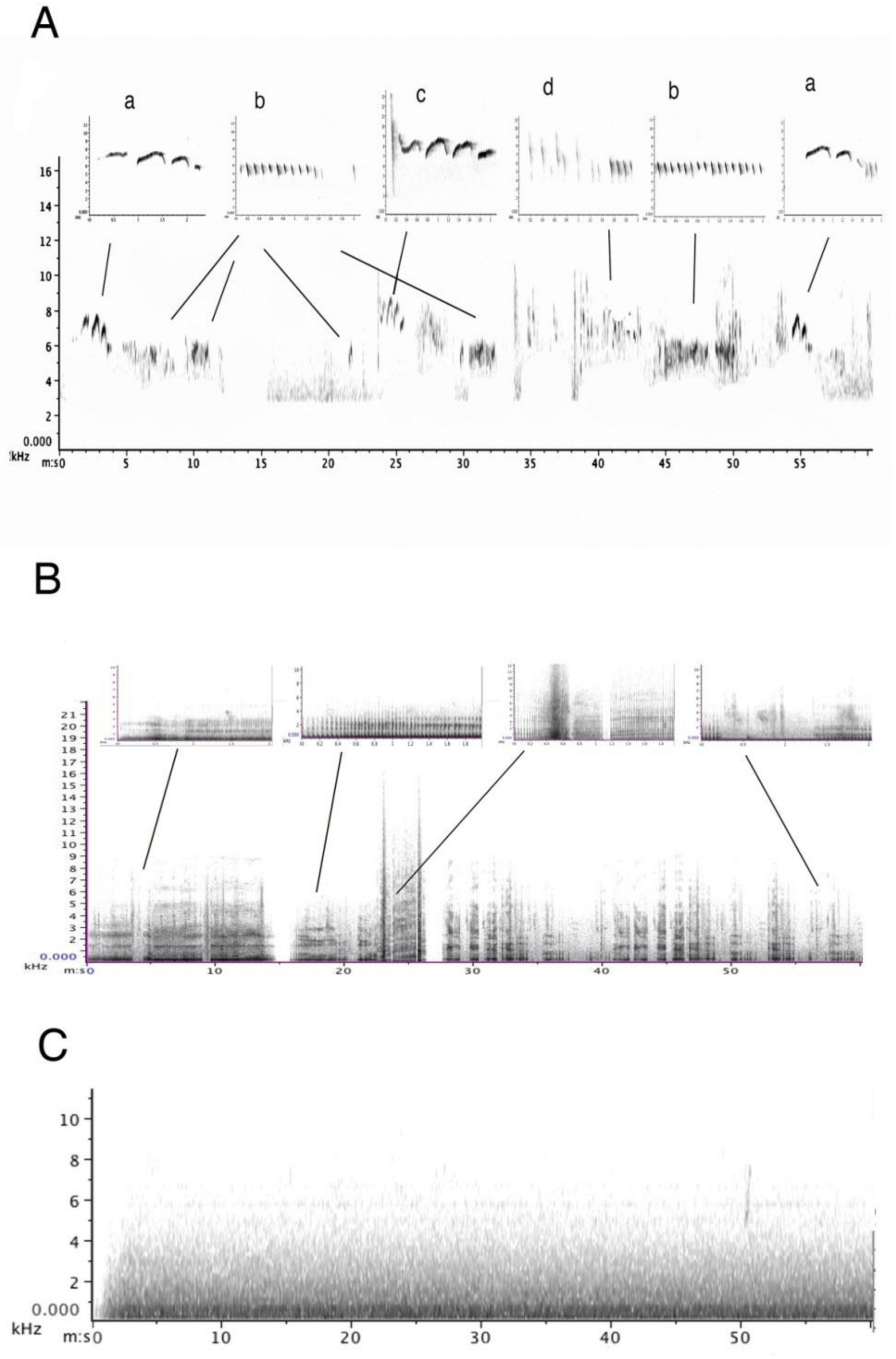


Figure 4.1. Spectrograms of the auditory stimuli used in this experiment and Experiments 3 and 4. kHz are shown on the y axis, time (secs) on the x axis. A – marmoset food-related calls, including excerpts a, b, c and d showing the different sequences , B – leopard growl with excerpts showing different sound structures (most of the energy of the growls is under 2 kHz). C – marmoset housing background noise.

calls together and using only one type of food-related call for the entire 60 seconds of playback, it was decided to use an entire sequence that was produced by one marmoset (Jardine, F, aged 51 months, family group 1, Table 2.1), rather than by marmosets from three different home-rooms because sounds travel between all three rooms and all marmosets are familiar with each other's calls. Moreover, Jardine belonged to the largest family group (Group 1) which, as Chapter 2 had shown, was housed in Room 1 (Table 2.1 and Fig. 2.1, respectively), adjacent to the room that housed Group 2, while Room 3, the room furthest away from Jardine (but could still receive vocal signals from Room 1) was again occupied by marmosets belonging to Group 1. Hence, no ‘stranger’ effect was thus likely.

Further, the sequence that was chosen, shown here in Figure 4.1 A, contained three calls and transitional sounds from one to the other that had been identified as food calls or food-related calls in previous research. One such call, found by Vitale *et al*. (2003), here shown in Figure 4.1. The insert (c), already described in Chapter 2 (details Fig. 2.7 A), was particularly common when live food was presented, such as mealworms or crickets, while another call, a chirp, shown in insert (b) in Figure 4.1 A above (detail also provided previously in Fig. 2.7 D) seemed to occur only when fruit was presented and had been found by Stewart (2009) to be significantly related to such food only. Another call shown in insert (a) of Fig. 4.1 A (also previously discussed in Ch.2 and shown there in Fig. 2.7 C), while it could not be identified clearly as a separate food call, was still found far more frequently in conjunction with the chirp than in any other context. Note that this call sounds to the ear like a phee call (phee shown in Fig. 2.7 B) but it has some crucial differences. The main energy of the phee call is around 10 kHz while the insert (a) in Fig. 4.1 A is not only of lower frequency (6-9 kHz) but also of shorter duration and moves through the frequencies in a different manner (note curving). Whether or not this call has any specific function or serves to link different food-related calls is not known. Still, it seemed important to keep the vocal responses to food as naturalistic as possible and hence include variations and utterances in conjunction with calls that had been identified as belonging to responses to food, particularly to fruit and marshmallow. Hence, the 60 seconds of playback include 3 call types as shown in Fig. 4.1 A (a, b, c) but also variations of the same and transitional elements from one call type to another as shown in insert (d). Reference to this stimulus is made as marmoset ‘food-related calls’.

4.2.1.2.2 Leopard growl: The leopard growl was a combination of shorter audio clips from junglewalk.com and grsites.com/archive/sounds (Fig. 4.1 B). The lengths of the original clips were 14 secs, 13 secs, 10 secs, 6 secs and 3 secs. These were lengthened and/or spliced together to create a natural sounding vocalisation using Goldwave version 5.25. The inserts provided in Figure 4.1 B show some structural variations within the growls typically of a range of 1.5-4.kHz, with the exception of some dramatic and high amplitude sounds (darker shade) reaching up to 14 kHz also shown.

4.2.1.2.3 Background noise: The background noise was recorded from the indoor rooms in the marmosets’ housing using a Marantz solid state digital recorder PMD670 and a gain 10 Sennheiser MKH 418S P48 microphone and consisted mostly of white noise and did not include marmoset vocalisations (Fig. 4.1 C). Several minutes had been recorded to ensure that the one-minute section chosen for testing did not have any unexpected or loud noises, or any marmoset vocalisations.

4.2.2 Experimental procedure

After being enticed into the indoor room and allowed to settle for five minutes, each marmoset was observed and video-recorded for 2 minutes pre-test, 1 minute test and 2 minutes post-test, as described in Chapter 2, Section 2.3. Olfactory stimuli were tested first, followed by visual and then auditory stimuli. However, the stimuli in each modality (aversive, pleasant and neutral) were presented in random order on different days so that no individual was tested more than once per day and there was a minimum of one day between stimulus presentations. Two trials were conducted for each stimulus, with a minimum of one day between presentations, to determine whether the behavioural responses of the marmosets were consistent.

4.2.2.1 Visual stimuli

As previously described (Ch. 2), at the end of the pre-test period the covered visual stimulus was placed on the table in the indoor room, within arm’s reach of the screened door (illustrated in Fig. 2.3, Ch. 2). The cover was then removed and the testing period began. At the end of the testing period (1 min) the visual stimulus was removed, marking the start of the post-test period.

4.2.2.2 Olfactory stimuli

All experiments were now conducted in the indoor rooms and so some alterations were made to the method of presenting olfactory stimuli described in Chapter 3. The tea infuser and cotton ball were placed inside a clear plastic container (6 cm deep, 8.5 cm in diameter) with a lid, in 50 mL of the odour solution. The container was placed inside a white ceramic bowl (6.5 cm deep, 10 cm diameter) (Fig. 4.2) of the same dimensions and colour as those used in other food-based experiments conducted with these marmosets.

The transparent lid of the plastic container was perforated (approximately 35 pinprick holes using a size 8 hand-sewing needle) to allow the odour molecules of the liquid to be detected by the marmosets, but only at very close range. They could easily see the tea infuser and were curious

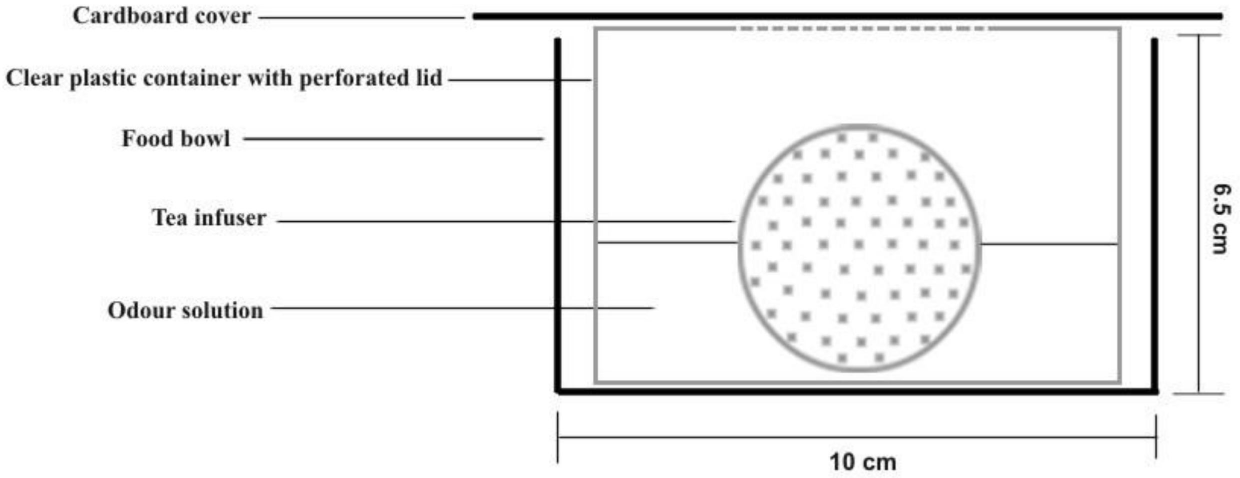


Figure 4.2. Side view of equipment used to present the odour solutions. The lid was perforated in the centre. The odour solution was poured into the plastic container prior to tests. The tea infuser contained a cotton ball for the aversive and pleasant solutions, to soak up the liquid and bring the odour closer to the perforated lid.

enough to sniff at the lid. The insulation of the lid effectively limited the spread of the odour plume, and also avoided direct contact between the marmosets and the liquid. A black cardboard cover was placed over the bowl to further limit the diffusion of the odour prior to the bowl being placed in the indoor room. The marmosets had been trained in a previous study (Brown *et al.*, 2010) to remove black cardboard lids from the food bowls to retrieve a food reward. This method ensured that the marmosets investigated the bowl and, subsequently, the odour. Only one food bowl, container, cardboard cover and tea infuser were used per odour to avoid contamination of the scents. The food bowl, container and tea infuser were washed in distilled water before and after each testing so that the odour did not build up in concentration over time. In other words, every precaution was taken to make each odour unique and specific to the trial, with minimal carry-over to the post-test period.

The zippered canvas door screen was installed for inconspicuous placement and removal of the stimulus. The olfactory stimuli were placed each time at the same location on the platform inside the indoor room, within the experimenter’s reach from the door (illustrated in Fig. 2.3, Ch. 2).

The testing period began when the marmoset had removed the cardboard cover and bent down over the bowl, bringing its nose within 2 cm of the perforated lid (Fig. 4.3). After one minute, the stimulus, including the cardboard cover, was removed from the room by the experimenter.

Cat faeces were collected from a cat that was fed a regular diet of tinned cat food (including chicken, beef, fish, lamb and turkey varieties) and kibble. The faeces were frozen and stored prior to use; samples were not used or kept after a month of storage.

Figure 4.3. Marmoset sniffing at the odour inside the bowl, after removing the cardboard cover.

Pink marshmallow (Coles supermarket brand) at 1:10 dilution was the most pleasant odour presented to the marmosets (Ch. 3). The marshmallow was kept in the refrigerator prior to making up a solution for testing and was not stored for more than a month. Fresh solutions of these odours were made up each day prior to testing. The tea infuser that was used as the neutral olfactory stimulus was clean and had never been used to convey any odour solutions.

4.2.2.3 Auditory stimuli

The auditory stimuli were delivered through a speaker (Logitech Z-5, USB digital) placed on the ledge of the one-way mirror inside the indoor room just above the height of the platform (90 cm from the ground), 50 cm behind the position where the visual and olfactory stimuli were placed in other tests. The speaker was connected to either a PC laptop (HP Pavilion dv9000) or an iPod in the observation room. The sounds were played at 60 dB_{SPL} with a 60-second loop.

The speaker was placed in the room prior to the pre-test period and remained there for the test and post-test periods. The testing period began on commencement of playing the audio clip. At the end of it, the sound was stopped but the speaker remained in the room. The marmosets showed no visible signs of aversion to the speaker.

4.2.3 Behaviour scored

From the video footage taken during the trials, the behaviour scored was: distance from the stimulus (visual or olfactory) location, activity (as movements between virtual room Sections), latency to approach/move, and looking up and down. Contact calls, mobbing/alarm vocalisations, food-related calls and latency to vocalise were analysed using spectrograms of the audio recordings. Detailed definitions of these behavioural responses are provided in Chapter 2 (Section 2.4). Behaviour was scored at five-second intervals. Latency to approach and vocalise was scored in seconds to two decimal places.

4.2.4 Statistical analysis

Firstly, the two trials of each stimulus were compared using two-tailed t-tests for normal data and Wilcoxon signed-rank tests for non-parametric data. When no significant differences were found, the mean of the two trials was taken for each marmoset and used for further analysis. Pre- and post-test values for behaviour that were counted, such as vocalisations and vigilance, were divided by 2 to standardise this for comparison with the one-minute test period. Analyses were conducted for significant differences between the pre-test, test and post-test periods of each stimulus, then between stimuli within each modality, and finally between the same type of stimuli of different modalities. The statistical analyses used are the same as detailed in Chapter 2 (Section 2.5).

4.3 Results

Trials 1 and 2 of the aversive and pleasant stimuli were not significantly different from each other for any behavioural measure across the pre-test, test and post-test periods (two-tailed t-test t values ranged from 0.24 to -1.86 with corresponding p values ranging from 0.81 to 0.09).

The presentations of the neutral stimuli of all three modalities were shown to have little effect on the behaviour of the marmosets from the pre-test scores. The stimuli, particularly the neutral visual (tube) and neutral olfactory (tea infuser odour), did elicit some curiosity in the first trial but the marmosets habituated to its presence rapidly (results of the statistical comparisons of the responses in trials 1 and 2, and the pre-test, test and post-test comparisons, within each neutral stimulus are shown in: visual - Appendix II A, olfactory – Appendix III A, auditory – Appendix IV A).

The data used in the analyses with the aversive and pleasant stimuli are shown in Appendices II (visual), III (olfactory) and IV (auditory) and are presented as either means for each individual (when there was no significant difference between trials) or only trial 1 data (when significant differences were found between the responses of trials 1 and 2). The results of the within-modality comparisons (as shown in: visual - Appendix II C, olfactory - Appendix III C, auditory - Appendix IV C) showed that the neutral stimuli were neither attractive nor repellent. The responses to the neutral stimuli are not discussed further in this chapter.

4.3.1 Responses to visual stimuli

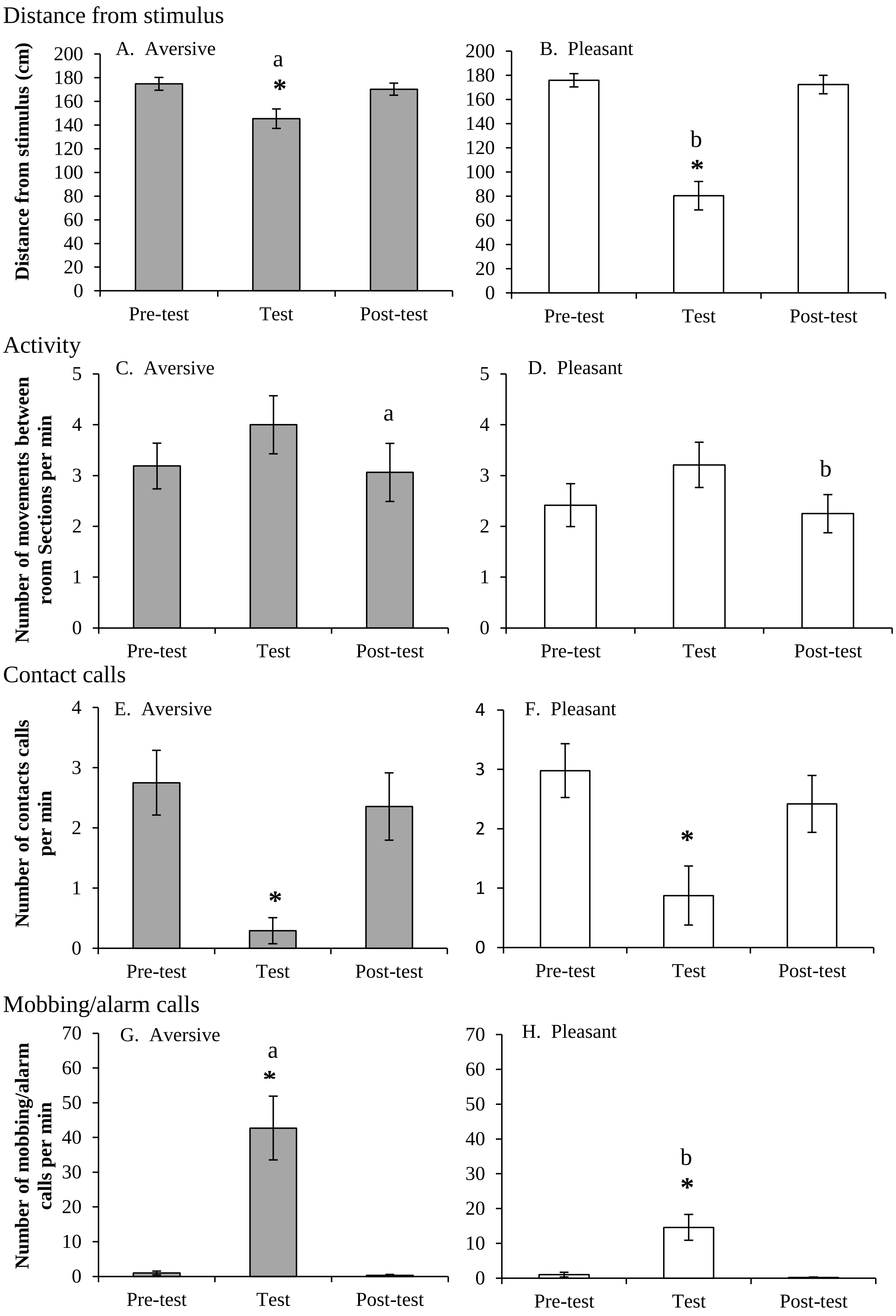
4.3.1.1 Aversive visual stimulus

Table 4.2 presents the results of the statistical analyses comparing the pre-test, test and post-test periods of the aversive visual stimulus (quoll).

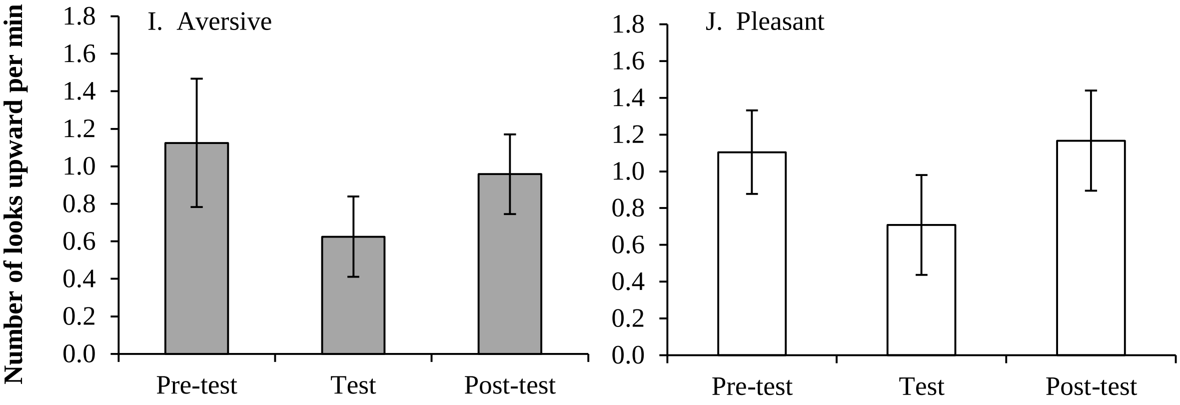
Table 4.2. Statistical comparisons of the responses to the aversive visual stimulus (quoll), pre-test, test and post-test. Tests of heterogeneity were first performed using a repeated measures ANOVA with 'Sphericity Assumed' correction for normal data and a Friedman's test for non-parametric data. *Post hoc* test results are shown where applicable; Bonferroni pairwise comparisons were used for normal data and Wilcoxon signed-rank tests were used to analyse non-parametric data. Significant differences are shown in bold. The '–' indicates when statistical tests were not applicable. The same styling applies to the other Tables in this chapter.

	Main or major effect	Pre-test versus test	Test versus post-test	Pre-test versus post-test
Mean distance from stimulus (cm)	**$F_{(2,22)} = 10.57$** **$p = 0.001$**	**$p = 0.01$**	**$p = 0.02$**	$p = 1.00$
Activity per min	$F_{(2,22)} = 2.22$ $p = 0.13$	–	–	–
Number of contact calls per min	**$X^2 = 12.00$** **p = 0.002**	**$Z = -2.81$** **$p = 0.01$**	**$Z = -2.80$** **$p = 0.01$**	$Z = -1.19$ $p = 0.23$
Number of mobbing/alarm calls per min	**$X^2 = 19.16$** **$p \leq 0.001$**	**$Z = -2.94$** **$p = 0.003$**	**$Z = -2.93$** **$p = 0.003$**	$Z = -0.94$ $p = 0.35$
Number of looks upward per min	$X^2 = 3.35$ $p = 0.19$	–	–	–
Number of looks downward per min	**$X^2 = 18.43$** **$p \leq 0.001$**	**$Z = -3.07$** **$p = 0.002$**	**$Z = -3.07$** **$p = 0.002$**	$Z = -0.81$ $p = 0.42$

As shown in Table 4.2, the presentation of the aversive visual stimulus altered the behaviour of the marmosets in all responses scored except activity (Fig. 4.4 C) and number of looks upward (Fig. 4.4 I). The marmosets' mean distance (cm) from the stimulus location was closer in the test period than it was in the pre- ($p = 0.01$) or post-test ($p = 0.02$) periods (Fig. 4.4 A).


Distance from stimulus
A. Aversive
B. Pleasant
Distance from stimulus (cm)
0
20
40
60
80
100
120
140
160
180
200
a
*
b
*
Pre-test
Test
Post-test
Activity
C. Aversive
D. Pleasant
Number of movements between room Sections per min
0
1
2
3
4
5
a
b
Pre-test
Test
Post-test
Contact calls
E. Aversive
F. Pleasant
Number of contacts calls per min
0
1
2
3
4
*
*
Pre-test
Test
Post-test
Mobbing/alarm calls
G. Aversive
H. Pleasant
Number of mobbing/alarm calls per min
0
10
20
30
40
50
60
70
a
*
b
*
Pre-test
Test
Post-test

Looking upward



Looking downward

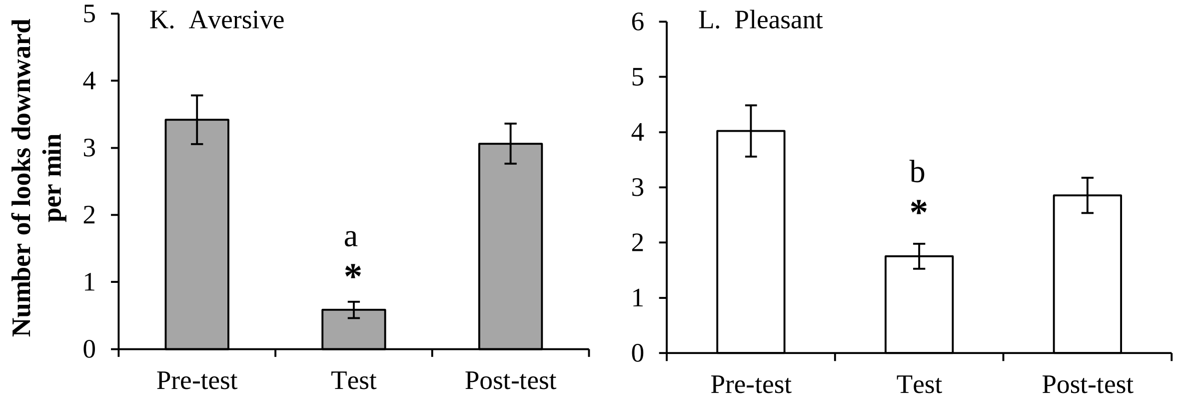


Figure 4.4. Comparison of the behavioural responses scored in the pre-test, test and post-test periods within and between the visual stimuli. The responses to the aversive stimulus (quoll) are plotted on the left (A, C, E, G, I, K; grey bars) and the responses to the pleasant stimulus (marshmallow) are plotted on the right (B, D, F, H, J, L; white bars). A, B – distance from the stimulus (cm), C, D – activity, E, F – contact calls, G, H – mobbing/alarm calls, I, J – looks upward, K, L – looks downward (means ± sem). The measures for pre- and post-test periods did not differ significantly from each other for any of the scores. An asterisk (*) is used to show significant differences between the test and pre-/post-test periods ($p \leq 0.05$). Responses to the aversive and pleasant stimuli have been compared; bars marked ‘a’ differ significantly from those marked ‘b’ ($p \leq 0.05$). Statistical details of these differences are shown in Tables 4.2, 4.3 and 4.4. The marmosets approached both stimuli, but gave more mobbing/alarm vocalisations to the quoll than to the marshmallow.

The number of contact calls produced was lower in the test period than in the pre- ($p = 0.01$) or post-test ($p = 0.01$) periods (Fig. 4.4 E), but the number of mobbing/alarm calls was higher (pre-test versus test: $p = 0.003$; test versus post-test: $p = 0.003$) (Fig. 4.4 G).

Mean distance (cm) was also plotted over time (5-second intervals) and is presented in Figure 4.5. The data were not analysed in this format, but this method of presentation shows the marmosets’ movements throughout the pre-test, test and post-test period.

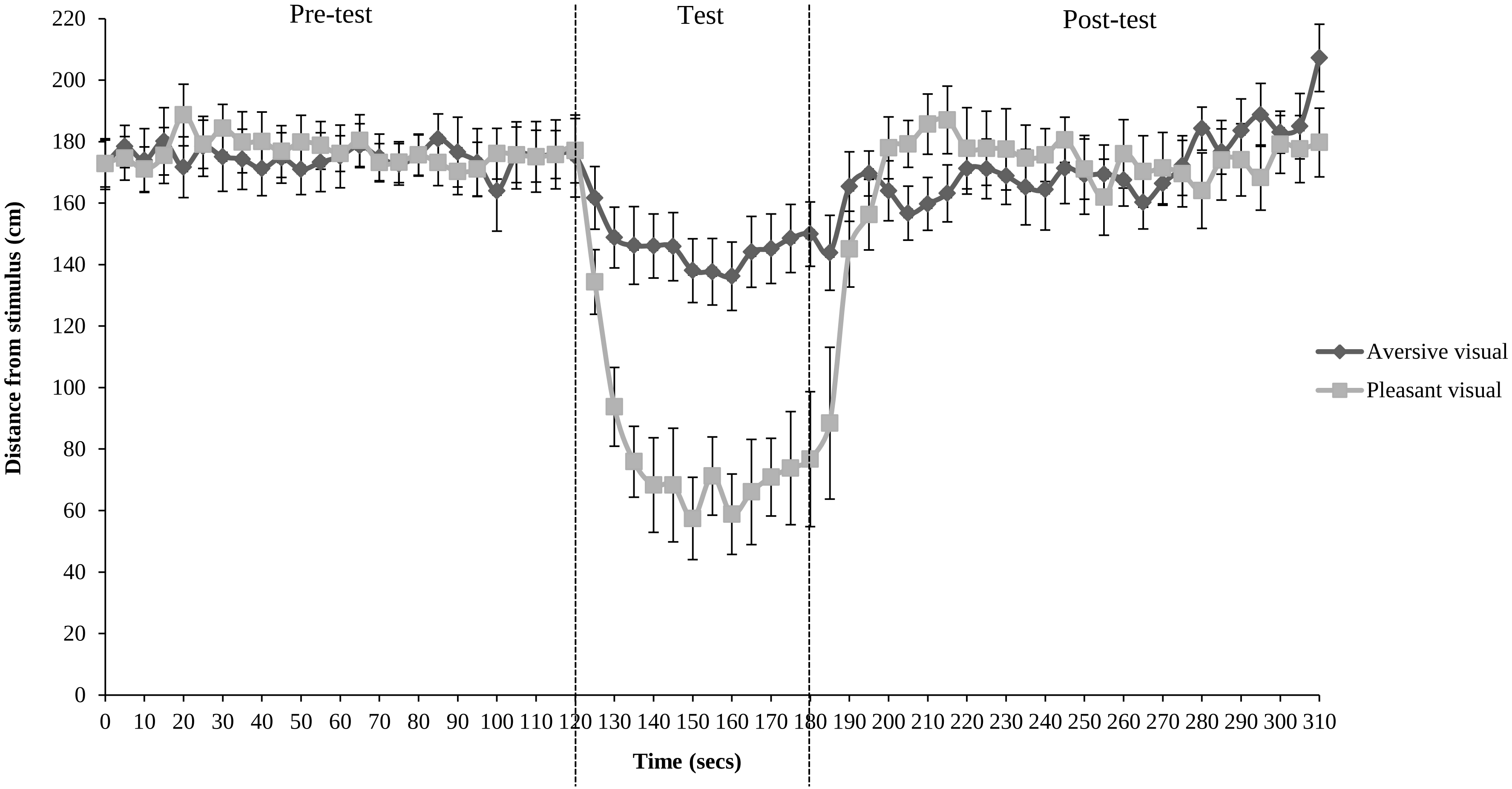


Figure 4.5. Distance (cm) over time (5-second intervals) from the visual stimuli, in the pre-test, test and post-test periods (means ± sem). Dark-grey line (◊ symbols) represents results showing the response to the quoll. Light-grey line (□ symbols) represents results showing the response to the marshmallow. Note that the marmosets approached the marshmallow more closely than they did the quoll and maintained that closeness for most of the presentation.

The number of looks downward also reduced in the test period compared to the pre-test score (p = 0.002), but increased again in the post-test period (p = 0.002) (Fig. 4.4 K). The pre- and post-test periods for all behavioural responses were not significantly different from each other (Table 4.2)

4.3.1.2 Pleasant visual stimulus

The results of the statistical analyses comparing the pre-test, test and post-test periods of the pleasant visual stimulus (marshmallow) are shown in Table 4.3.

Table 4.3. Statistical comparisons of the responses to the pleasant visual stimulus (marshmallow), pre-test, test and post-test.

	Main or major effect	Pre-test versus test	Test versus post-test	Pre-test versus post-test
Mean distance from stimulus (cm)	**X^2 = 18.67** **$p \leq 0.001$**	**Z = -3.06** **p = 0.002**	**Z = -3.06** **p = 0.002**	Z = -0.47 p = 0.64
Activity per min	$F_{(2,22)}$ = 2.78 p = 0.08	**-**	**-**	**-**
Number of contact calls per min	**X^2 = 13.15** **p = 0.001**	**Z = -2.56** **p = 0.01**	**Z = -2.52** **p = 0.01**	Z = -1.07 p = 0.28
Number of mobbing/alarm calls per min	**X^2 = 12.63** **p = 0.002**	**Z = -2.59** **p = 0.01**	**Z = -2.94** **p = 0.003**	Z = -1.51 p = 0.13
Number of food-related calls per min	**X^2 = 18.00** **$p \leq 0.001$**	**Z = -2.67** **p = 0.01**	**Z = -2.67** **p = 0.01**	**-**
Number of looks upward per min	X^2 = 1.72 p = 0.42	-	-	-
Number of looks downward per min	**$F_{(2,22)}$ = 15.86** **$p \leq 0.001$**	**t = 4.93** **p = 0.001**	**t = -3.07** **p = 0.03**	**t = 3.05** **p = 0.03**

Again, the marmosets' activity and number of looks upward did not change across the pre-test, test and post-test periods (Table 4.3; Fig. 4.4 D and J, respectively). The marmosets' mean distance from the stimulus location was less in the test period than it was in the pre- (p = 0.002) or post-test (p = 0.002) periods (Fig. 4.4 B). Mean distance (cm) over time (5-second intervals) is shown in Figure 4.5.

Contact calling again was reduced but mobbing/alarm calling increased in the test period in comparison to the pre- (*p* = 0.01 and *p* = 0.01, respectively) and post-test (*p* = 0.01 and *p* = 0.003, respectively) periods (Fig. 4.4 F and H, respectively). Food-related calls were only scored in the test period of the pleasant visual stimulus (8.63 ± 2.33 food-related calls per min); this was significantly different from the pre- (*p* = 0.01) and post-test (*p* = 0.01) scores. The mean number of food-related calls per minute is not included in Figure 4.4.

The number of looks downward decreased in the test period from the pre-test (*p* = 0.001) and increased again in the post-test (*p* = 0.03); however, the number of these looks made in the post-test was lower than scored in the pre-test (*p* = 0.03) (Fig. 4.4 L).

4.3.1.3 Comparison of visual stimuli

Responses to the aversive and pleasant visual stimuli were compared by examining the pre-test, test and post-test periods separately; the statistical results are shown in Table 4.4.

Although the marmosets approached both stimuli they did so more closely when the pleasant visual stimulus was presented ($p \leq 0.001$) (Fig. 4.4A, above); the closest distance scored from the stimulus location was significantly smaller in response to the pleasant visual stimulus than the aversive visual stimulus (*p* = 0.002) (Fig. 4.6A, below). Closest distance of approach from the marshmallow was not 0 cm as three marmosets did not retrieve the food in one trial each (but did in the other trial).

Table 4.4. Statistical comparisons of the responses to the aversive (quoll) and pleasant (marshmallow) visual stimulus, pre-test, test and post-test.

	Pre-test	Test	Post-test
Distance from stimulus (cm)	$t = -0.56$ $p = 0.80$	**$t = -6.78$** **$p \leq 0.001$**	$t = -0.28$ $p = 0.79$
Closest distance to stimulus (cm)	**-**	**$Z = -3.06$** **$p = 0.002$**	**-**
Latency to approach (secs)	-	$t = -1.79$ $p = 0.10$	-
Activity per min	$t = 1.24$ $p = 0.24$	$t = 1.25$ $p = 0.24$	**$t = 2.21$** **$p = 0.05$**
Number of contact calls per min	$Z = -0.80$ $p = 0.42$	$Z = -1.62$ $p = 0.11$	$Z = 0.00$ $p = 1.00$
Number of mobbing/alarm calls per min	$Z = -0.42$ $p = 0.67$	**$Z = -2.98$** **$p = 0.003$**	$Z = -0.27$ $p = 0.79$
Number of food-related calls per min	**-**	**$Z = -2.67$** **$p = 0.01$**	**-**
Latency to vocalise (secs)	**-**	**$Z = -1.96$** **$p = 0.05$**	**-**
Number of looks upward per min	$Z = -0.31$ $p = 0.76$	$Z = -0.53$ $p = 0.60$	$Z = -0.54$ $p = 0.61$
Number of looks downward per min	$t = -1.37$ $p = 0.20$	**$t = 4.10$** **$p = 0.002$**	$t = 0.47$ $p = 0.65$
Number of looks at the stimulus per min	**-**	**$t = 2.41$** **$p = 0.04$**	**-**

While mean activity per minute showed no significant difference between periods within each visual stimulus, there was a significant difference between the post-test periods of the two visual stimuli ($p = 0.05$) (Fig. 4.4 C and D). The marmosets were more active after the aversive stimulus had been removed than after the presentation of the pleasant stimulus ($p = 0.05$). There was no significant difference in latency to approach ($p = 0.10$) (Fig. 4.6 B).

Mobbing/alarm calls increased in response to both visual stimuli but the marmosets gave more of these calls in response to the aversive visual stimulus ($p = 0.003$) (Figs. 4.4 G and H). There was a significant difference in the number of food-related calls produced in the test periods of the aversive and pleasant visual stimuli; the marmosets gave food-related calls only in response to the pleasant stimulus ($p = 0.01$). The marmosets vocalised sooner in response to the aversive visual stimulus than they did to the pleasant visual stimulus ($p = 0.05$) (Fig. 4.6 C).

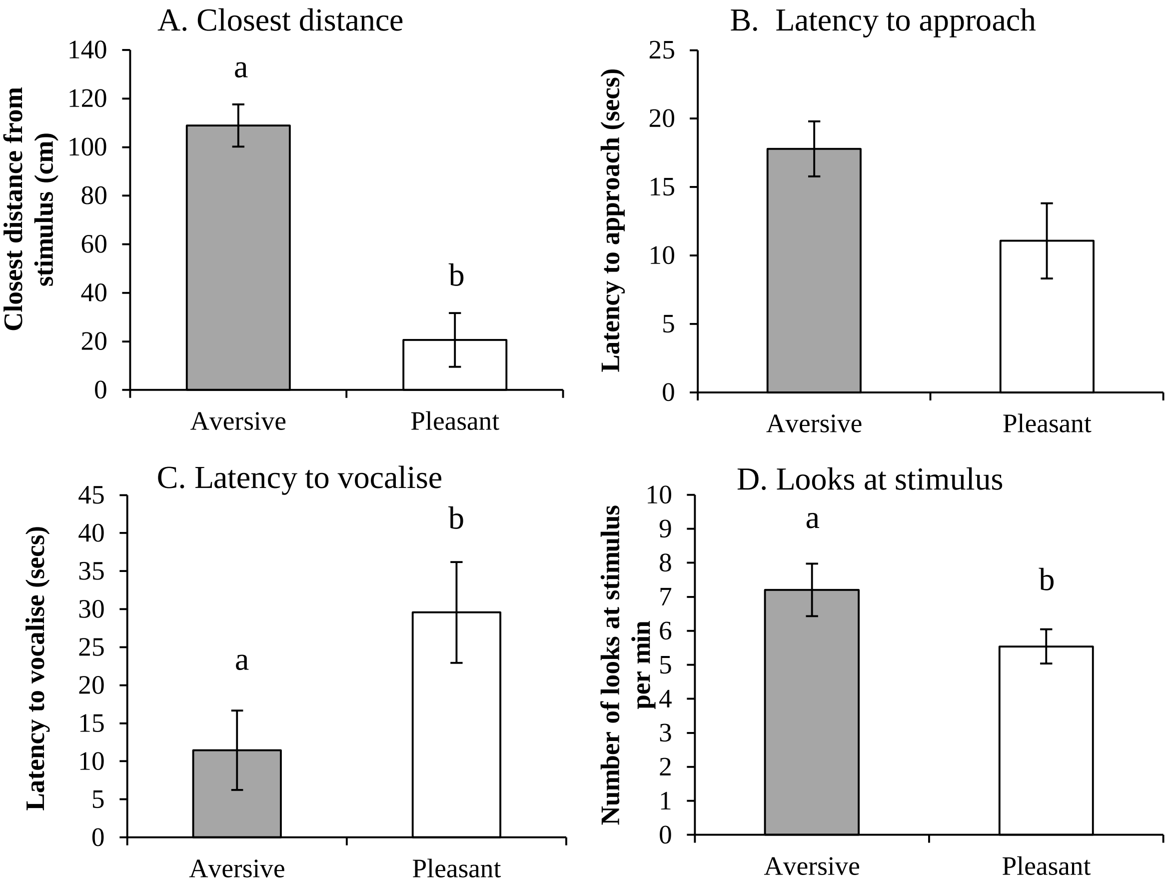


Figure 4.6. Comparison of the behavioural responses to the presentation of the visual stimuli for measurements appropriate only in the test period. The response to the aversive stimulus (quoll) is plotted as grey bars and the response to the pleasant stimulus (marshmallow) as white bars. A – closest distance to the stimulus (cm), B – latency to approach (secs), C – latency to vocalise (secs), D – looks at the stimulus (means ± sem). Bars marked ‘a’ differ significantly from those marked ‘b’ ($p \leq 0.05$). The marmosets began vocalising sooner and were more visually fixated on the quoll than on the marshmallow. Additionally, the mean closest distance to the marshmallow was not 0 cm as three individuals did not retrieve the marshmallow in one trial, but did in the other trial.

The number of looks downward was lower when the aversive visual stimulus was presented than when the pleasant visual stimulus was presented ($p = 0.002$) (Fig. 4.4 K and L). The marmosets looked at the aversive visual stimulus more often than they looked at the pleasant visual stimulus ($p = 0.04$) (Fig. 4.6 D).

4.3.2. Responses to olfactory stimuli

Mean distance from the stimulus location was not compared between the pre-test and test or between the test and post-test periods. This was because the test period started when the marmosets were sniffing the odour and were at a distance of 0 cm, automatically skewing the test-period score to a closer distance.

4.3.2.1 Aversive olfactory stimulus

The results of the statistical analyses comparing the pre-test, test and post-test periods of the aversive olfactory stimulus (cat faeces odour) are shown in Table 4.5.

Table 4.5. Statistical comparisons of the responses to the aversive olfactory stimulus (odour of cat faeces), pre-test, test and post-test.

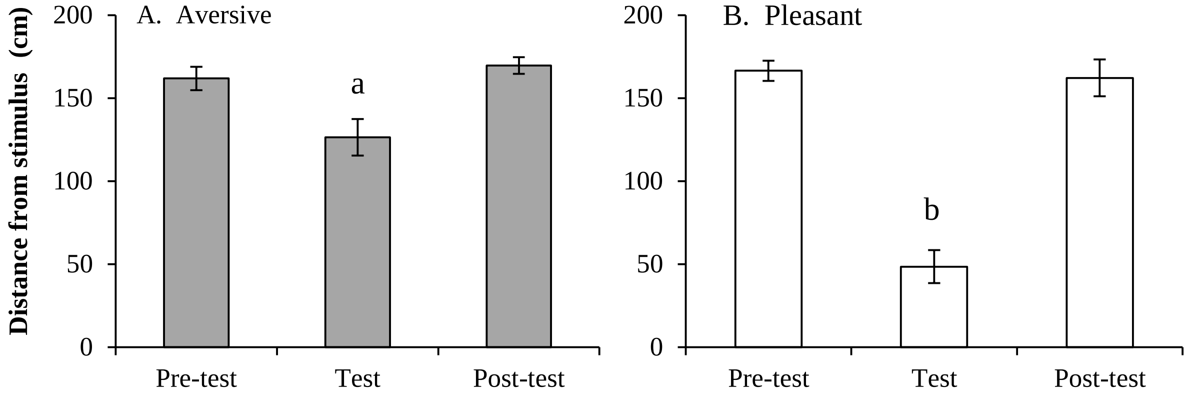
	Main or major effect	Pre-test versus test	Test versus post-test	Pre-test versus post-test
Mean distance from stimulus (cm)	**-**	-	-	$Z = -1.02$ $p = 0.31$
Activity per min	$F_{(2,22)} = 2.31$ $p = 0.12$	**-**	**-**	**-**
Number of contact calls per min	$\mathbf{F_{(2,22)} = 8.47}$ $\mathbf{p = 0.002}$	$\mathbf{p = 0.03}$	$\mathbf{p = 0.03}$	$p = 1.00$
Number of mobbing/alarm calls per min	$X^2 = 4.08$ $p = 0.13$	-	-	-
Number of looks upward per min	$X^2 = 1.00$ $p = 0.61$	-	-	-
Number of looks downward per min	$F(_{2,22}) = 2.00$ $p = 0.17$	-	-	-

Only one of the behavioural responses scored was found to be significantly different across the pre-test, test and post-test periods for the aversive olfactory stimulus (Table 4.5). The number of contact calls given was significantly lower in the test period than it was in the pre- ($p = 0.03$) and post-test ($p = 0.03$) periods (Fig. 4.7 E).

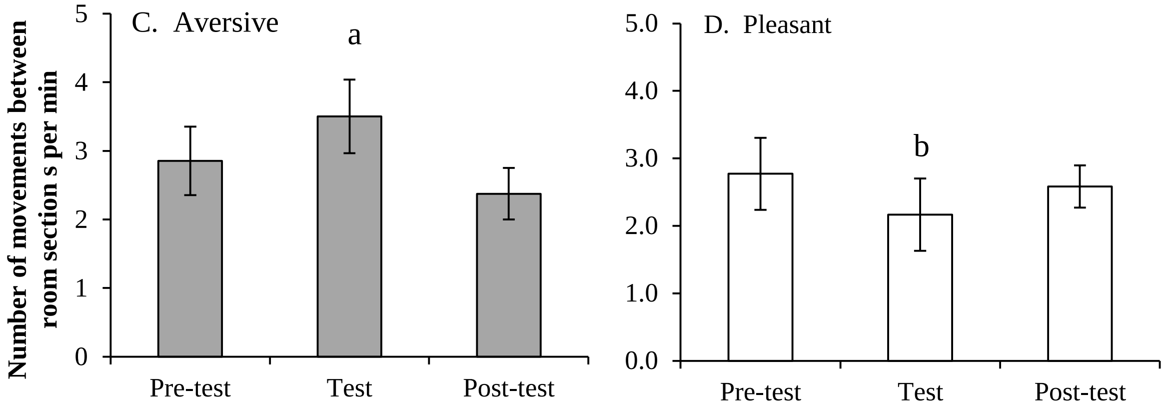
4.3.2.2 Pleasant olfactory stimulus

Table 4.6 presents the results of the statistical analyses comparing the pre-test, test and post-test periods of the pleasant olfactory stimulus (marshmallow odour).

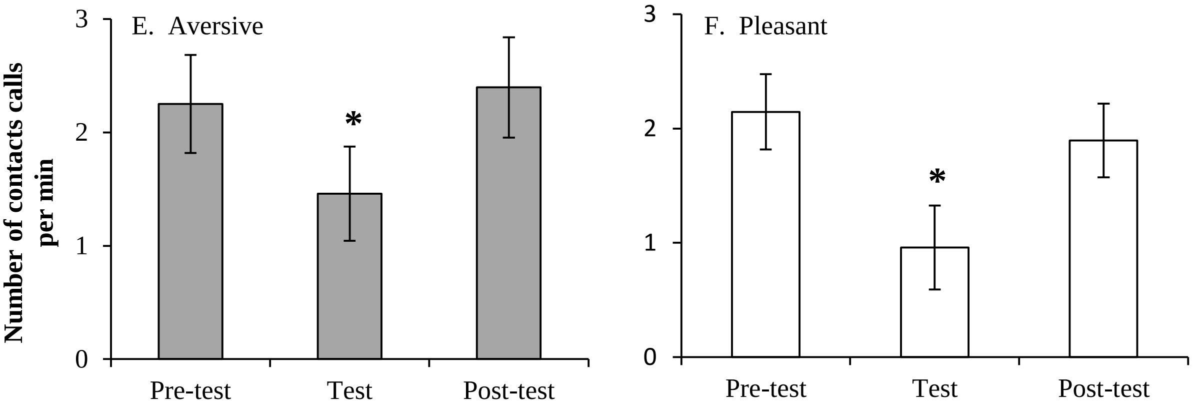
Distance from stimulus



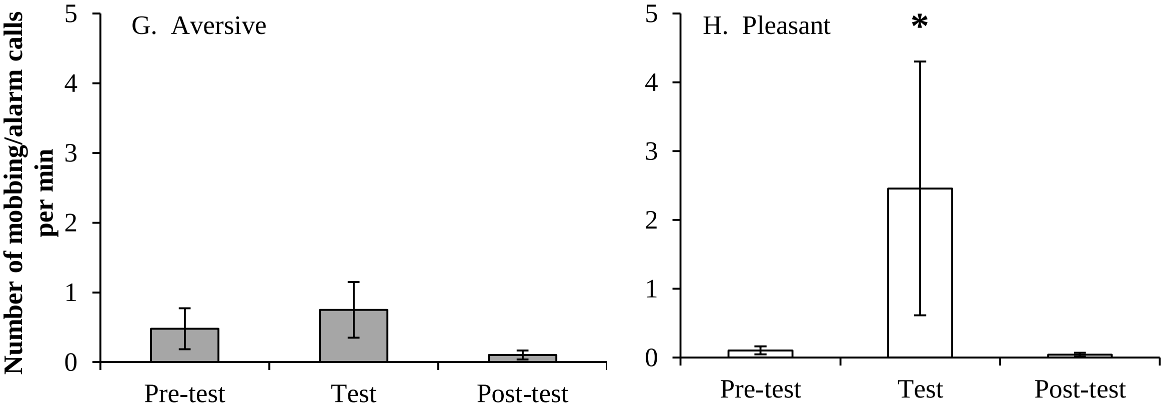
Activity



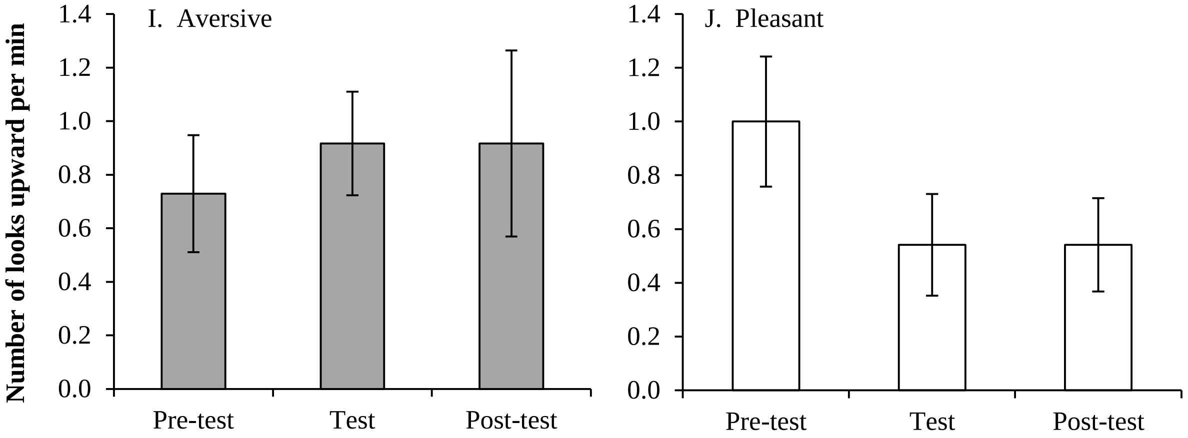
Contact calls



Mobbing/alarm calls



Looking up



Looking down

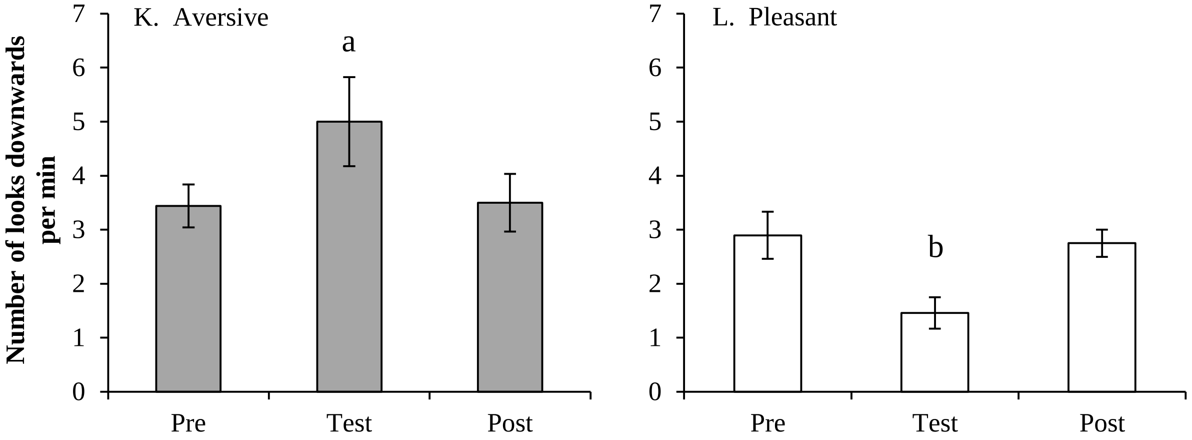


Figure 4.7. Comparison of the behavioural responses (means ± sem) scored in the pre-test, test and post-test periods within and between the olfactory stimuli. The responses to the aversive stimulus (cat faeces odour) are shown on the left (A, C, E, G, I, K; grey bars) and the responses to the pleasant stimulus (marshmallow odour) are shown on the right (B, D, F, H, J, L; white bars). The data are presented as in Figure 4.4. The pre- and post-test scores for A and B were not statistically compared to the test period as this score was skewed due to the 0 cm distance starting point. Statistical details of these differences are shown in Tables 4.5, 4.6 and 4.7. An asterisk (*) is used to show significant differences between the test and pre-/post-test periods ($p \leq 0.05$). Responses to the aversive and pleasant stimuli have been compared; bars marked 'a' differ significantly from those marked 'b' ($p \leq 0.05$). The marmosets remained in closer proximity to the marshmallow odour than they did to the cat faeces odour.

As evident in Table 4.6 below, the three types of vocalisations scored were all significantly different in the test period presenting marshmallow odour than in the pre- and post-test periods. The number of contact calls per minute was lower in the test period than it was in the pre- (p = 0.05) or post-test (p = 0.05) (Fig. 4.7 F). However, the number of mobbing/alarm calls showed the opposite trend (pre-test versus test: p = 0.05; test versus post-test: p = 0.02) (Fig. 4.7 H). Other than one food-related call made in the post-test, food-related calls were scored only during the test period of the pleasant olfactory stimulus (1.79 ± 0.68 per min). This was significantly different from the pre-test (p = 0.02) and post-test (p = 0.02). As food-related calls were observed only in this instance (no food-related calls were scored during the aversive odour test), they were not included in Figure 4.7.

Table 4.6. Statistical comparisons of the responses to the pleasant olfactory stimulus (marshmallow odour), pre-test, test and post-test.

	Main or major effect	Pre-test versus test	Test versus post-test	Pre-test versus post-test
Distance from stimulus (cm)	-	-	-	$Z = -0.63$ $p = 0.53$
Activity per min	$F_{(2,22)} = 0.77$ $p = 0.48$	-	-	-
Number of contact calls per min	**$F_{(2,22)} = 5.94$** **$p = 0.01$**	**$p = 0.05$**	**$p = 0.05$**	$p = 1.00$
Number of mobbing/alarm calls per min	**$X^2 = 6.41$** **$p = 0.04$**	**$Z = -1.98$** **$p = 0.05$**	**$Z = -2.33$** **$p = 0.02$**	$Z = -0.97$ $p = 0.33$
Number of food-related calls per min	**$X^2 = 10.75$** **$p = 0.01$**	**$Z = -2.37$** **$p = 0.02$**	**$Z = -2.38$** **$p = 0.02$**	$Z = -1.00$ $p = 0.32$
Number of looks upward per min	$X^2 = 3.00$ $p = 0.22$	-	-	-
Number of looks downward per min	$X^2 = 3.96$ $p = 0.14$	-	-	-

4.3.2.3 Comparison of olfactory stimuli

Table 4.7 shows the statistical results of the comparisons of the responses (including the test period-only behavioural responses) to the aversive and pleasant olfactory stimuli.

Over the test period, the marmosets remained in closer proximity to the pleasant odour than to the aversive odour ($p \leq 0.001$) (Table 4.7, Fig. 4.7 A and B, above). Movements during the test periods are plotted in Figure 4.8 (below), showing that the marmosets remained near the pleasant stimulus for longer than they did to the aversive stimulus after their initial sniff. Activity per minute was higher in response to the aversive olfactory stimulus than it was when the pleasant olfactory stimulus was presented (p = 0.02) (Fig. 4.7 C and D).

Table 4.7. Statistical comparisons of the responses to the aversive (odour of cat faeces) and pleasant (marshmallow odour) olfactory stimulus, pre-test, test and post-test.

	Pre-test	Test	Post-test
Distance from stimulus (cm)	$t = -0.50$ $p = 0.63$	**$t = 7.59$** **$p \leq 0.001$**	$Z = -0.24$ $p = 0.81$
Activity per min	$t = -0.15$ $p = 0.89$	**$t = 2.66$** **$p = 0.02$**	$t = -0.56$ $p = 0.59$
Number of contact calls per min	$t = 0.23$ $p = 0.82$	$t = 1.73$ $p = 0.11$	$t = -0.15$ $p = 0.89$
Number of mobbing/alarm calls per min	$Z = -0.42$ $p = 0.67$	$Z = -0.34$ $p = 0.74$	$Z = 1.44$ $p = 0.18$
Number of food-related calls per min	-	**$Z = -2.37$** **$p = 0.02$**	$Z = -1.00$ $p = 0.32$
Latency to vocalise (secs)	-	$t = 1.26$ $p = 0.24$	-
Number of looks upward per min	$Z = -0.89$ $p = 0.37$	$Z = -0.28$ $p = 0.78$	$Z = -0.77$ $p = 0.44$
Number of looks downward per min	$Z = -1.19$ $p = 0.23$	**$Z = -2.14$** **$p = 0.03$**	$Z = -1.37$ $p = 0.17$

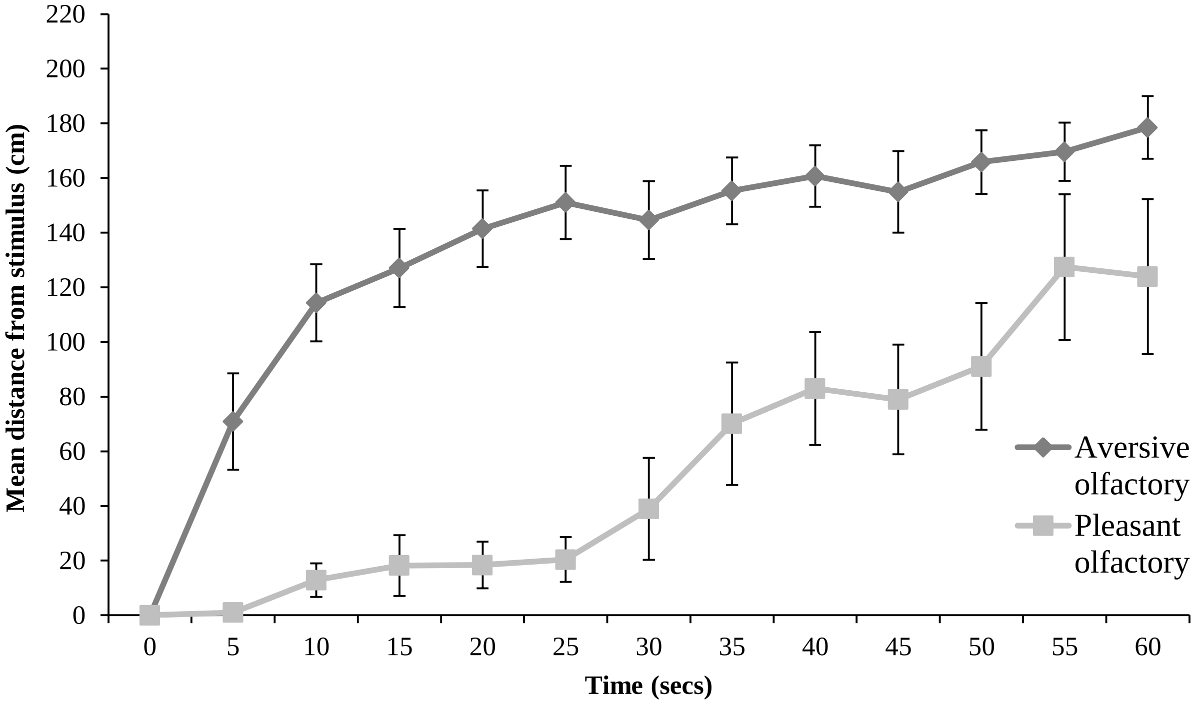


Figure 4.8. Distance (cm) over time (5-second intervals; test period) from the olfactory stimuli (means ± sem). Dark-grey line (◊ symbols) shows the response to the odour of cat faeces. Light-grey line (□ symbols) shows the response to the marshmallow odour. Note that the marmosets lingered around the marshmallow odour for longer than they did in response to the cat faeces odour.

The marmosets gave more food-related calls to the pleasant odour than they did to the aversive odour (p = 0.02). The number of looks downward per minute was higher in response to the aversive odour than it was to the pleasant odour (p = 0.03) (Fig. 4.7 K and L), although there had been no differences between periods for each stimulus.

Although there had been significant differences found for the number of vocalisations made within and between stimuli, there was no significant difference in latency to vocalise between the test-period presentations of the odours (Table 4.7).

4.3.3. Responses to auditory stimuli

4.3.3.1 Aversive auditory stimulus

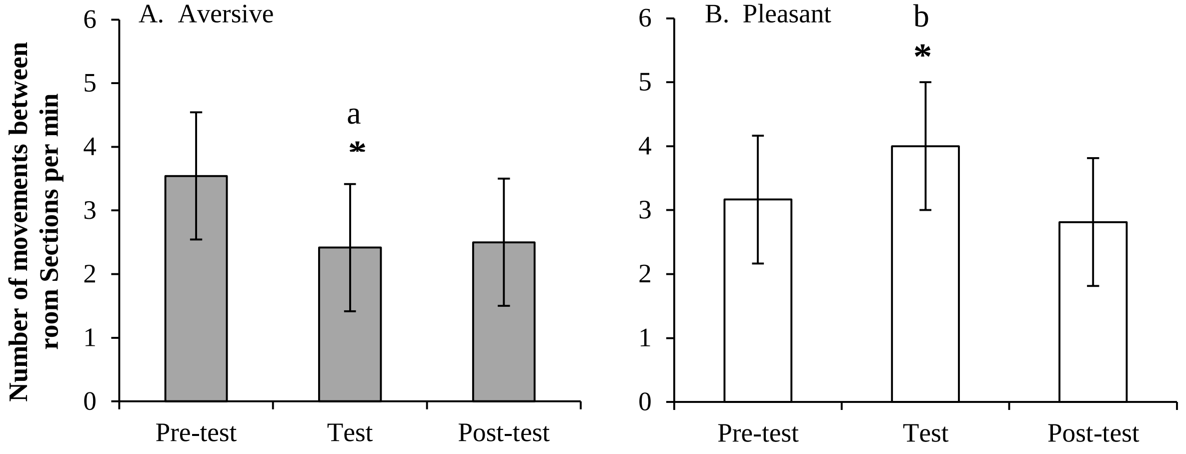
The results of the statistical analyses comparing the pre-test, test and post-test periods of the aversive auditory stimulus (leopard growl) are shown in Table 4.8.

Table 4.8. Statistical comparisons of the responses to the aversive auditory stimulus (leopard growl), pre-test, test and post-test.

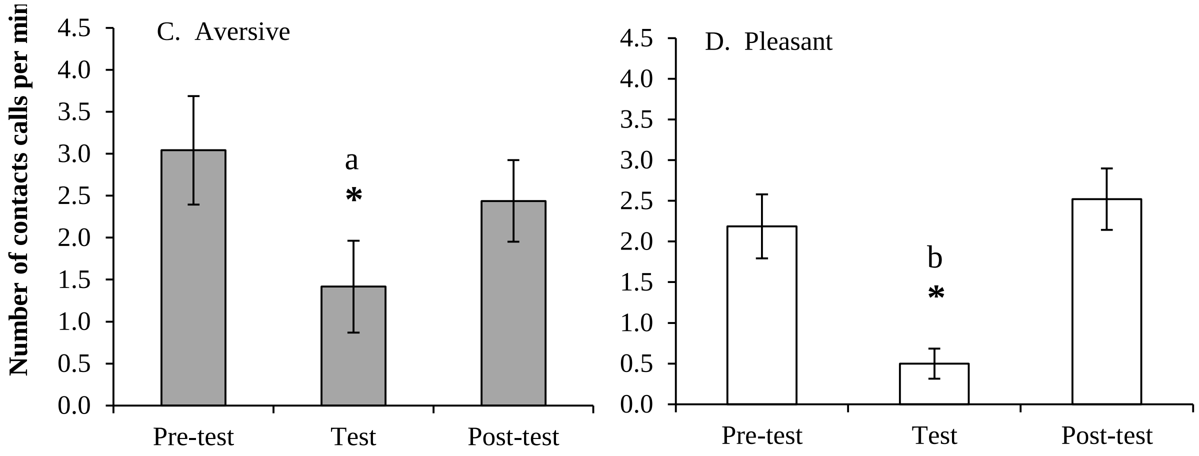
	Main or major effect	Pre-test versus test	Test versus post-test	Pre-test versus post-test
Activity per min	**$F_{(2,22)} = 4.72$** **$p = 0.05$**	$p = 0.14$	$p = 1.00$	$p = 0.11$
Number of contact calls per min	**$X^2 = 14.65$** **$p = 0.001$**	**$Z = -2.91$** **$p = 0.004$**	**$Z = -2.95$** **$p = 0.003$**	$Z = -1.38$ $p = 0.17$
Number of mobbing/alarm calls per min	$X^2 = 0.67$ $p = 0.72$	-	-	-
Number of looks upward per min	$X^2 = 3.05$ $p = 0.22$	-	-	-
Number of looks downward per min	$F_{(2,22)} = 0.77$ $p = 0.48$	-	-	-

The only significant difference found between responses in the pre-test, test and post-test periods was contact calls per minute (Fig. 4.9 C).

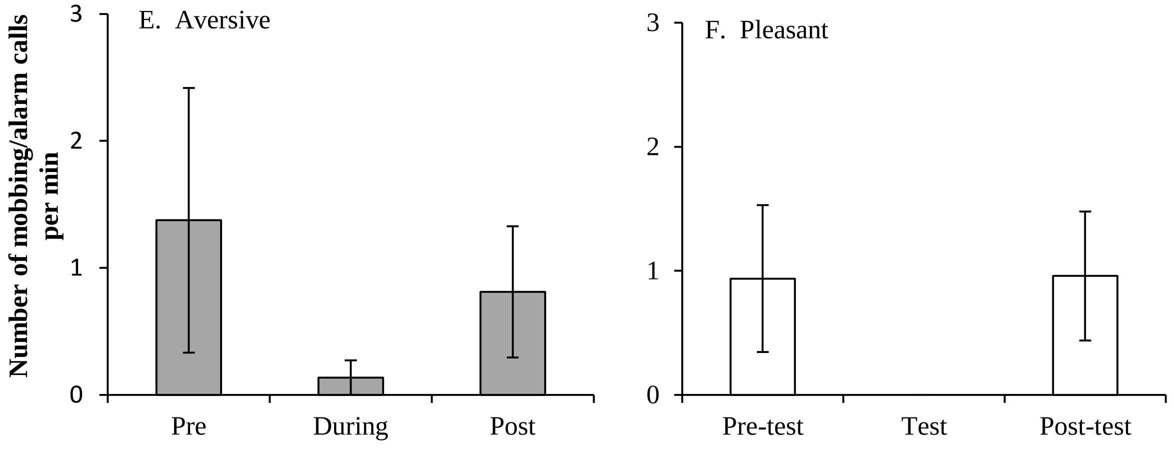
Activity



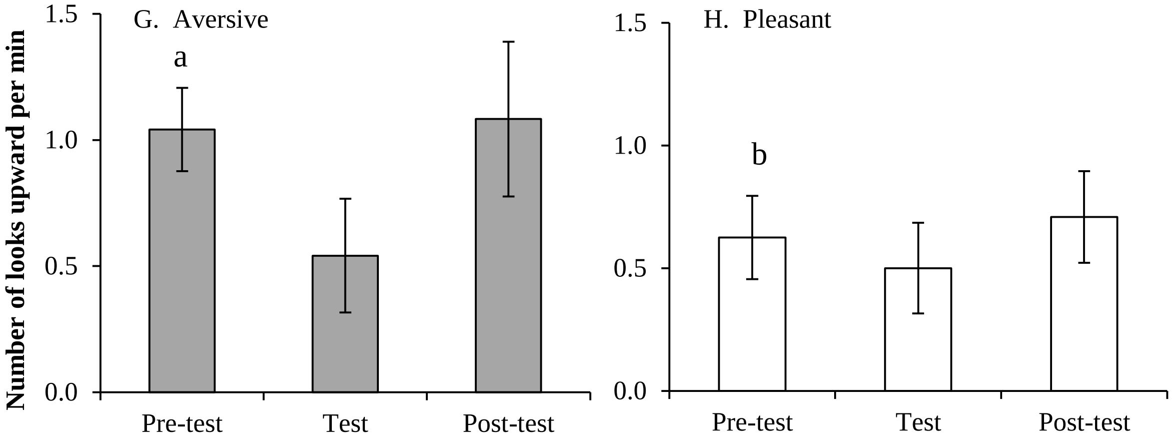
Contact calls



Mobbing/alarm calls



Looking upward



Looking downward

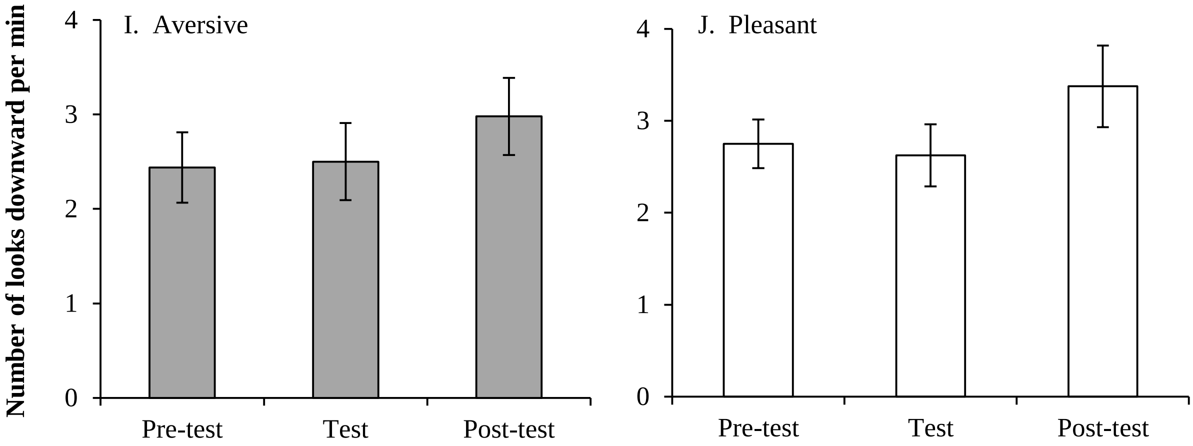


Figure 4.9. Comparison of the pre-test, test and post-test periods within and between the auditory stimuli. Behavioural responses to auditory stimuli (means ± sem). The responses to the aversive stimulus (leopard growl) are shown on the left (A, C, E, G, I; grey bars) and the responses to the pleasant stimulus (marmoset food-related calls) are shown on the right (B, D, F, H, J; white bars). The data are presented as in Figure 4.4. Mean distance was not scored. Due to an outlier in the test period of E, the scores presented were from 11 instead of 12 marmosets. The measures for pre- and post-test periods did not differ significantly from each other for any behaviour scored, except for activity before and after the presentation of the aversive stimulus. Statistical details of these differences are shown in Tables 4.8, 4.9 and 4.10. An asterisk (*) is used to show significant differences between the test and pre-/post-test periods ($p \leq 0.05$). Responses to the aversive and pleasant stimuli have been compared; bars marked ‘a’ differ significantly from those marked ‘b’ ($p \leq 0.05$). Note that the marmosets reduced activity and gave more contact calls in response to the leopard growl than to the marmoset food-related calls. Additionally, note that the marmosets reduced all vocalisations in response to both auditory stimuli.

The marmosets dramatically reduced their vocalisations when the aversive auditory stimulus was presented (from the pre-test scores, $p = 0.004$). Contact calling increased from the test scores in the post-test ($p = 0.003$).

Significant heterogeneity was found for activity per minute, but *post hoc* analysis found no significant differences between the periods (Table 4.8).

4.3.3.2 Pleasant auditory stimulus

The results of the statistical analyses comparing the pre-test, test and post-test periods of the pleasant auditory stimulus (marmoset food-related calls) are shown in Table 4.9.

Table 4.9. Statistical comparisons of the responses to the pleasant auditory stimulus (marmoset food-related calls), pre-test, test and post-test.

	Main or major effect	Pre-test versus test	Test versus post-test	Pre-test versus post-test
Activity per min	$\boldsymbol{F_{(2,22)} = 5.09}$ $\boldsymbol{p = 0.02}$	$p = 0.12$	$\boldsymbol{p = 0.04}$	$p = 1.00$
Number of contact calls per min	$\boldsymbol{X^2 = 18.96}$ $\boldsymbol{p \leq 0.001}$	$\boldsymbol{Z = -3.07}$ $\boldsymbol{p = 0.002}$	$\boldsymbol{Z = -3.07}$ $\boldsymbol{p = 0.002}$	$Z = -0.56$ $p = 0.57$
Number of mobbing/alarm calls per min	$X^2 = 4.73$ $p = 0.09$	-	-	-
Number of looks upward per min	$X^2 = 0.93$ $p = 0.63$	-	-	-
Number of looks downward per min	$X^2 = 3.65$ $p = 0.16$	-	-	-

The results of Table 4.9 show two behavioural responses that were affected by the presentation of the pleasant auditory stimulus. Activity per minute was significantly different only between the test and the post-test periods ($p = 0.04$), showing activity levels decreasing in the post-test (Fig. 4.9 B, above). There was no significant difference between the pre-test and test periods or the pre- and post-test periods (Table 4.9). The marmosets gave significantly fewer contact calls (Fig. 4.9 D) in the test period than they had in the pre- ($p = 0.002$) or post-test ($p = 0.002$) periods. There was a trend for a reduction in the number of mobbing/alarm calls per minute from the pre-test, as no mobbing/alarm calls were scored in the test period (Table 4.9; Fig. 4.9 F); there was no significant difference as the pre- and post-test scores were quite low.

4.3.3.3 Comparison of auditory stimuli

The results are shown in Table 4.10.

Table 4.10. Statistical comparisons of the responses to the aversive (leopard growl) and pleasant (marmoset food-related calls) auditory stimulus, pre-test, test and post-test.

	Pre-test	Test	Post-test
Activity per min	t = 0.98 p = 0.35	**t = -2.24** **p = 0.05**	Z = 0.55 p = 0.62
Latency to move (secs)	-	t = 0.66 p = 0.52	-
Number of contact calls per min	Z = -1.72 p = 0.09	**Z = -2.16** **p = 0.03**	Z = -0.40 p = 0.69
Number of mobbing/alarm calls per min	Z = -0.53 p = 0.60	Z = -1.60 p = 0.11	Z = -0.32 p = 0.75
Latency to vocalise (secs)	-	t = 1.85 p = 0.09	-
Number of looks upward per min	**Z = -2.11** **p = 0.04**	Z = -0.09 p = 0.93	Z = -1.26 p = 0.21
Number of looks downward per min	Z = -1.20 p = 0.23	Z = -0.31 p = 0.76	Z = -0.71 p = 0.48

Behavioural responses to the aversive (leopard growl) and pleasant (marmoset food-related calls) auditory stimulus were significantly different in the test period for activity (p = 0.05) (Fig. 4.9 A and B, above) and the number of contact calls per minute (p = 0.03) (Fig. 4.9 C and D). The marmosets displayed higher activity in response to the pleasant auditory stimulus, but produced fewer contact calls, than to the aversive auditory stimulus. The pre-test scores for number of looks upward for both auditory stimuli were significantly different (p = 0.04); the marmosets looked up more often before the aversive auditory stimulus was presented than before presentation of the pleasant auditory stimulus (Fig. 4.9 10 and H). However, there was no significant difference between the pre-test and test periods for either stimulus (Tables 4.8 and 4.9). To reiterate, there had been no significant difference in this behaviour between the pre-test, test and post-test periods of both stimuli. There was some reduction in the number of looks up during the presentation of the leopard growl which may be why no significant difference was found between responses in the test periods of the leopard growl and food-related calls.

Interestingly, there was no significant difference between the responses to the stimuli in latency to move (secs) and latency to vocalise (secs) (Table 4.10; Fig. 4.10 A and B, respectively). There were no significant differences between periods for the aversive (Table 4.8) or pleasant (Table 4.9) stimuli or between these stimuli (Table 4.10) for mean number of looks downward per minute (Fig. 4.9 I and J).

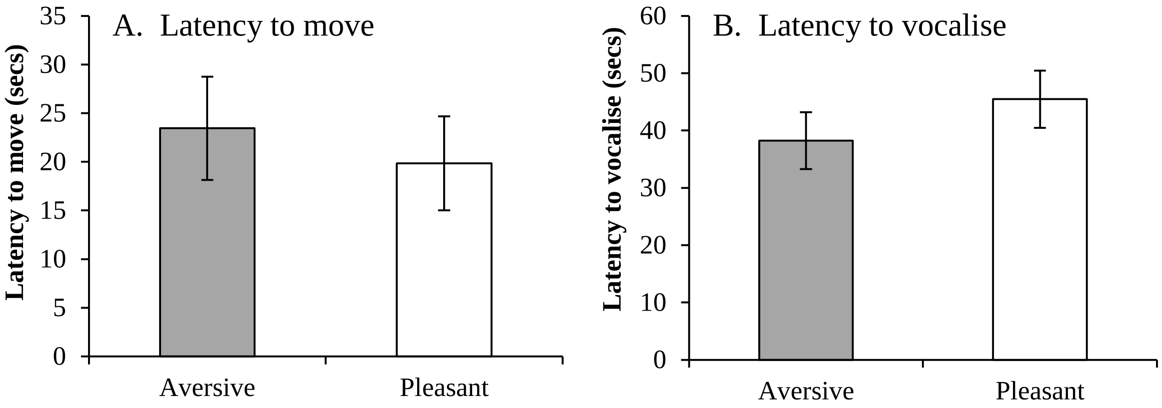


Figure 4.10. Behavioural responses to the presentation of the auditory stimuli for measurements appropriate only in the test period. The responses to the aversive stimulus (leopard growl) are plotted in the grey bars and the responses to the pleasant stimulus (marmoset food-related calls) in the white bars. A – latency to move (secs), B – latency to vocalise (secs) (means ± sem). There were no significant differences between responses to the aversive and auditory stimuli. Statistical details are shown in Table 4.10.

4.3.4. Comparison between modalities

So far the stimuli have been compared between types (aversive and pleasant) within each modality. In this section, the stimuli are compared within type, but between modalities.

The pre- and post-test periods were tested for heterogeneity for each behavioural response scored. Except for two occasions, no significant differences were found between stimuli for these periods (repeated measures ANOVAs $F_{(2,22)}$ values ranged from 0.40 to 1.18 with corresponding p values ranged from 0.92 to 0.31; Friedman test X^2 values ranged from 0.17 to 2.57 with corresponding p values ranged from 0.92 to 0.28). The pre-tests of the mean number of looks downward per minute for both the aversive (repeated measures ANOVA, $F_{(2,22)} = 6.39$, $p = 0.01$) and pleasant (repeated measures ANOVA, $F_{(2,22)} = 3.84$, $p = 0.04$) stimuli showed significant heterogeneity; *post hoc* tests showed that the score for the aversive auditory stimulus was significantly lower than the score for visual (Bonferroni pairwise comparison, $p = 0.01$) or olfactory (Bonferroni pairwise comparison, $p = 0.05$) stimuli, and the score for the pleasant auditory stimulus was lower than the score for the visual stimulus (Bonferroni pairwise comparison, $p = 0.05$). Significant differences between the test periods for these stimuli therefore had to be considered carefully.

The results of the test period comparisons are reported in Sections 4.3.4.1 (aversive stimuli) and 4.3.4.2 (pleasant stimuli).

4.3.4.1 Aversive stimuli

The statistical results of comparing the test-period responses to the aversive visual (quoll), aversive olfactory (cat faeces odour) and aversive auditory (leopard growl) stimuli are shown in Table 4.11.

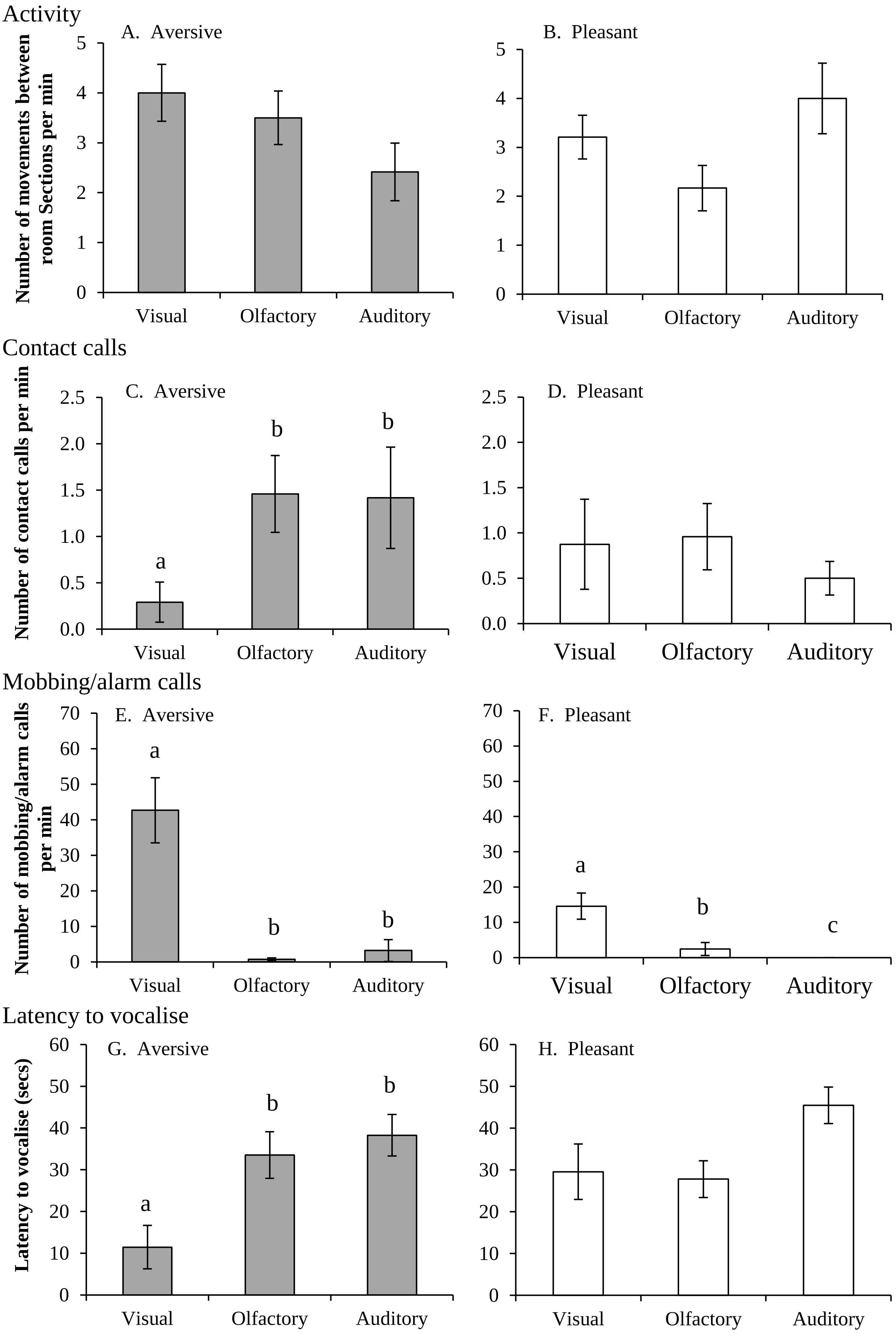
Significant differences were found between the aversive visual stimulus and the aversive olfactory and aversive auditory stimuli (no significant difference was found between the aversive olfactory and auditory stimuli). Activity and number of looks upward per minute did not differ significantly between the three aversive stimuli (Fig. 4.11 A and I, respectively). The marmosets gave fewer contact calls per minute during the presentation of the aversive visual stimulus than

Table 4.11. Statistical comparisons of the responses to the aversive visual (quoll), aversive olfactory (odour of cat faeces) and aversive auditory (leopard growl) stimulus (test period only).

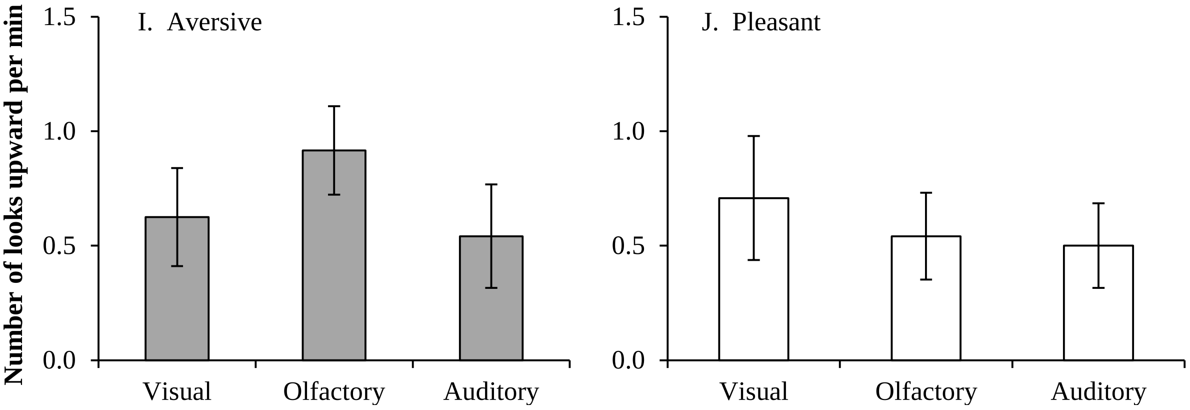
	Main or major effect	Visual versus olfactory	Visual versus auditory	Olfactory versus auditory
Activity per min	$F_{(2,22)} = 2.99$ $p = 0.07$	-	-	-
Number of contact calls per min	$\mathbf{X^2 = 7.35}$ $\mathbf{p = 0.03}$	$\mathbf{Z = 2.32}$ $\mathbf{p = 0.02}$	$\mathbf{Z = -2.17}$ $\mathbf{p = 0.03}$	$Z = -0.82$ $p = 0.41$
Number of mobbing/alarm calls per min	$\mathbf{X^2 = 15.44}$ $\mathbf{p \leq 0.001}$	$\mathbf{Z = -2.93}$ $\mathbf{p = 0.003}$	$\mathbf{Z = -2.49}$ $\mathbf{p = 0.01}$	$Z = -0.42$ $p = 0.67$
Latency to vocalise (secs)	$\mathbf{X^2 = 17.64}$ $\mathbf{p \leq 0.001}$	$\mathbf{Z = -2.93}$ $\mathbf{p = 0.003}$	$\mathbf{Z = -2.93}$ $\mathbf{p = 0.003}$	$Z = -1.16$ $p = 0.25$
Number of looks upward per min	$X^2 = 0.49$ $p = 0.78$	-	-	-
Number of looks downward per min	$\mathbf{X^2 = 18.60}$ $\mathbf{p \leq 0.001}$	$\mathbf{Z = -2.96}$ $\mathbf{p = 0.003}$	$\mathbf{Z = -2.81}$ $\mathbf{p = 0.01}$	$Z = -0.05$ $p = 0.96$

they did during the presentation of the olfactory ($p = 0.02$) and auditory ($p = 0.03$) stimuli (Fig. 4.11 C). The aversive visual stimulus elicited significantly more mobbing/alarm calls than the aversive olfactory ($p = 0.003$) or aversive auditory ($p = 0.01$) stimuli (Fig. 4.11 E). Latency to vocalise (Figure 4.11G) was shorter in response to the visual stimulus than it was in response to the olfactory ($p = 0.003$) or auditory ($p = 0.003$) stimuli.

As mentioned previously, there were fewer looks downward in the pre-test of the aversive auditory stimulus than in the pre-test period of the visual and olfactory stimuli. However, in the test period of the aversive visual stimulus the marmosets looked down less often than they did for the auditory stimulus ($p = 0.01$) (Fig. 4.11 K).


Activity
A. Aversive
B. Pleasant
Number of movements between room Sections per min
0
1
2
3
4
5
Visual
Olfactory
Auditory
Contact calls
C. Aversive
D. Pleasant
Number of contact calls per min
0.0
0.5
1.0
1.5
2.0
2.5
a
b
b
Visual
Olfactory
Auditory
Mobbing/alarm calls
E. Aversive
F. Pleasant
Number of mobbing/alarm calls per min
0
10
20
30
40
50
60
70
a
b
b
a
b
c
Visual
Olfactory
Auditory
Latency to vocalise
G. Aversive
H. Pleasant
Latency to vocalise (secs)
0
10
20
30
40
50
60
a
b
b
Visual
Olfactory
Auditory

Looking upward



Looking downward

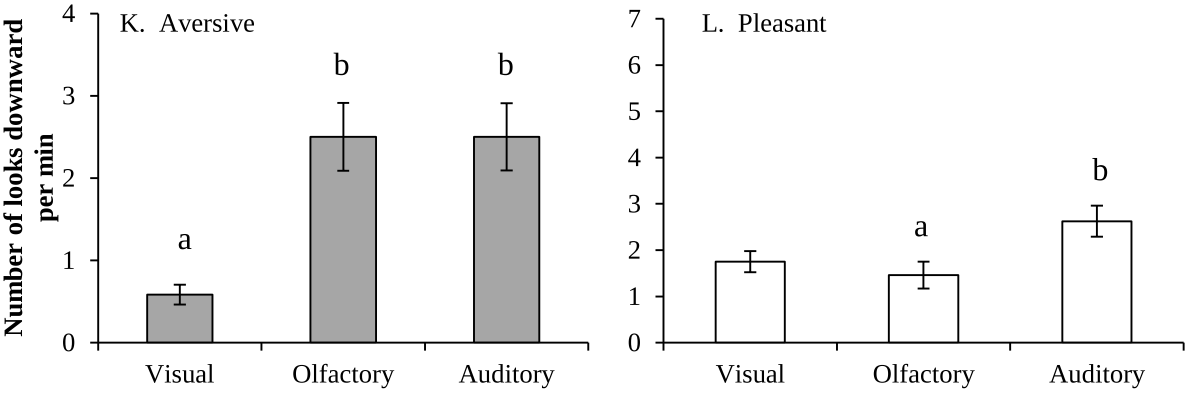


Figure 4.11. Within-type comparison of the behavioural responses in the test periods of the aversive and pleasant stimuli. The responses to the aversive stimuli (quoll, odour of cat faeces and leopard growl) are shown on the left (A, C, E, G, I, K; grey bars) and the responses to the pleasant stimuli (marshmallow, marshmallow odour and marmoset food-related calls) are shown on the right (B, D, F, H, J, L; white bars). A, B – activity, C, D – contact calls, E, F – mobbing/alarm calls, G, H – latency to vocalise (secs), I, J – looks upward, K, L – looks downward (means ± sem). Statistical details of these differences are shown in Tables 4.11 and 4.12. Bars marked ‘a’ are significantly different ($p \leq 0.05$) from those marked ‘b’, and ‘c’ is significantly different from both ‘a’ and ‘b’. Bars without labels represent scores that were not statistically different from each other.

Meanwhile, there was no significant difference in the number of looks downward between the test periods of the auditory and olfactory stimuli ($p = 0.96$). There was a significant difference between the aversive visual and olfactory stimuli ($p = 0.003$).

4.3.4.2 Pleasant stimuli

The statistical results of comparing the test-period responses to the pleasant visual (marshmallow), pleasant olfactory (marshmallow odour) and pleasant auditory (marmoset food-related calls) stimuli are shown in Table 4.12.

Table 4.12. Statistical comparisons of the responses to the pleasant visual (marshmallow), pleasant olfactory (marshmallow odour) and pleasant auditory (marmoset food-related calls) stimulus (test period only).

	Main or major effect	Visual versus olfactory	Visual versus auditory	Olfactory versus auditory
Activity per min	**$F_{(2,22)} = 4.24$** **$p = 0.03$**	$p = 0.16$	$p = 0.80$	$p = 0.08$
Number of contact calls per min	$X^2 = 0.40$ $p = 0.82$	-	-	-
Number of mobbing/alarm calls per min	**$X^2 = 18.20$** **$p \leq 0.001$**	**$Z = -2.13$** **$p = 0.03$**	**$Z = -2.93$** **$p = 0.03$**	**$Z = -2.41$** **$p = 0.02$**
Number of food-related calls per min	**$X^2 = 14.61$** **$p = 0.001$**	**$Z = -2.38$** **$p = 0.02$**	**$Z = -2.67$** **$p = 0.01$**	**$Z = -2.37$** **$p = 0.02$**
Latency to vocalise (secs)	$X^2 = 4.72$ $p = 0.09$	-	-	-
Number of looks upward per min	$X^2 = 0.77$ $p = 0.68$	-	-	-
Number of looks downward per min	**$X^2 = 6.40$** **$p = 0.04$**	$Z = -0.99$ $p = 0.32$	$Z = -1.84$ $p = 0.07$	**$Z = -2.24$** **$p = 0.03$**

A significant difference in heterogeneity was found for activity between the three pleasant stimuli ($p = 0.03$) (Fig. 4.11 B), but *post hoc* analysis found no significant differences between stimuli (Table 4.12).

Significant differences were found between all pleasant stimuli for the mean number of mobbing/alarm calls given per minute (visual versus olfactory: $p = 0.03$; visual versus auditory: $p = 0.01$; olfactory versus auditory: $p = 0.02$) (Fig. 4.11 F). The marmosets gave significantly more food-related calls during the presentation of the marshmallow than they did to its odour ($p = 0.02$) or the food-related calls ($p = 0.01$); there were also significantly more such calls made per minute in response to the olfactory stimulus than there were to the auditory stimulus ($p = 0.02$).

The number of looks downward per minute differed significantly between the olfactory and auditory stimuli ($p = 0.03$). Although there had been a significant difference between the pre-test periods for number of looks downward per minute between the pleasant visual and auditory stimuli, only a trend for fewer looks downward during the presentation of the marshmallow than during the presentation of the food-related calls was found ($p = 0.07$).

4.4 Discussion

As predicted, the results of this study show that the marmosets displayed strong mobbing behaviour in response to the quoll. The leopard growl also produced a strong reaction, but in a different way. Upon hearing the leopard growl the marmosets froze, many trembled, and their locomotion around the room was significantly reduced. Even when the vocalisation was stopped the marmosets remained cautious, moving little. In contrast, once the quoll was removed from the room, the marmosets' behaviour returned to pre-test levels. Only the occasional glance in the direction of where the quoll had been suggested a lingering concern. These results suggest that the auditory cue of a predator elicited a longer-lasting reaction than the visual cue. In contrast, there was not a strong response to the cat faeces after the first contact. The marmosets simply then avoided the stimulus.

The marshmallow and its odour produced behaviour that showed a strong attraction. The marmosets remained in close proximity to the stimuli and attempted to gain access to the marshmallows. Presentation of the food-related calls elicited an increase in activity, measured as room use, which was not seen during the presentation of the leopard growls. Hence, the marmosets displayed some degree of reaction to all of the aversive and pleasant stimuli regardless of modality, but in different ways. Whether one modality is more important than another in eliciting a response to a combination of sensory cues from a stimulus is discussed and explored in detail in Chapter 5.

This experiment was designed to test the strength of the marmosets' response to the stimuli, to determine if habituation would occur, and to provide baseline data for experiments of combining related stimuli (Ch. 5) and presenting conflicting combinations (Ch. 6). Responses to any of the aversive or pleasant stimuli presented were not significantly different from each in the two trials, hence habituation did not occur. In the case of the results obtained for the most aversive and most pleasant visual stimuli, non-habituation seems an enduring feature of the stimuli. For example, the number of mobbing/alarm vocalisations produced in both trials in response to presentation of the quoll presented in this chapter was not significantly different from the number scored in an experiment by Gordon in 2007, using the same marmosets. In case of the auditory and olfactory stimuli there was a potential for longer and repeated exposure to result in some level of habituation. Other studies (e.g. Dacier *et al*., 2006; Raderschall *et al*, 2011) have found that habituation to predatory or aversive stimuli occurred only when the prey animals had learnt that the actual threat level was low. However, since the next experiments (Chapters 5 and 6) presented in this thesis use constantly changing combinations, the risk of habituation might have also been lowered. Habituation did occur in response to the neutral stimuli, particularly the PVC tube and the tea infuser odour. This result was not unexpected and justified their use as neutral stimuli.

The results here also showed that a strong reaction of attraction or withdrawal across all modalities cannot be measured using just one particular behaviour. A suite of behavioural responses needed to be measured and, furthermore, the response of the marmosets was affected by the modality presented (as summarised in Table 4.13). This is important because, as mentioned in Chapter 1 (Section 1.5.2), the number of behavioural responses measured can alter the outcome of a signal classification for combined stimuli. The next two chapters report results of experiments that used combinations only of the stimuli tested in this chapter.

Table 4.13. Summary of the results presented in this chapter, indicating changes in responses from the pre-test scores during the presentation of the aversive and pleasant visual, olfactory and auditory stimuli. Arrows indicate the direction of change (increase or decrease), '-' indicates that no change occurred and n/a shows that distance was not relevant either for the stimulus (auditory) or not comparable between the pre-test and test periods (olfactory).

	Behaviour scored						
Stimulus	Mean distance	Activity	Contact calls	Mobbing/ alarm calls	Food calls	Looks up	Looks down
Quoll	↓	–	↓	↑	–	–	↓
Marshmallow	↓	–	↓	↑	↑	–	↓
Cat faeces odour	n/a	–	↓	–	–	–	–
Marshmallow odour	n/a	–	↓	↑	↑	–	–
Leopard growl	n/a	–	↓	–	–	–	–
Marmoset food-related calls	n/a	–	↓	–	–	–	–

Interestingly, the marmosets responded to the aversive and pleasant stimuli within each modality in similar ways. In most cases the direction of response was the same. For example, the marmosets approached both the quoll and the marshmallow, and reduced contact calling in response to both auditory and olfactory aversive and pleasant stimuli. These findings suggest that different stimuli of a specific modality do not necessarily elicit completely opposite responses (attraction or repellence), but may produce responses of different strength and differences on a continuum (e.g., measures of distance from stimulus). It is important to note, however, that there were some instances in which the marmosets showed opposite reactions to the aversive and pleasant stimuli. The marmosets had a higher activity rate and looked downward more often in response to the cat faeces than they did to the marshmallow odour. This may suggest that the marmosets perceived some information in the odour of cat faeces absent in the marshmallow odour requiring them to scan below table level.

The results of the aerial and terrestrial scans showed that the marmosets had a tendency to look down more than up, regardless of any stimulus being presented. It has been suggested that marmosets are more vulnerable to aerial attack (Caine and Weldon, 1989), but the captive marmosets in our colony may have recognised the ceiling as a barrier. Lizards, insects and mice have been occasionally observed on the floor of the playroom and general terrestrial scanning may be an effect of these encounters. However, as the marmosets also tend to rest and move about in the top third, and certainly the top half, of the room, there is more space and there are also more obstacles in and behind which a threat could be hidden in the lower section of the playroom. Black spider monkeys (*Ateles paniscus*) have been observed to scan terrestrially more than aerially (Neal, 2009). This species dwells in the high canopy of the South American rainforests and it is suggested that this may be a factor in the direction of vigilance, different from that of middle-storey-dwelling primates (Neal, 2009). Wild marmosets are typically found mid-storey (Rylands, 1993). The marmosets looked down more often during the presentation of the odour of cat faeces and leopard growl than they did when they saw the quoll or heard the food-related calls of marmosets. This is not surprising given that the quoll was a visual point upon which the marmosets could fixate and the marmosets would not expect to find conspecifics in the lower storey of the room. Moreover, the odour of cat faeces suggests that there may be something important going on below, important for a species that seeks arboreal refuge.

Activity was significantly higher after the presentation of the quoll than it was after the marshmallow (post-test period); however, there was no significant difference between the pre-test, test and post-test periods of the quoll. Still, this is interesting because increased activity, as mentioned in Chapter 3, has been considered as a response to pleasant stimuli, which a decrease in activity typically occurs when an animal is in the presence of fearful stimuli (Abramsky *et al*., 1996; Dielenberg *et al*., 2001; Gall and Brodie, Jr., 2009). Indeed, there was a trend for increased activity during the presentation of the marshmallow from the pre-test score (Table 4.3). However, this difference in activity between the aversive and pleasant stimuli was found in the post-test period, not during the presentations. This suggests that the marmosets may have been slightly aroused by the quoll and this had some long-term effects that the marshmallow did not.

Presenting both aversive (predatory) and pleasant (food-based) stimuli provided an opportunity to compare not only different types of response but also extremes of response. Chapter 5 presents an experiment in which two and three stimuli from different sensory modalities but of the same type (either all aversive or all pleasant) are combined to test whether these responses intensify with multiple stimuli. Stimuli eliciting opposite responses (conflicting stimuli) were presented together and tested in a separate experiment; this is described in Chapter 6.

CHAPTER FIVE

EXPERIMENT 3: RESPONSES TO RELATED MULTIMODAL COMBINATIONS

5.1 Introduction

The previous experiment established that responses were dependent on the modality in which a stimulus was presented but, of course, this result was based on presenting one stimulus only. Darwin suggested in 1872 that multiple, concurrent stimuli should be important in the communication systems of animals (Darwin, 1872). Tinbergen reiterated this view in 1959 (Tinbergen, 1959). It has been widely acknowledged that many signals and stimuli in nature are multimodal (Guilford and Dawkins, 1991; Rowe and Guilford, 1996) and the question has arisen how these are processed, together or independently (Hebets and Papaj, 2005; Partan and Marler, 1999; Rowe and Guilford, 1996; Smith, 1994). This chapter is therefore concerned with testing compatible bi- and trimodal combinations of aversive or pleasant stimuli, while Chapter 6 reports on results obtained from presenting conflicting combinations (i.e. aversive together with pleasant stimuli).

The experiment presented here aimed to test whether the responses to the individually presented stimuli would be altered by presenting multiple predator- or food-based stimuli, or whether one modality might dominate. When these stimuli were to be presented simultaneously, it was possible that the marmosets would either not associate the stimuli with each other and try to respond to each one separately (independence) or focus on only one stimulus (dominance). As mentioned in Chapter 1, Partan and Marler (1999, 2005) also suggested that responses might be modulated or display entirely new behavioural patterns. However, their theory was based on social signal displays by a single animal using multiple modalities to communicate. In the natural world, information is received from various sensory sources daily and needs to be processed so as to enhance the probability that objects and events will be detected and identified correctly and rapidly, and responded to appropriately (Stein and Wallace, 1999). Importantly, multiple signals or stimuli from a common event or entity, regardless of modality, are thought to be coupled for processing in the brain (Calvert *et al*., 2004; Nakamura *et al*., 2007). This is known as the ‘binding problem’ (von der Malsburg, 1981). The core of this problem was first realised by Immanuel Kant in 1781, although he termed it ‘synthesis’ (Revonsuo and Newman, 1999). Kant theorised that the world is made up of perceived objects, and in order for the brain to produce a unified and complex representation of one’s environment, the mind must first have some way of relating the different objects it experiences together (Revonsuo and Newman, 1999). In my study, multiple stimuli were derived from different sources, despite their commonalities, which the marmosets may or may not associate with each other even when the stimuli are presented simultaneously. It is hence not so much a matter of whether the marmosets in this study are predator-naive or whether presentations of two or three stimuli arise from the same source or not. It has already been shown that each selected stimulus was consistently aversive or pleasant, as the case may be. The question is whether combining two or more of the same type of stimulus intensifies the response, elicits change in new or specific directions, suggesting a different impact of multimodal over unimodal information.

Furthermore, presenting multiple and aversive stimuli simultaneously may increase the level of risk perceived. The threat-sensitivity predator-avoidance hypothesis (Helfman, 1989) suggests that prey animals actively assess the degree of threat posed by a predator and alter their behavioural response accordingly. The results of Experiment 2 (Ch. 4) suggested that the odour of the cat faeces was unpleasant, but that the marmosets perceived both the quoll and the leopard growl as not just aversive stimuli, but also as risks. The threat-sensitivity hypothesis suggests that when these stimuli are combined and presented simultaneously, the animal’s response should increase in intensity as the threat appears to increase. That is, neither stimulus is dominant, but perceived together they provide more information than their parts. To express this differently, as mentioned in Chapter 1 (Section 1.5), this is an example of modulated, non-redundant signalling, as described by Partan and Marler, (1999, 2005).

However, this hypothesis has been mostly tested on predator-experienced animals that were able to associate the stimuli as coming from a single event or entity, e.g. a predator. Since the experience of the marmosets to bind the aversive stimuli together was at least questionable, it was predicted that responses would reflect a hierarchy of modality, i.e. the aversive visual stimulus would have a greater impact than the auditory stimulus, and the olfactory stimulus would have the least impact. For the pleasant stimuli, however, it was predicted that a combination of any of the three would intensify the response shown to the individual stimulus, reflected, for instance, in reduced response time. This prediction was based on evidence that indicates that vision and olfaction together are important modalities for primates in identification of odours (Zellner *et al*., 1991) and determining food palatability (Dominy 2004; Dominy *et al*., 2001; Hiramatsu *et al*., 2009), and auditory cues (food-related calls) elicit approach and searching by conspecifics (Vitale *et al*., 2003).

5.2 Materials and methods

Twelve common marmosets (6 females/6 males; aged 24 to 197 months) were tested individually for their responses to related combinations of the aversive and pleasant stimuli that were tested separately in Experiment 2 (Ch. 4).

5.2.1 Combinations tested

Bimodal and trimodal combinations were tested, using either only aversive or only pleasant stimuli within each combination. Altogether eight combinations were tested. These were:

Aversive –

1. Visual (quoll) + olfactory (cat faeces odour)
2. Visual (quoll) + auditory (leopard growl)
3. Olfactory (cat faeces odour) + auditory (leopard growl)
4. Visual (quoll) + olfactory (cat faeces odour) + auditory (leopard growl)

Pleasant –

1. Visual (marshmallow) + olfactory (marshmallow odour)
2. Visual (marshmallow) + auditory (marmoset food-related calls)
3. Olfactory (marshmallow odour) + auditory (marmoset food-related calls)
4. Visual (marshmallow) + olfactory (marshmallow odour) + auditory (marmoset food-related calls)

5.2.2 Experimental procedure

The combinations were presented in a set order (visual/olfactory, visual/auditory, olfactory/auditory, then trimodal combinations), but aversive and pleasant were randomised within that order. This was to ensure that there was sufficient time – at least four weeks – between the presentations of any stimulus, particularly aversive stimuli, to reduce the risk of habituation. Each combination was presented once, with a minimum of one day between presentations.

As described in the General Methods (Ch. 2), an individual marmoset was enticed into the indoor room and left to explore the room for a few minutes. The marmoset was then observed and filmed for a two-minute pre-test period, followed by a two-minute test period in which a combination was presented and further observed for a two-minute post-test period.

Care was taken to ensure that the stimuli were presented simultaneously to improve the chances of these being perceived simultaneously. This required some adaptations for the visual/olfactory combination, especially for the aversive combination. Experiment 3 (Ch. 4) had shown that the marmosets did not approach the quoll closely enough to get right next to the bowl and detect an odour inside. To improve the design, the tea infuser was placed on a piece of black cardboard. This method of presentation allowed the odour molecules to disperse more readily than was possible when using the bowl with the perforated lid, improving the chances of detection without the marmosets having to approach the quoll closely. The visual and olfactory stimuli were then covered with a piece of calico, as used in Experiment 2 (Ch. 4), and placed on the platform in the indoor room within arm’s reach of the door, with the tea infuser and cardboard placed next to (< 5 cm) the visual stimulus. The calico cover was then removed and the testing period started. The cotton ball inside the tea infuser was soaked in the solution and removed from the solution just prior to testing. To humans, both the cat faeces and marshmallow odours were detectable from the tea infuser at least one metre away. This method of presenting the olfactory cue was used only for combinations that also included a visual component.

The visual/auditory stimuli were presented simultaneously by covering the visual stimulus with calico before placing it on the platform in the indoor room (within arm’s reach of the door). Thus, playing of the auditory stimulus could begin when the cover was removed from the visual stimulus. At the end of the test period the sound was stopped and the visual stimulus was removed from the room.

Presenting olfactory/auditory combinations simultaneously involved first placing the olfactory stimulus on the platform. Here, the original method could be used (olfactory stimulus in a bowl with a cardboard cover that the marmoset had to remove). The auditory stimulus was played only when the marmoset had approached the olfactory stimulus and removed the cardboard cover. At the end of the two-minute test period, the bowl was removed and the auditory stimulus turned off. The aim of the cardboard cover was to limit the dispersal of the odour. The removal of the lid was used as a clear indicator of proximity to, and potential detection of, the olfactory stimulus. It was judged (from tests on humans) that at that distance (< 5 cm) the marmosets should perceive the odour, and it was already known that olfactory perception in marmosets is far more acute than in humans (Stephan *et al*., 1970).

The trimodal combinations were presented using a combination of the methods described above. The visual stimulus was covered before being placed on the platform in the indoor room at the same time as the tea infuser on the piece of cardboard; the tea infuser was again positioned less than 5 cm away from the visual cue. As the same time as the calico cover was removed from the visual stimulus the auditory stimulus was played; hence all three stimuli were presented simultaneously.

5.2.3 Behaviour scored

The behaviour scored included distance from the stimulus (visual or olfactory) location, activity (as movements between virtual room sections), latency to approach, contact calls, mobbing/alarm vocalisations, food-related calls, latency to vocalise, and looking up and down. Detailed definitions of these behavioural responses were provided in Chapter 2 (Section 2.4). Behaviour was scored at five-second intervals. Latency to approach and vocalise was scored in seconds to two decimal places.

5.2.4 Statistical analysis

Each combination, except for the olfactory/auditory combinations, was analysed for significant differences between the pre-test, test and post-test periods for all behavioural responses; mean distance from the stimulus was compared between the pre- and post-test periods only, as the test period began at 0 cm from the stimulus. The full two minutes of the test period were used in the comparisons with the pre- and post-test periods. The first and second minutes of the test period of the combination stimuli were also compared using t-tests and Wilcoxon signed-rank tests (presented in Appendix V). This was to test for changes over time. The results of each combination were compared to the results of each individually presented stimulus (as described in the previous chapter); the pre-test, test and post-test periods were all compared separately. Individual stimuli had been tested for one minute; hence, for comparisons between test periods, only the first minute of the presentation of the combination was used. This was because it was important to compare only the initial reaction to the combination to the response to the individually presented stimuli, not a mean taken over the two minutes.

The pre-test, test and post-test periods of each combination were compared with each other, separately. Comparisons of three or more stimuli (i.e. a bimodal combination with the two individually presented stimuli) were made using repeated measures ANOVAs for normal data and Friedman’s test for non-parametric data. *Post hoc* analyses were Bonferroni tests and Wilcoxon signed-rank tests, respectively. Some behavioural responses could only tested between two stimuli or periods; for instance, in the visual/auditory combination, distance from the stimulus could be measured only in regard to the visual component and compared to the individually presented visual stimulus. For these analyses, two-tailed t-tests were used for normal data and Wilcoxon signed-rank tests for non-parametric data.

5.3 Results

5.3.1 Comparison of pre-test, test and post-test results, within each combination

The behavioural responses to the combinations were first tested for significant differences across the pre-test, test and post-test periods and are presented in sections 5.3.1.1 and 5.3.1.2. The data used in these analyses are shown in Appendix V.

5.3.1.1 Aversive combinations

The results of the statistical analyses for the aversive combinations across the pre-test, test and post-test periods are shown in Table 5.1. None of the post-test scores were significantly different from the pre-test scores.

Table 5.1. Statistical comparisons of the pre-test, test and post-test responses for each aversive combination. Tests of heterogeneity were first performed using a Friedman's test for non-parametric data; *post hoc* Wilcoxon signed-rank tests are shown where applicable. Pairwise comparisons were made using two-tailed t-tests for normal data and Wilcoxon signed-rank tests for non-parametric data. Significant results are bolded. The '–' indicates that statistical tests were not applicable. The same styling applies to the other tables in this chapter.

	Main or major effect	Pre-test versus test	Test versus post-test	Post-test versus pre-test
Aversive visual/olfactory combination				
Mean distance from stimulus (cm)	X^2 = 2.60 p = 0.27	–	–	–
Activity per 2 mins	X^2 = 4.80 p = 0.09	–	–	–
Number of contact calls per 2 mins	**$F_{(2,22)}$ = 8.56** **p = 0.002**	**p = 0.03**	**p = 0.03**	p = 1.00
Number of mobbing/alarm calls per 2 mins	**X^2 = 16.27** **$p \leq 0.001$**	**Z = -2.93** **p = 0.003**	**Z = -2.85** **p = 0.004**	Z = -0.73 p = 0.47
Number of food-related calls per 2 mins	X^2 = 2.00 p = 0.37	–	–	–
Number of looks upward per 2 mins	X^2 = 5.69 p = 0.06	–	–	–
Number of looks downward per 2 mins	**$F_{(2,22)}$ = 4.78** **p = 0.02**	p = 0.06	p = 0.12	p = 0.92
Aversive visual/auditory combination				
Mean distance from stimulus (cm)	**$F_{(2,22)}$ = 3.41** **p = 0.05**	p = 0.82	p = 0.06	p = 0.44
Activity per 2 mins	$F_{(2,22)}$ = 0.33 p = 0.72	–	–	–
Number of contact calls per 2 mins	**X^2 = 10.91** **p = 0.004**	**Z = -2.45** **p = 0.01**	**Z = -2.35** **p = 0.02**	Z = -1.20 p = 0.23

Continued from previous page				
	Main or major effect	Pre-test versus test	Test versus post-test	Post-test versus pre-test
Number of mobbing/alarm calls per 2 mins	**X^2 = 13.72** **p = 0.01**	**Z = -2.54** **p = 0.01**	**Z = -2.71** **p = 0.01**	Z = -1.84 p = 0.07
Number of food-related calls per 2 mins	X^2 = 2.00 p = 0.37	–	–	–
Number of looks upward per 2 mins	X^2 = 0.32 p = 0.85	–	–	–
Number of looks downward per 2 mins	**$F_{(2,22)}$ = 5.35** **p = 0.01**	p = 0.08	p = 0.47	p = 0.10
Aversive olfactory/auditory combination				
Mean distance from stimulus (cm)	–	–	–	t = -1.94 p = 0.08
Activity per 2 mins	X^2 = 4.98 p = 0.08	–	–	–
Number of contact calls per 2 mins	$F_{(2,22)}$ = 1.17 p = 0.33	–	–	–
Number of mobbing/alarm calls per 2 mins	X^2 = 0.88 p = 0.65	–	–	–
Number of food-related calls per 2 mins	X^2 = 2.00 p = 0.37	–	–	–
Number of looks upward per 2 mins	X^2 = 1.37 p = 0.51	–	–	–
Number of looks downward per 2 mins	$F_{(2,22)}$ = 1.79 p = 0.20	–	–	–
Aversive visual/olfactory/auditory combination				
Mean distance from stimulus (cm)	X^2 = 0.55 p = 0.76	–	–	–
Activity per 2 mins	$F_{(2,22)}$ = 0.33 p = 0.72	–	–	–
Number of contact calls per 2 mins	X^2 = 5.14 p = 0.08	–	–	–
Number of mobbing/alarm calls per 2 mins	**X^2 = 8.07** **p = 0.02**	**z = -2.38** **p = 0.02**	**z = -2.38** **p = 0.02**	z = 0.00 p = 1.00
Number of looks upward per 2 mins	X^2 = 5.42 p = 0.07	–	–	–
Number of looks downward per 2 mins	$F_{(2,22)}$ = 1.52 p = 0.24	–	–	–

5.3.1.1.1 Aversive visual/olfactory combination: The results of Table 5.1 show that there were significant differences between the periods for contact calls and mobbing/alarm calls. The marmosets gave significantly fewer contact calls per two minutes during the test period than they did in the pre- (p = 0.03) or post-test (p = 0.03) period (Fig. 5.1 A). In contrast, the number of mobbing/alarm calls per two minutes increased in the test period from the pre-test levels (p = 0.003) and then decreased to pre-test scores in the post-test (p = 0.004) (Fig. 5.1 B).

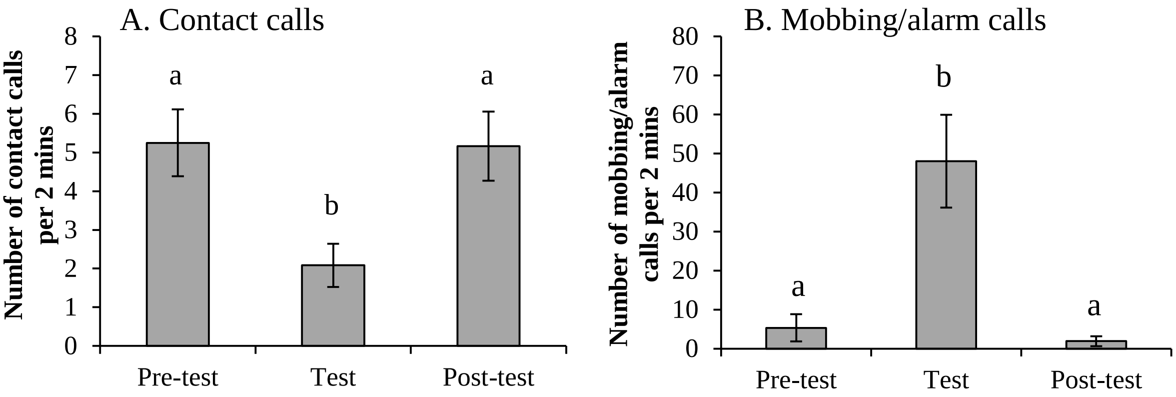


Figure 5.1. Comparison of responses in the pre-test, test and post-test periods: aversive visual/olfactory (quoll/odour of cat faeces) combination (2 mins). A – contact calls B – mobbing/alarm calls (means ± sem). Bars marked 'a' are significantly different from those marked 'b'. The marmosets produced significantly fewer contact calls but more mobbing/alarm calls during the test, compared to the pre- and post-test periods.

5.3.1.1.2 Aversive visual/auditory combination: The statistical results presented in Table 5.1 show that the marmosets gave fewer contact calls per two minutes in the test period than they did in the pre- (*p* = 0.01) or post-test (*p* = 0.02) period (Fig. 5.2 A). The marmosets produced significantly more mobbing/alarm calls per two minutes in the test period than they did in the pre- (*p* = 0.01) or post-test (*p* = 0.01) period (Fig. 5.2 B); there was also a weak trend for significantly fewer mobbing/alarm calls in the post-test period versus the pre-test (*p* = 0.07).

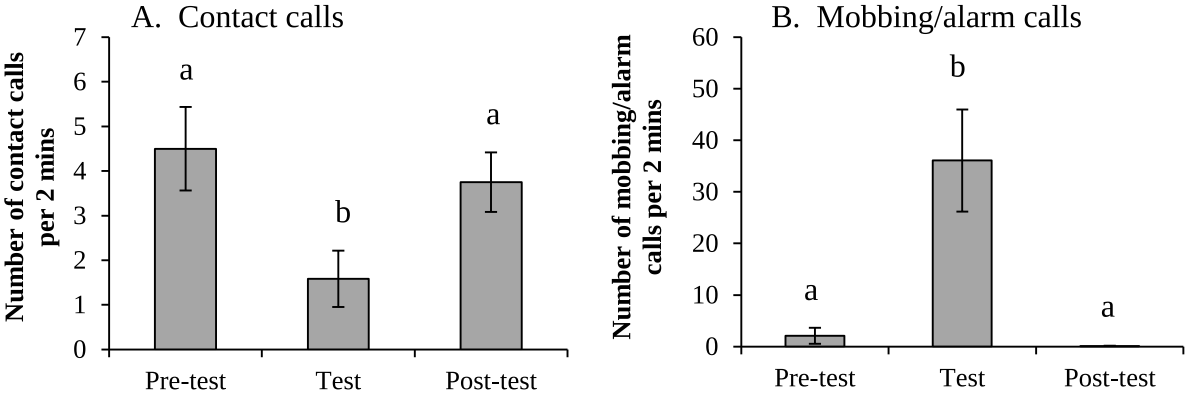


Figure 5.2. Comparison of responses in the pre-test, test and post-test periods: aversive visual/auditory (quoll/leopard growl) combination (2 mins). A – contact calls, B – mobbing/alarm calls (means ± sem). Bars marked 'a' are significantly different from those marked 'b'. The marmosets produced significantly fewer contact calls, but more mobbing/alarm calls, in the test period than in the pre- and post-test periods.

5.3.1.1.3 Aversive olfactory/auditory combination: As is evident in Table 5.1, no significant differences were found between the time periods for this combination. However, there was a weak trend for a greater mean distance (cm) from the position of the stimulus in the post-test than there was in the pre-test ($p = 0.07$).

5.3.1.1.4 Aversive visual/olfactory/auditory combination: The only significant difference found, between test periods for this trimodal combination was for the number of mobbing/alarm calls per two minutes: more in the test period than in the pre- ($p = 0.02$) or post-test ($p = 0.02$) period (Fig. 5.3).

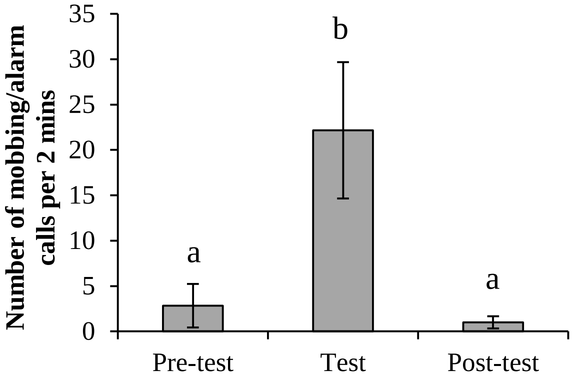


Figure 5.3. Comparison of responses in the pre-test, test and post-test periods: aversive trimodal (quoll/odour of cat faeces/leopard growl) combination (2 mins) - mobbing/alarm calls (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’.

5.3.1.2 Pleasant combinations

The behavioural responses to the pleasant combinations were first tested for significant differences across the pre-test, test and post-test periods. It is important to note that, except for one case (Section 5.3.1.2.1), the pre- and post-test periods of the pleasant combinations were not significantly different from each other.

Table 5.2. Statistical comparisons of the responses to the pleasant combinations between the pre-test, test and post-test periods.

	Main or major effect	Pre-test versus test	Test versus post-test	Post-test versus pre-test
Pleasant visual/olfactory combination				
Mean distance from stimulus (cm)	**$X^2 = 18.00$** **$p \leq 0.001$**	**$Z = -3.06$** **$p = 0.002$**	**$Z = -3.06$** **$p = 0.002$**	$Z = -0.47$ $p = 0.64$
Activity per 2 mins	$X^2 = 0.86$ $p = 0.65$	–	–	–
Number of contact calls per 2 mins	**$X^2 = 12.19$** **$p = 0.002$**	**$Z = -2.81$** **$p = 0.01$**	**$Z = -2.59$** **$p = 0.01$**	**$Z = -2.44$** **$p = 0.02$**
Number of mobbing/alarm calls per 2 mins	**$X^2 = 8.69$** **$p = 0.01$**	**$Z = -2.20$** **$p = 0.03$**	**$Z = -2.53$** **$p = 0.01$**	$Z = -1.38$ $p = 0.17$
Number of food-related calls per 2 mins	**$X^2 = 10.00$** **$p = 0.01$**	**$Z = -2.02$** **$p = 0.04$**	**$Z = -2.02$** **$p = 0.04$**	$Z = 0.00$ $p = 1.00$
Number of looks upward per 2 mins	$X^2 = 4.00$ $p = 0.14$	–	–	–
Number of looks downward per 2 mins	**$X^2 = 14.21$** **$p = 0.001$**	**$Z = -2.87$** **$p = 0.004$**	**$Z = -2.68$** **$p = 0.01$**	$Z = -0.36$ $p = 0.72$
Pleasant visual/auditory combination				
Mean distance from stimulus (cm)	**$X^2 = 18.67$** **$p \leq 0.001$**	**$Z = -3.06$** **$p = 0.002$**	**$Z = -3.06$** **$p = 0.002$**	$Z = -0.39$ $p = 0.70$
Activity per 2 mins	$X^2 = 3.00$ $p = 0.22$	–	–	–
Number of contact calls per 2 mins	**$X^2 = 12.70$** **$p = 0.002$**	**$Z = -2.82$** **$p = 0.01$**	**$Z = -2.67$** **$p = 0.01$**	$Z = -0.36$ $p = 0.72$
Number of mobbing/alarm calls per 2 mins	**$X^2 = 6.61$** **$p = 0.04$**	**$Z = -2.09$** **$p = 0.04$**	**$Z = -2.04$** **$p = 0.04$**	$Z = 0.00$ $p = 1.00$
Number of food-related calls per 2 mins	**$X^2 = 8.40$** **$p = 0.02$**	**$Z = -2.03$** **$p = 0.04$**	$Z = -1.84$ $p = 0.07$	$Z = -1.00$ $p = 0.32$
Number of looks upward per 2 mins	$X^2 = 1.85$ $p = 0.40$	–	–	–
Number of looks downward per 2 mins	$F_{(2,22)} = 0.62$ $p = 0.55$	–	–	–
Pleasant olfactory/auditory combination				
Mean distance from stimulus (cm)	–	–	–	$Z = -0.71$ $p = 0.48$
Activity per 2 mins	$X^2 = 5.77$ $p = 0.06$	–	–	–
Number of contact calls per 2 mins	**$F_{(2,22)} = 3.88$** **$p = 0.04$**	$p = 0.07$	$p = 0.15$	$p = 1.00$
Number of mobbing/alarm calls per 2 mins	$X^2 = 0.40$ $p = 0.82$	–	–	–
Number of food-related calls per 2 mins	$X^2 = 2.00$ $p = 0.37$	–	–	–
Number of looks upward per 2 mins	$X^2 = 4.10$ $p = 0.13$	–	–	–
Number of looks downward per 2 mins	$X^2 = 4.85$ $p = 0.09$	–	–	–
Pleasant visual/olfactory/auditory combination				
Mean distance from stimulus (cm)	**$F_{(2,22)} = 13.72$** **$p = 0.003$**	**$p = 0.002$**	**$p = 0.03$**	$p = 1.00$
Activity per 2 mins	$F_{(2,22)} = 1.66$ $p = 0.22$	–	–	–
Number of contact calls per 2 mins	**$F_{(2,22)} = 15.32$** **$\mathrm{p} \leq 0.001$**	**$p = 0.002$**	**$p = 0.003$**	$p = 0.48$

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	Main or major effect	Pre-test versus test	Test versus post-test	Post-test versus pre-test
Number of mobbing/alarm calls per 2 mins	$X^2 = 5.20$ $p = 0.07$	–	–	–
Number of food-related calls per 2 mins	$X^2 = 6.00$ $p = 0.05$	$Z = -1.60$ $p = 0.11$	$Z = -1.60$ $p = 0.11$	$Z = -0.00$ $p = 1.00$
Number of looks upward per 2 mins	$X^2 = 3.66$ $p = 0.16$	–	–	–
Number of looks downward per 2 mins	**$F_{(2,22)} = 7.31$** **$p = 0.01$**	**$p = 0.05$**	**$p = 0.002$**	$p = 1.00$

5.3.1.2.1 Pleasant visual/olfactory combination: As shown in Table 5.2, significant differences were found in all but two behavioural responses. The marmosets approached the combination to a closer mean distance in the test period than they did in the pre- ($p = 0.002$) and post-test ($p = 0.002$) periods (Fig. 5.4 A).

The number of contact calls was lower in the test period than in the pre- ($p = 0.01$) or post-test ($p = 0.01$) period (Fig. 5.4 B), but the number of mobbing/alarm calls and food-related calls was higher in the test period than in the pre- ($p = 0.03$ and p = 0.04, respectively) and post-test ($p = 0.01$ and $p = 0.04$, respectively) periods (Fig. 5.4 C and D, respectively). There was one significant difference found between pre- and post-test periods in the number of contact calls: the marmosets gave more of these calls in the pre- than in the post-test period ($p = 0.02$).

The marmosets also looked down significantly less often during the presentation of this combination than they did in the pre- ($p = 0.004$) or post-test ($p = 0.01$) period (Fig. 5.4 E).

All marmosets retrieved the marshmallow.

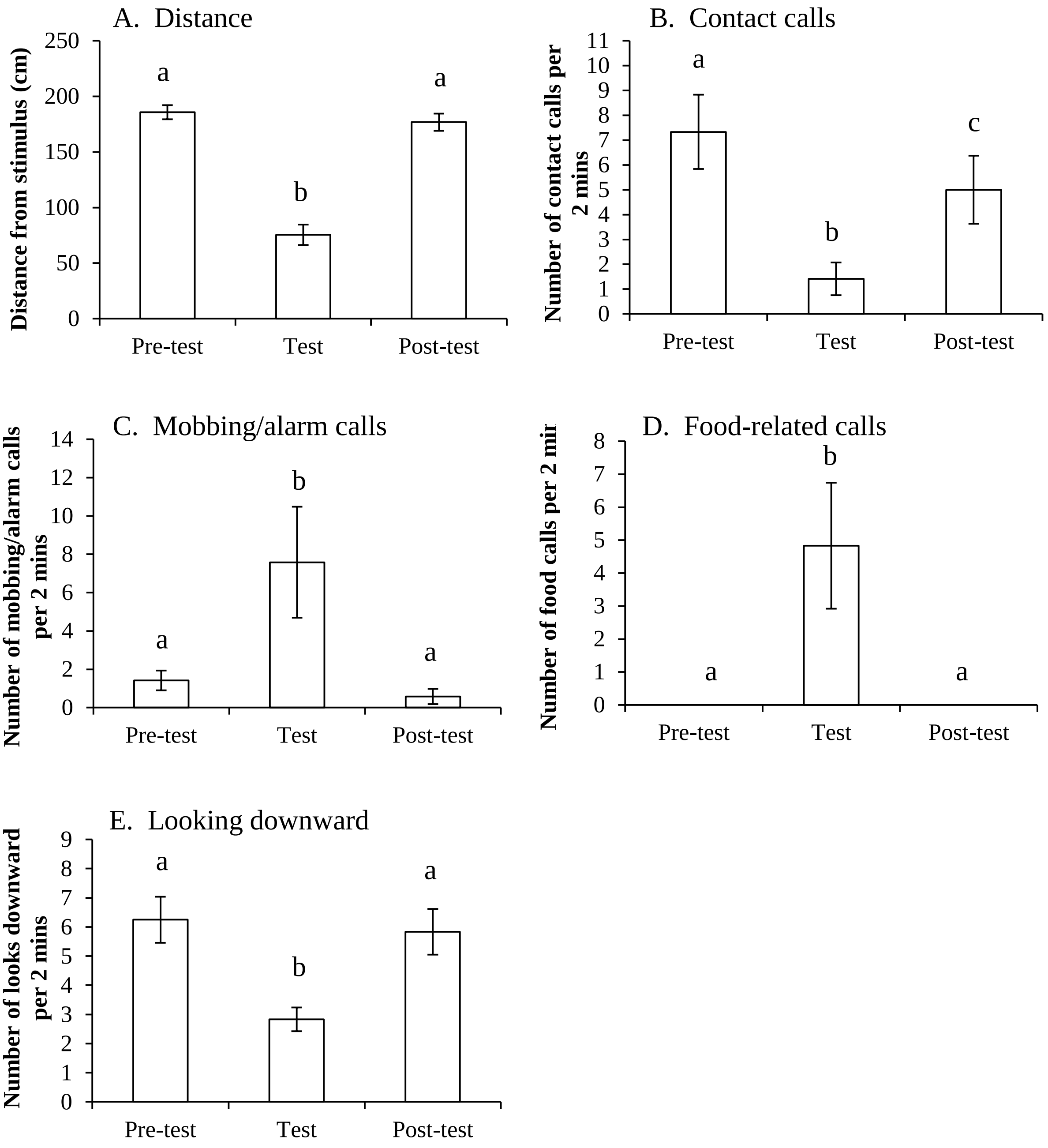


Figure 5.4. Comparison of responses in the pre-test, test and post-test periods: pleasant visual/olfactory (marshmallow/marshmallow odour) combination (2 mins). A – distance from stimulus (cm), B – contact calls, C – mobbing/alarm calls, D – food-related calls, E – looks downward (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’, and ‘c’ is significantly different from both ‘a’ and ‘b’. The marmosets had a closer mean distance, made fewer contact calls but more mobbing/alarm calls and food-related calls, and looked down less frequently in the test period than they did in the pre-test.

<u>5.3.1.2.2 Pleasant visual/auditory combination</u>: Table 5.2 shows that the presentation of this combination strongly affected the behaviour of the marmosets. The mean distance from the position of the stimulus was closer in the test period than it was in either the pre- (p = 0.002) or

post-test (*p* = 0.002) period (Fig. 5.5 A, below). Again the marmosets made fewer contact calls in the test period than in the pre- (*p* = 0.01) and post-test (*p* = 0.01) periods (Fig. 5.5 B), but more mobbing/alarm calls and food-related calls in the test period than in the pre-test (*p* = 0.04 and *p* = 0.04, respectively) (Fig. 5.5 C and D, respectively); only the number of mobbing/alarm calls was higher in the test period than in the post-test (*p* = 0.03). There was no significant difference in the number of food-related calls in the test period compared to the post-test (*p* = 0.07).

One marmoset did not retrieve the marshmallow.

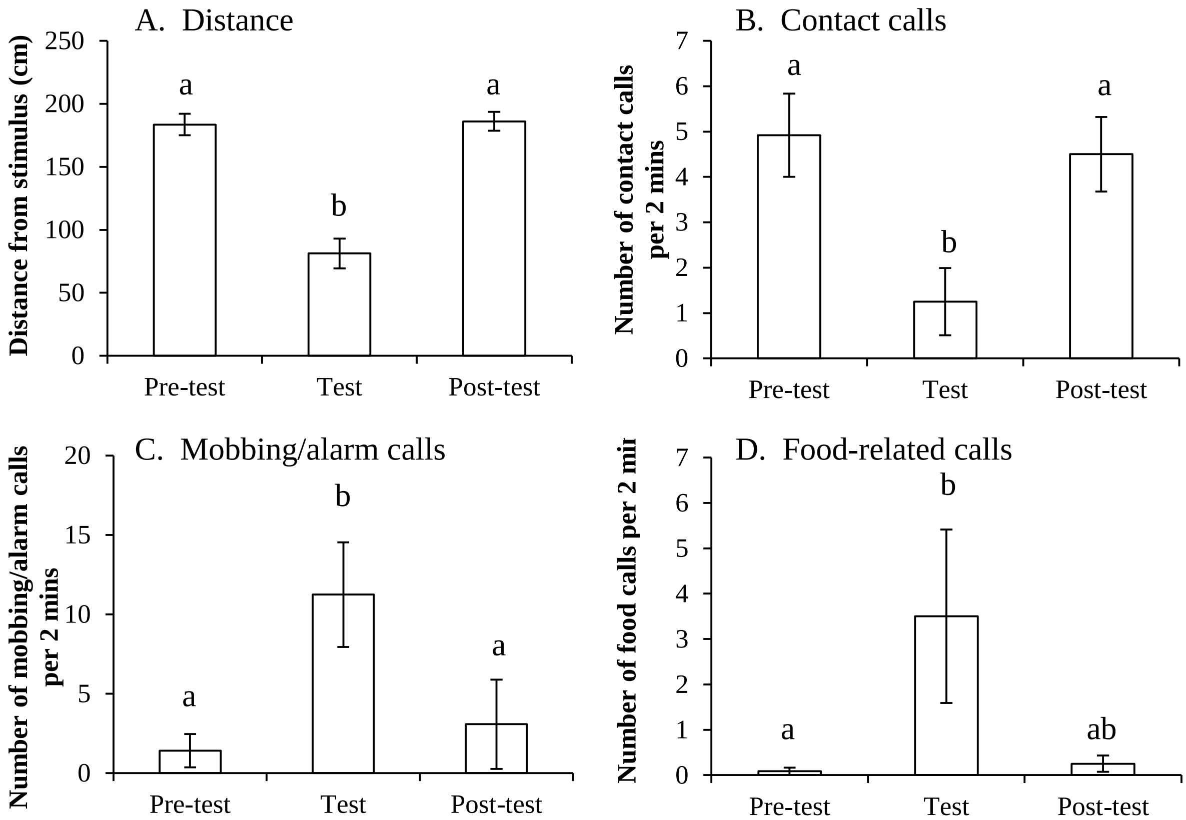


Figure 5.5. Comparison of responses in the pre-test, test and post-test periods: pleasant visual/auditory (marshmallow/marmoset food-related calls) combination (2 mins). A – distance from stimulus (cm), B – contact calls, C – mobbing/alarm calls, D – food-related calls (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’; ‘ab’ is not significantly different from either ‘a’ or ‘b’. In comparison to the pre-test h,et marmosets came closer and reduced their contact calling, but increased their mobbing/alarm calling and food-related calling, during the presentation of the combination.

5.3.1.2.3 Pleasant olfactory/auditory combination: As seen in Table 5.2, a significant difference was found only for heterogeneity in the number of contact calls per two minutes across the three time periods (*p* = 0.04). *Post hoc* tests revealed no significant differences (Table 5.2), but there was a weak trend for fewer calls in the test period than in the pre-test (*p* = 0.07).

5.3.1.2.4 Pleasant visual/olfactory/auditory combination: Three behavioural responses were affected by the presentation of the pleasant trimodal combination (Table 5.2). Mean distance was closer to the stimulus location in the test period than it was in the pre- (*p* = 0.002) or post-test (*p* = 0.03) period (Fig. 5.6 A).

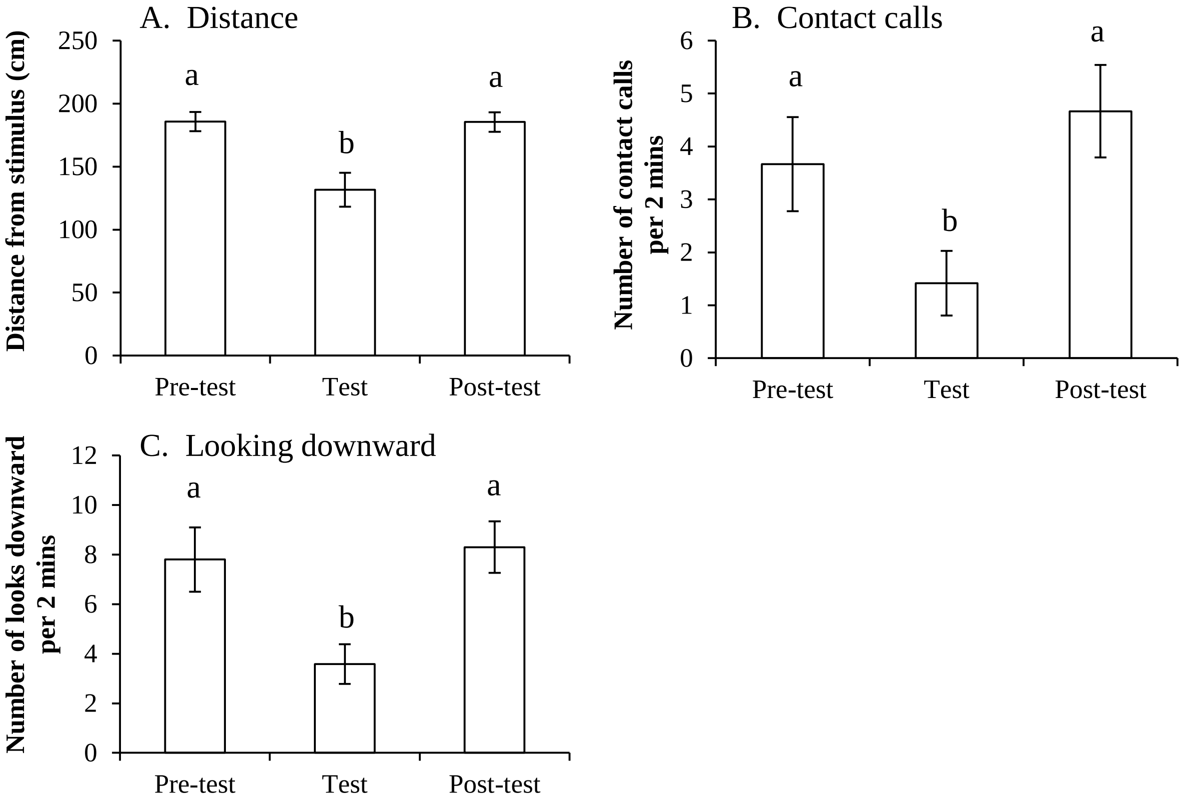


Figure 5.6. Comparison of responses in the pre-test, test and post-test periods: pleasant trimodal (marshmallow/marshmallow odour/marmoset food-related calls) combination (2 mins). A – distance from stimulus (cm), B – contact calls , C – looks downward (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’. The marmosets came closer and reduced their contact calling and looking downward during the presentation of the combination.

The marmosets reduced the number of contact calls made during the trimodal stimulus presentation in comparison to the pre- ($p = 0.002$) and post-test ($p = 0.003$) periods (Fig. 5.6 B). Significant heterogeneity was found for the number of food-related calls made across the three time periods ($p = 0.05$), but *post hoc* tests found no significant differences between the time periods.

The marmosets looked down significantly less often during the presentation of the trimodal stimulus than they did before ($p = 0.05$) or after ($p = 0.002$) presentation (Fig. 5.6 C, above).

5.3.2 Comparison of the responses to the combinations and the individually presented stimuli

The first and second minutes of the test period of the combinations were compared to determine whether the behaviour scored remained consistent over the test period. These results are shown in Appendix VI. Of the 64 comparisons made between minutes 1 and 2, eight showed significant differences. The first-minute results of the combination trials were then compared to the results of their respective individual stimuli (as presented in Ch. 4). The results of the comparisons of the test periods are shown below (Sections 5.3.2.1 to 5.3.2.8).

Comparisons were made between responses to the combinations and to the stimuli presented alone. Appendix VII presents the statistical results of the pre- and post-test comparisons, conducted to ensure that pre-test behaviour was comparable between tests and to determine whether there was a difference in post-test responses between singular and multiple stimuli presentations; test-period comparisons are presented in Sections 5.3.2.1 to 5.3.2.8. Three significant differences were found in the pre-test comparisons and four in the post-test comparisons. In the pre-test comparisons, mean distance was significantly greater in the pre-test of the quoll/leopard grow combination (184.48 ± 6.07 cm) than the quoll alone (174.92 ± 5.42

cm) (two-tailed t-test, $t = 2.37$, $p = 0.04$). The number of looks downward per two minutes was significantly smaller in the pre-test of the leopard growl (4.88 ± 0.75) than it was in that of either the quoll/leopard growl combination (8.08 ± 1.10) (repeated measures ANOVA, $F_{(2,22)} = 9.65$, $p = 0.001$; Bonferroni pairwise comparison, $p = 0.004$) or the odour of cat faeces/leopard growl combination (7.75 ± 0.74) (repeated measures ANOVA, $F_{(2,22)} = 16.88$, $p \leq 0.001$; Bonferroni pairwise comparison, $p = 0.03$). There was also significantly fewer looks downward in the pre-test of the faecal odour (3.44 ± 0.40) than there was for the odour of cat faeces/leopard growl combination (Bonferroni pairwise comparison, $p \leq 0.001$).

In the comparisons of behaviour in the post-test periods, mean distance was significantly greater after the presentation of the quoll/leopard growl (196.99 ± 5.48 cm) (two-tailed t-test, $t = 3.67$, $p = 0.004$) and quoll/odour of cat faeces/leopard growl (193.90 ± 4.07 cm) (two-tailed t-test, $t = 4.06$, $p = 0.002$) combinations than after the presentation of the quoll (170.33 ± 5.13 cm). Mean distance was also significantly greater after the presentation of the odour of cat faeces/leopard growl (203.78 ± 11.84 cm) (Wilcoxon signed-rank test, $Z = -2.28$, $p = 0.02$) than the odour alone (169.59 ± 5.00 cm). Finally, the marmosets looked up more often per two minutes after the presentation of the marshmallow/marshmallow odour/marmoset food-related calls combination (2.17 ± 0.52) than they did after the presentation of the marmoset food-related calls alone (1.42 ± 0.37) (repeated measures ANOVA, $F_{(3,33)} = 3.11$, $p = 0.04$; Bonferroni pairwise comparison, $p = 0.01$).

The comparisons of the responses to the individually presented stimuli relevant to each combination are also shown in the tables in this section to provide a reference point of differences in responses to the stimuli.

5.3.2.1 Comparison of responses to the aversive visual/olfactory combination and the stimuli presented alone

Table 5.3 shows the statistical results of the test-period comparisons between the aversive visual/olfactory combination and the aversive visual (quoll) and aversive olfactory (odour of cat faeces) stimuli on their own.

Table 5.3. Responses to the aversive visual/olfactory (quoll/odour of cat faeces) combination versus the individually presented stimuli. Statistical comparisons of the first minute responses (test periods).

	Main or major effect	Combination versus aversive visual	Combination versus aversive olfactory	Aversive visual versus aversive olfactory
Mean distance from stimulus (cm)	–	$t = -0.19$ $p = 0.85$	–	–
Closest distance to stimulus (cm)	–	$t = -0.99$ $p = 0.35$	–	–
Latency to approach (seconds)	–	$Z = -1.78$ $p = 0.07$	–	–
Activity per min	$F_{(2,22)} = 0.25$ $p = 0.69$	–	–	–
Number of contact calls per min	**$X^2 = 6.53$** **$p = 0.04$**	$Z = -1.22$ $p = 0.22$	$Z = -1.07$ $p = 0.28$	**$Z = -2.32$** **$p = 0.02$**
Number of mobbing/alarm calls per min	**$X^2 = 16.48$** **$p \leq 0.001$**	$Z = -1.81$ $p = 0.07$	**$Z = -2.93$** **$p = 0.003$**	**$Z = -2.93$** **$p = 0.003$**
Latency to vocalise (secs)	**$X^2 = 11.90$** **$p = 0.003$**	$Z = -0.17$ $p = 0.87$	**$Z = -2.31$** **$p = 0.02$**	**$Z = 2.93$** **$p = 0.003$**
Number of looks upward per min	$X^2 = 2.39$ $p = 0.30$	–	–	–
Number of looks downward per min	**$X^2 = 12.18$** **$p = 0.002$**	**$Z = -2.44$** **$p = 0.02$**	$Z = -1.26$ $p = 0.21$	**$Z = -2.96$** **$p = 0.003$**
Number of looks at the stimulus per min	–	$t = -1.83$ $p = 0.10$	–	–

As shown in Table 5.3, the marmosets gave significantly more mobbing/alarm calls per minute towards the quoll/odour of cat faeces combination than they did to the faecal odour stimulus presented on its own ($p = 0.003$) (Fig. 5.7 A). There was a significantly shorter latency to vocalise (seconds) on presentation of the aversive combination than the individually presented cat faeces odour ($p = 0.02$), but not the individually presented quoll ($p = 0.87$) (Fig. 5.7 B).

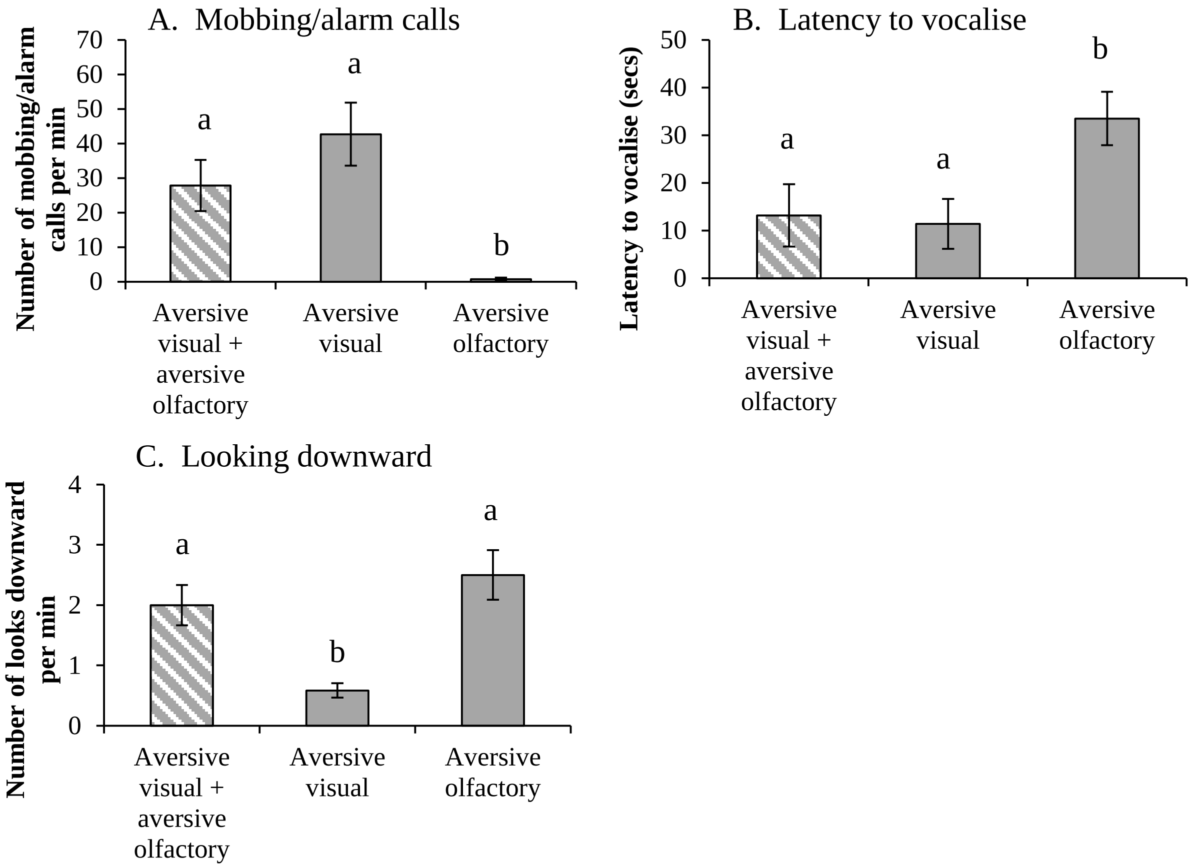


Figure 5.7. Comparison of responses during the test period: aversive visual/olfactory (quoll/odour of cat faeces) combination and individually presented stimuli (1 min). A – mobbing/alarm calls, B – latency to vocalise (secs), C – looks downward (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’.

The marmosets looked down more often during the presentation of the combination than during the presentation of the quoll alone ($p = 0.02$) (Fig. 5.7 C).

5.3.2.2 Comparison of responses to the aversive visual/auditory combination and the stimuli presented alone

The results of the test-period comparisons between the combination and the quoll and leopard growl on their own stimuli are shown in Table 5.4.

Table 5.4. Responses to the aversive visual/auditory (quoll/leopard growl) combination versus the individually presented stimuli. Statistical comparisons of the first minute responses (test periods).

	Main or major effect	Combination versus aversive visual	Combination versus aversive auditory	Aversive visual versus aversive auditory
Mean distance from stimulus (cm)	–	**t = -2.16** **p = 0.05**	–	–
Closest distance to stimulus (cm)	–	t = 0.55 p = 0.59	–	–
Latency to approach (secs)	–	Z **= -1.96** **p = 0.05**	–	–
Activity per min	$F_{(2,22)}$ = 3.03 p = 0.07	–	–	–
Number of contact calls per min	**X^2 = 7.66** **p = 0.02**	Z = -1.79 p = 0.07	Z = -1.27 p = 0.21	Z **= -2.17** **p = 0.03**
Number of mobbing/alarm calls per min	**X^2 = 10.00** **p = 0.01**	**Z = -2.59** **p = 0.01**	**Z = -2.19** **p = 0.03**	**Z = -2.49** **p = 0.01**
Latency to vocalise (secs)	**X^2 = 12.84** **p = 0.002**	Z = -1.78 p = 0.07	Z **= -1.96** **p = 0.05**	Z **= -2.93** **p = 0.003**
Number of looks upward per min	X^2 = 0.18 p = 0.92	–	–	–
Number of looks downward per min	**X^2 = 8.83** **p = 0.01**	**Z = -2.10** **p = 0.04**	Z = -1.03 p = 0.31	Z **= -2.81** **p = 0.01**
Number of looks at the stimulus per min	–	Z = -1.85 p = 0.07	–	–

Several significant differences were found between responses to the quoll/leopard growl combination and the individually presented stimuli, as seen in Table 5.4. The marmosets moved significantly further away from the quoll when it was presented together with the leopard growl than when presented alone (p = 0.05) (Fig. 5.8 A). The marmosets also took significantly longer to approach the quoll/leopard growl combination than the quoll alone (p = 0.05) (Fig. 5.8 B).

There were no significant differences, despite the significant major effect, in the number of contact calls per minute in response to the aversive visual/aversive auditory combination and to the two individual stimuli, even though the marmosets gave significantly fewer contact calls during the presentation of the quoll than the leopard growl (p = 0.03). The number of mobbing/alarm calls per minute, however, was significantly different in all comparisons: the marmosets gave fewer mobbing/alarm calls per minute to the aversive combination than they did

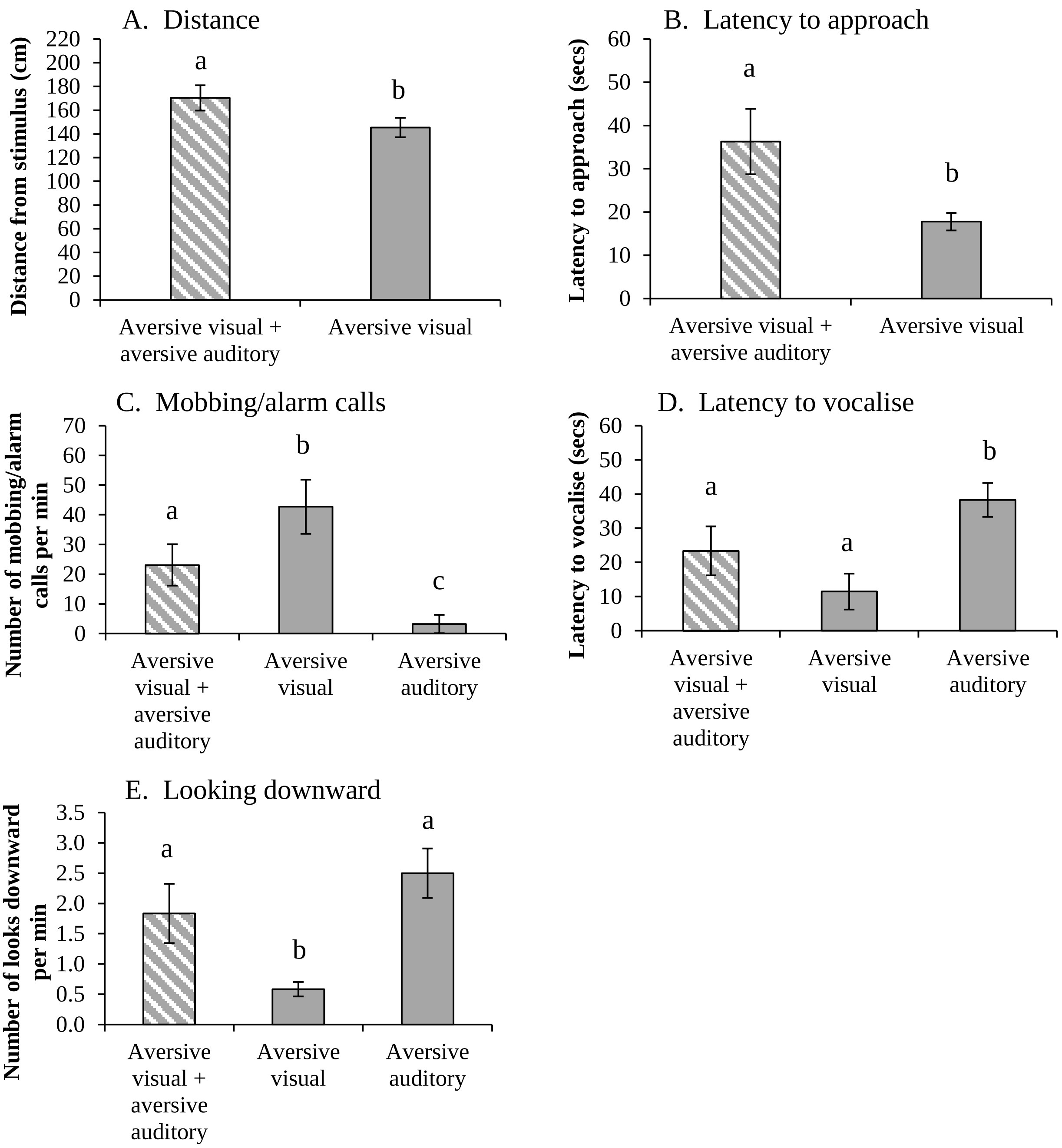


Figure 5.8. Comparison of responses during the test period: aversive visual/auditory (quoll/leopard growl) combination and individually presented stimuli (1 min). A – latency to approach (secs), B – mobbing/alarm calls, C – latency to vocalise (secs), D – looks downward (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’, and ‘c’ is significantly different from both ‘a’ and ‘b’.

to the quoll alone (*p* = 0.01), but more than they did to the auditory stimulus alone (*p* = 0.03) (Fig. 5.8 C).

Distance over time (5-second intervals) is also shown in Figure 5.9.

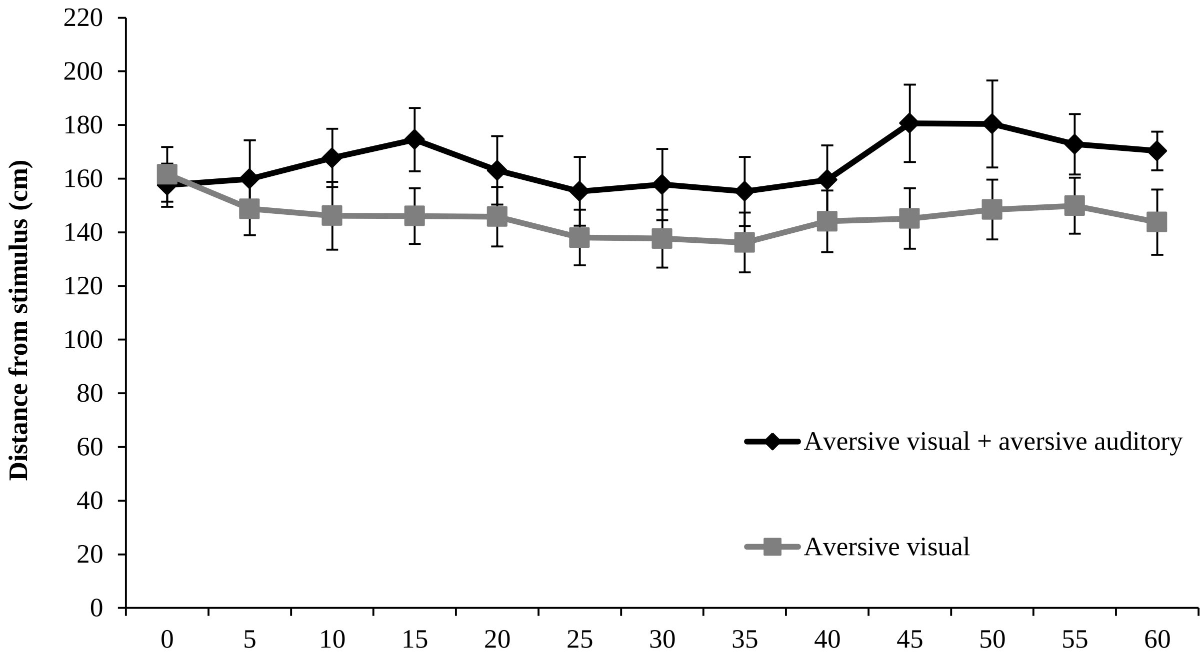


Figure 5.9. Distance (cm) over time (5-second intervals; test period) from the aversive visual/auditory (quoll/leopard growl) combination and the individually presented visual stimulus (means ± sem). Black line (♦ symbols) shows the response to the aversive visual/auditory combination. Dark-grey line (□ symbols) shows the response to the aversive visual stimulus alone. The marmosets were consistently further away during the presentation of the combination than when only the visual stimulus is presented.

Latency to vocalise (seconds) was significantly different only between the combination and the leopard growl ($p = 0.05$), and the two individual stimuli ($p = 0.003$) (Fig. 5.8 D). Also, the marmosets looked down significantly more often during the presentation of the combination than during the presentation of the quoll alone ($p = 0.04$), although the two individual stimuli were significantly different from each other (Fig. 5.8 E).

5.3.2.3 Comparison of responses to the aversive olfactory/auditory combination and the stimuli presented alone

The results of the test-period comparisons between the combination and the faecal odour and leopard growl are shown in Table 5.5.

Table 5.5. Responses to the aversive olfactory/auditory (odour of cat faeces/leopard growl) combination versus the individually presented stimuli. Statistical comparisons of the first minute responses (test periods).

	Main or major effect	Combination versus aversive olfactory	Combination versus aversive auditory	Aversive olfactory versus aversive auditory
Mean distance from stimulus (cm)	–	**$t = 2.62$ $p = 0.02$**	–	–
Activity per min	$X^2 = 3.49$ $p = 0.18$	–	–	–
Number of contact calls per min	$X^2 = 1.90$ $p = 0.39$	–	–	–
Number of mobbing/alarm calls per min	$X^2 = 5.43$ $p = 0.07$	–	–	–
Latency to vocalise (secs)	$F_{(2,22)} = 0.49$ $p = 0.62$	–	–	–
Number of looks upward per min	$X^2 = 0.44$ $p = 0.80$	–	–	–
Number of looks downward per min	**$F_{(2,22)} = 8.00$ $p = 0.002$**	**$p = 0.03$**	**$p = 0.02$**	$p = 1.00$

The marmosets' mean distance from the stimulus (cm) was significantly greater when the aversive olfactory/auditory combination was presented than when the olfactory stimulus was presented individually ($p = 0.02$) (Fig. 5.10 A; Table 5.5). Mean distance (cm) is also presented over time (5-second intervals), as shown in Figure 5.11, tracking the marmosets' movements over the entire test period.

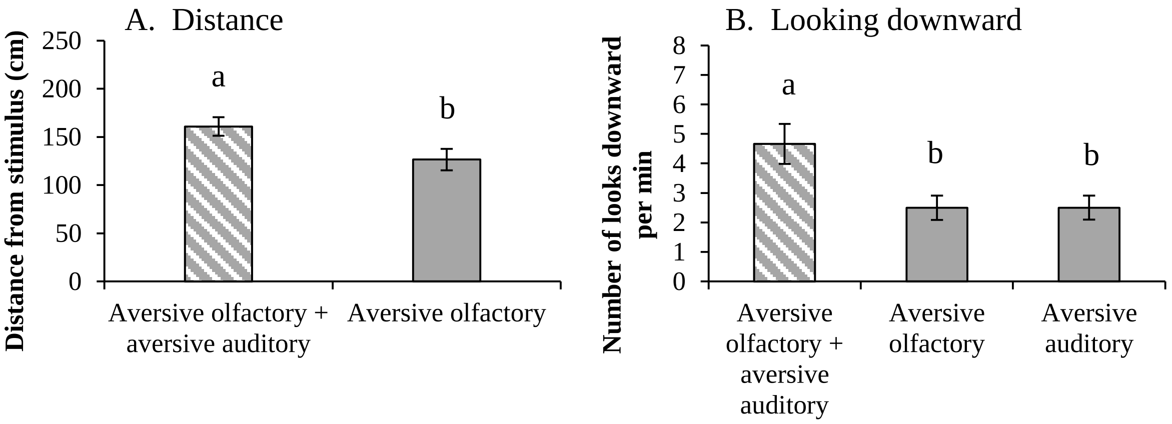


Figure 5.10. Comparison of responses during the test period: aversive olfactory/auditory (odour of cat faeces/leopard growl) combination and individually presented stimuli (1 min). A – distance from stimulus (cm), B – looks downward (means ± sem). Bars marked 'a' are significantly different from those marked 'b'.

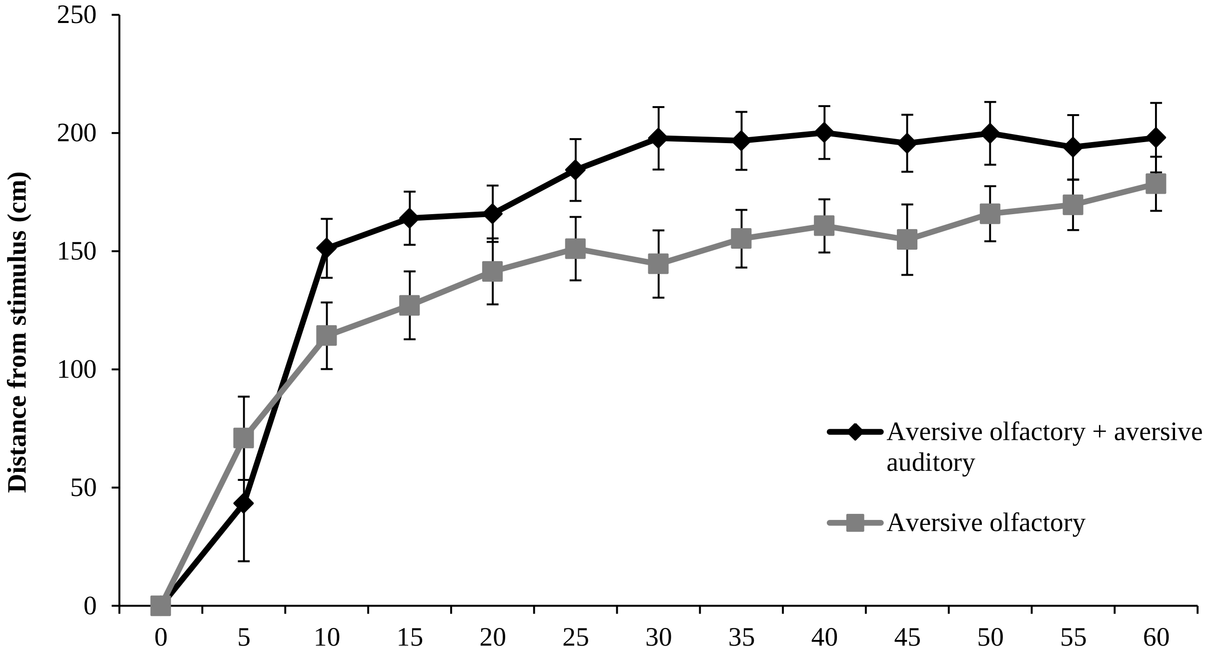


Figure 5.11. Distance (cm) over time (5-second intervals; test period) from the aversive olfactory/auditory (odour of cat faeces/leopard growl) combination and the odour of cat faeces alone (means ± sem). Black line (♦ symbols) shows the response to the combination. Dark-grey line (□ symbols) shows the response to the faecal odour alone. There was a significant difference between the mean of these two data sets.

The marmosets looked down significantly more often during the presentation of the aversive olfactory/aversive auditory combination than when the faecal odour or leopard growl was presented individually ($p = 0.01$ and $p = 0.01$, respectively) (Fig. 5.10 B).

5.3.2.4 Comparison of responses to the aversive visual/olfactory/auditory combination and the stimuli presented alone

The results of the test-period comparisons between the aversive visual/olfactory/auditory combination and the aversive visual (quoll), aversive olfactory (odour of cat faeces) and aversive auditory (leopard growl) stimuli are shown in Table 5.6.

Table 5.6. Responses to the aversive trimodal (quoll/odour of cat faeces/leopard growl) combination versus the individually presented stimuli. Statistical comparisons of the first minute responses (test periods).

	Main or major effect	Combination versus aversive visual	Combination versus aversive olfactory	Combination versus aversive auditory
Mean distance from stimulus (cm)	–	**$t = 2.95$ $p = 0.01$**	–	–
Closest distance to stimulus (cm)	–	t = 1.05 $p = 0.32$	–	–
Latency to approach (secs)	–	**$Z = -2.98$ $p = 0.003$**	–	–
Activity per min	$F_{(3,33)} = 2.21$ $p = 0.11$	–	–	–
Number of contact calls per min	**$X^2 = 9.16$ $p = 0.03$**	**$Z = -2.32$ $p = 0.02$**	$Z = -1.13$ $p = 0.26$	$Z = -1.12$ $p = 0.26$
Number of mobbing/alarm calls per min	**$X^2 = 20.33$ $p \leq 0.001$**	**$Z = -2.93$ $p = 0.003$**	**$Z = -2.10$ $p = 0.04$**	$Z = -1.36$ $p = 0.17$
Latency to vocalise (secs)	**$X^2 = 15.92$ $p = 0.001$**	**$Z = -2.30$ $p = 0.02$**	$Z = -0.05$ $p = 0.96$	$Z = -0.45$ $p = 0.66$
Number of looks upward per min	$X^2 = 1.37$ p = 0.71	–	–	–
Number of looks downward per min	**$X^2 = 20.33$ $p \leq 0.001$**	**$Z = -2.75$ $p = 0.01$**	$Z = -0.17$ $p = 0.87$	$Z = -0.22$ $p = 0.82$
Number of looks at the stimulus per min	–	**$Z = -3.07$ $p = 0.002$**	–	–

The aversive trimodal presentation produced highly significant results when compared with the responses to the individually presented stimuli: only three behavioural responses were not significantly different (Table 5.6). The marmosets' mean distance was significantly greater during the trimodal presentation than it was when only the quoll was presented ($p = 0.01$) (Fig. 5.12 A); however, the closest approach was not significantly different.

Mean distance over time (5-second intervals) has also been plotted to show the marmosets' movements during the test period (Fig. 5.13). Latency to approach (secs) was significantly longer for the trimodal combination than it was for the quoll on its own ($p = 0.003$) (Fig. 5.12 B).

Significantly more contact calls were produced per minute in the test period of the trimodal combination than for the quoll on its own ($p = 0.02$) (Fig. 5.12 C); the opposite was found for mobbing/alarm calls ($p = 0.003$) (Fig. 5.12 D).

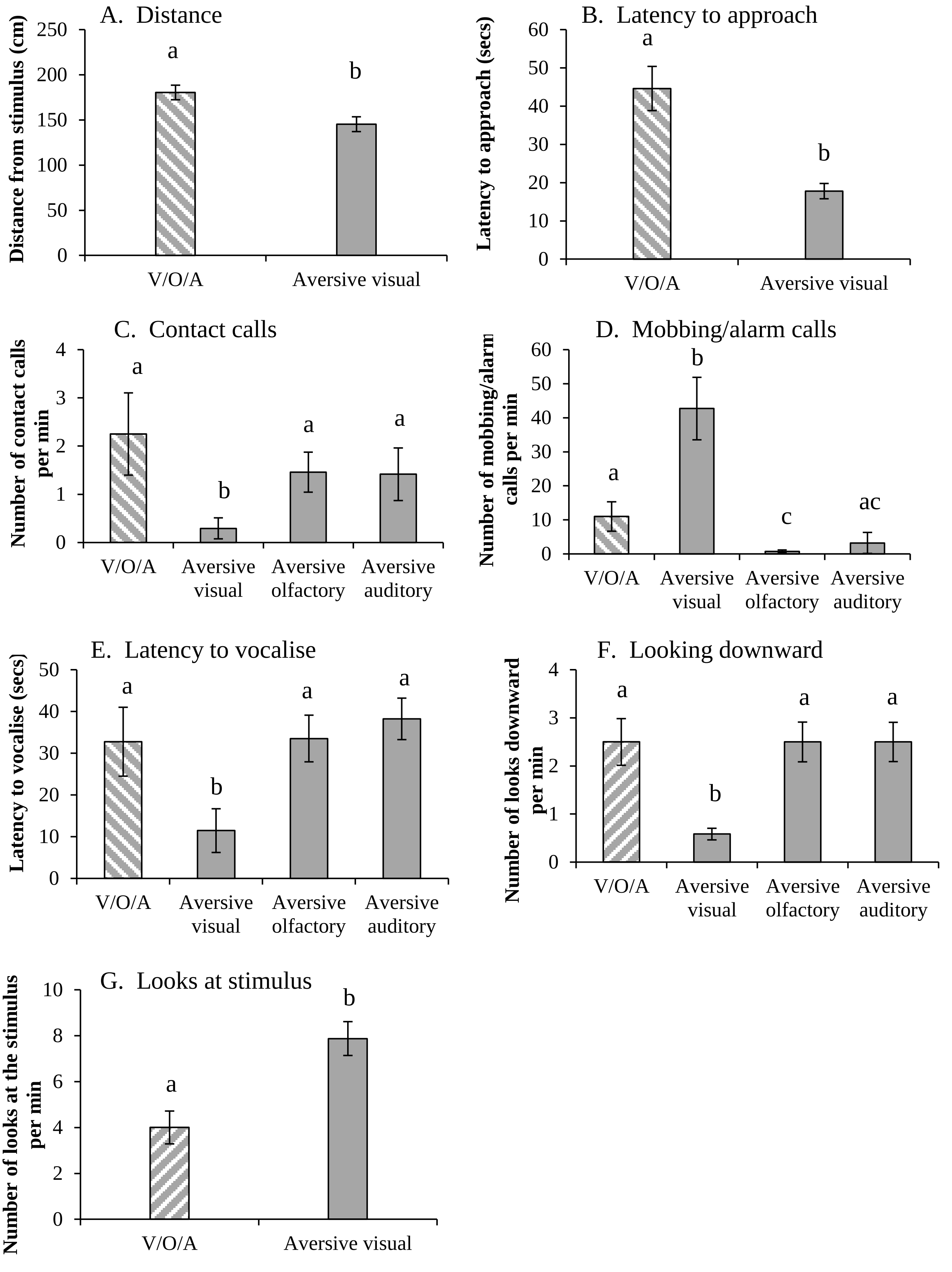


Figure 5.12. Comparison of responses during the test period: aversive trimodal (quoll/odour of cat faeces/leopard growl) combination (V/O/A) and individually presented stimuli (1 min). A – distance from stimulus (cm), B – latency to approach (secs), C – contact calls, D – mobbing/alarm calls, E – latency to vocalise (secs), F – looks downward, G – looks at the stimulus (means ± sem). Bars marked 'a' are significantly different from those marked 'b', and 'c' is significantly different from both 'a' and 'b'; 'ac' is not significantly different from either 'a' or 'c'. Note that most differences were between the trimodal combination and the quoll on its own.

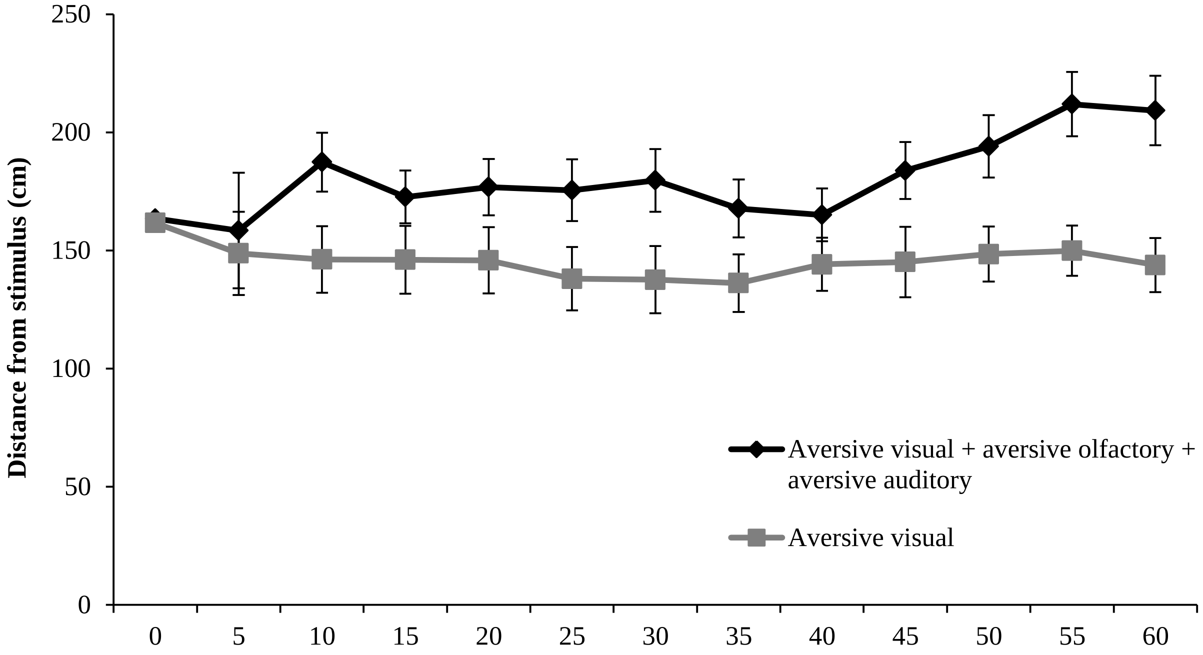


Figure 5.13. Distance (cm) over time (5-second intervals; test period) from the trimodal (quoll/odour of cat faeces/leopard growl) combination and the quoll alone over time (means ± sem). Black line (♦ symbols) shows the response to the trimodal combination. Dark-grey line (□ symbols) shows the response to quoll alone. There was a significant difference between the means of these two data sets.

Further, there were significantly more mobbing/alarm calls per minute in response to the trimodal combination than to the faecal odour alone (p = 0.04). Latency to vocalise (secs) was significantly shorter when only the quoll was presented (p = 0.02) (Fig. 5.12 E).

The marmosets looked downward more often per minute in response to the trimodal combination than to the quoll alone (p = 0.01) (Fig. 5.12 F). There were fewer recorded looks at the visual component of the trimodal combination per minute than to the quoll when presented on its own (p = 0.002) (Fig. 5.12 G).

5.3.2.5 Comparison of responses to the pleasant visual/olfactory combination and the stimuli presented alone

The results of the comparisons of the test-periods between the combination and its individual stimuli are shown in Table 5.7.

Table 5.7. Responses to the pleasant visual/olfactory (marshmallow/marshmallow odour) combination versus the individually presented stimuli. Statistical comparisons of the first minute responses (test periods).

	Main or major effect	Combination versus pleasant visual	Combination versus pleasant olfactory	Pleasant visual versus pleasant olfactory
Mean distance from stimulus (cm)	–	$t = -1.72$ $p = 0.11$	–	–
Closest distance to stimulus (cm)	–	$Z = -1.83$ $p = 0.07$	–	–
Latency to approach (secs)	–	$\boldsymbol{Z = -2.40}$ $\boldsymbol{p = 0.02}$	–	–
Activity per min	$F_{(2,22)} = 2.64$ $p = 0.09$	–	–	–
Number of contact calls per min	$X^2 = 1.09$ $p = 0.58$	–	–	–
Number of mobbing/alarm calls per min	$\boldsymbol{X^2 = 12.76}$ $\boldsymbol{p = 0.002}$	$\boldsymbol{Z = -2.76}$ $\boldsymbol{p = 0.01}$	$Z = -1.42$ $p = 0.16$	$\boldsymbol{Z = -2.13}$ $\boldsymbol{p = 0.03}$
Number of food-related calls per min	$X^2 = 4.29$ $p = 0.12$	–	–	–
Latency to vocalise (secs)	$X^2 = 0.00$ $p = 1.00$	–	–	–
Number of looks upward per min	$X^2 = 0.29$ $p = 0.87$	–	–	–
Number of looks downward per min	$F_{(2,22)} = 0.56$ $p = 0.58$	–	–	–
Number of looks at the stimulus per min	–	$t = -0.69$ $p = 0.51$	–	–

Table 5.7 shows that the response to the combination was significantly different from the response to the individually presented marshmallow for latency to approach and the number of mobbing/alarm calls. The marmosets had a significantly shorter latency to approach (secs) the marshmallow when it was paired with its odour than they did when it was presented alone ($p = 0.02$) (Fig. 5.14 A).

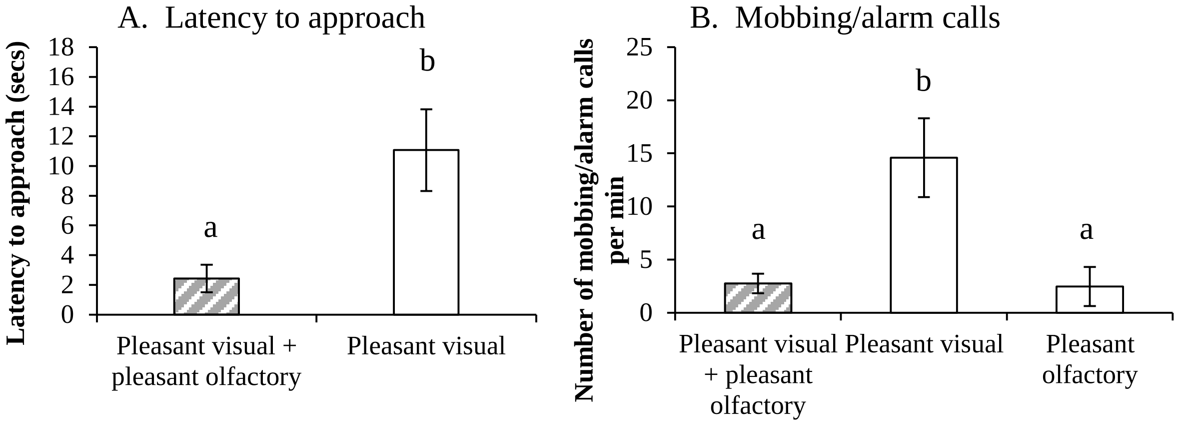


Figure 5.14. Comparison of responses during the test period: pleasant visual/olfactory (marshmallow/marshmallow odour) combination and individually presented stimuli (1 min). A – latency to approach (secs), B – mobbing/alarm calls (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’.

They also produced significantly fewer mobbing/alarm calls per minute towards the combination than they did to the marshmallow alone, but statistically the same number as they did towards the marshmallow odour alone (*p* = 0.01) (Fig. 5.14 B).

5.3.2.6 Comparison of responses to the pleasant visual/auditory combination and the stimuli presented alone

The results are shown in Table 5.8.

Significant differences were found only for the number of mobbing/alarm calls per minute and the number of food-related calls per minute. The marmosets gave fewer mobbing/alarm calls to the combination than they did to the marshmallow on its own (*p* = 0.02), but more than to the pleasant auditory stimulus presented individually (*p* = 0.01) (Fig. 5.15 A).

They also gave more food-related calls per minute during the presentation of both the combination and the marshmallow alone than they did to the pleasant auditory stimulus alone (*p* = 0.03 and *p* = 0.01, respectively) (Fig. 5.15 B).

Table 5.8. Responses to the pleasant visual/auditory (marshmallow/marmoset food-related calls) combination versus the individually presented stimuli. Statistical comparisons of the first minute responses (test periods).

	Main or major effect	Combination versus pleasant visual	Combination versus pleasant auditory	Pleasant visual versus pleasant auditory
Mean distance from stimulus (cm)	–	$t = -1.45$ $p = 0.17$	–	–
Closest distance to stimulus (cm)	–	$Z = -1.83$ $p = 0.07$	–	–
Latency to approach (secs)	–	$Z = -0.71$ $p = 0.48$	–	–
Activity per min	$F_{(2,22)} = 0.81$ $p = 0.46$	–	–	–
Number of contact calls per min	$X^2 = 3.15$ $p = 0.21$	–	–	–
Number of mobbing/alarm calls per min	**$X^2 = 17.32$ $p \leq 0.001$**	**$Z = -2.28$ $p = 0.02$**	**$Z = -2.67$ $p = 0.01$**	**$Z = -2.93$ $p = 0.003$**
Number of food-related calls per min	**$X^2 = 11.37$ $p = 0.003$**	$Z = -1.89$ $p = 0.06$	**$Z = -2.21$ $p = 0.03$**	**$Z = -2.67$ $p = 0.01$**
Latency to vocalise (secs)	$F_{(2,22)} = 2.78$ $p = 0.08$	–	–	–
Number of looks upward per min	$X^2 = 0.55$ $p = 0.76$	–	–	–
Number of looks downward per min	$X^2 = 5.44$ $p = 0.07$	–	–	–
Number of looks at the stimulus per min	–	$t = -1.34$ $p = 0.21$	–	–

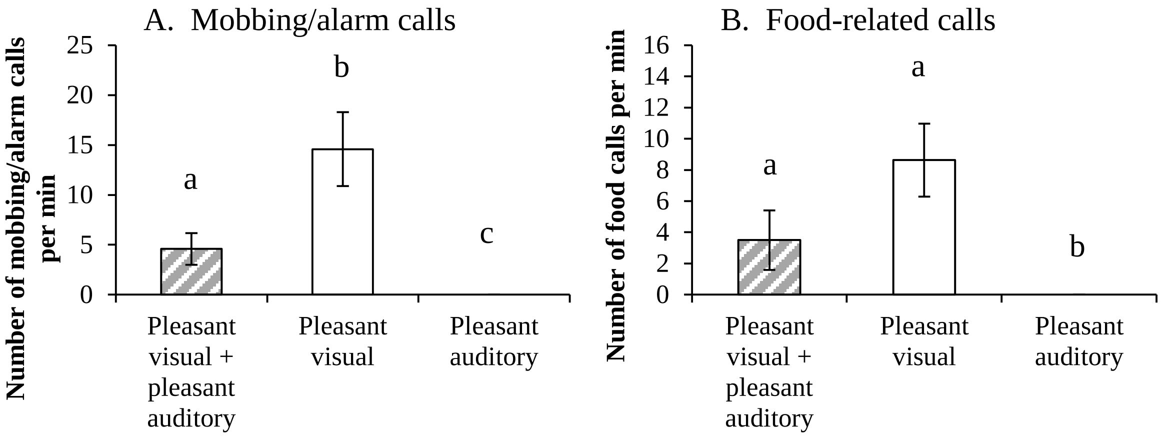


Figure 5.15. Comparison of responses during the test period: pleasant visual/auditory (marshmallow/marmoset food-related calls) combination and individually presented stimuli (1 min). A – mobbing/alarm calls, B – food-related calls (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’, and ‘c’ is significantly different from both ‘a’ and ‘b’.

5.3.2.7 Comparison of responses to the pleasant olfactory/auditory combination and the stimuli presented alone

Table 5.9 presents the results of the test-period comparisons.

Table 5.9. Responses to the pleasant olfactory/auditory (marshmallow odour/marmoset food-related calls) combination versus the individually presented stimuli. Statistical comparisons of the first minute responses (test periods).

	Main or major effect	Combination versus pleasant olfactory	Combination versus pleasant auditory	Pleasant olfactory versus pleasant auditory
Mean distance from stimulus (cm)	–	**$t = 4.95$ $p \leq 0.001$**	–	–
Activity per min	**$F_{(2,22)} = 3.39$ $p = 0.05$**	$p = 0.82$	$p = 0.54$	$p = 0.08$
Number of contact calls per min	$X^2 = 0.51$ $p = 0.77$	–	–	–
Number of mobbing/alarm calls per min	**$X^2 = 10.18$ $p = 0.01$**	**$Z = -2.76$ $p = 0.01$**	$Z = -1.42$ $p = 0.16$	**$Z = -2.13$ $p = 0.03$**
Number of food-related calls per min	**$X^2 = 12.76$ $p = 0.002$**	**$Z = -1.98$ $p = 0.05$**	$Z = -1.00$ $p = 0.32$	**$Z = -2.41$ $p = 0.02$**
Latency to vocalise (secs)	**$F_{(2,22)} = 5.14$ $p = 0.02$**	**$p = 0.05$**	$p = 1.00$	**$p = 0.05$**
Number of looks upward per min	$X^2 = 2.65$ $p = 0.27$	–	–	–
Number of looks downward per min	**$X^2 = 6.93$ $p = 0.03$**	**$Z = -2.14$ $p = 0.03$**	$Z = -0.89$ $p = 0.37$	**$Z = -2.24$ $p = 0.03$**

The marmosets' mean distance from the olfactory stimulus position was greater when coupled with the marmoset food-related calls than when presented individually ($p \leq 0.001$) (Fig. 5.16 A). Mean distance (cm) over time (5-second intervals) is also shown in Figure 5.17. Although there was a significant heterogeneity found for activity per minute ($p = 0.05$), *post hoc* tests found no significant differences between the paired comparisons.

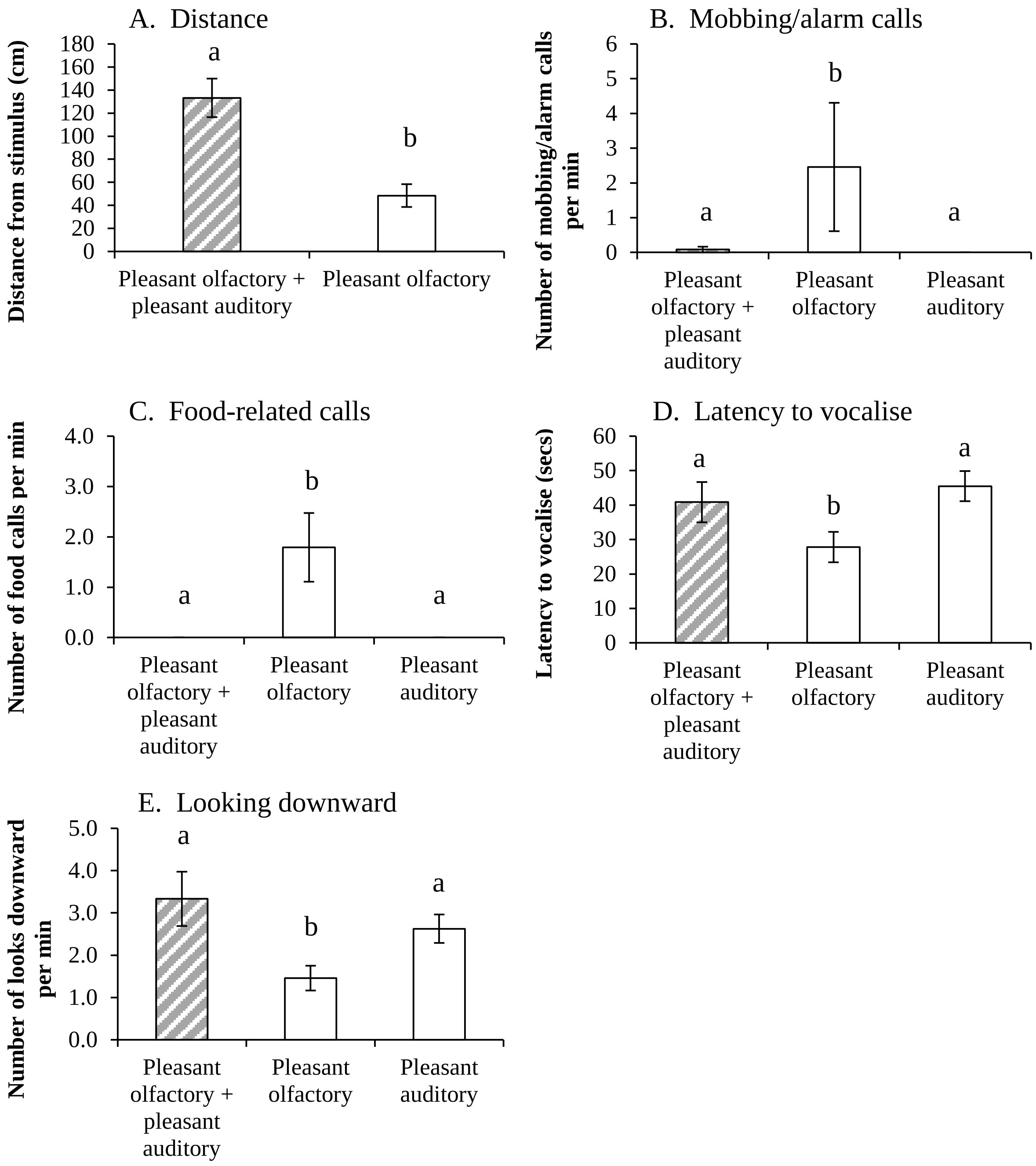


Figure 5.16. Comparison of responses during the test period: pleasant olfactory/auditory (marshmallow odour/marmoset food-related calls) combination and individually presented stimuli (1 min). A – distance from stimulus (cm), B – mobbing/alarm calls, C – food-related calls, D – latency to vocalise (secs), E – looks downward (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’.

There were fewer mobbing/alarm calls produced during the presentation of the combination than during the presentation of the marshmallow odour alone ($p = 0.01$); the responses to the two individual stimuli were also significantly different (Fig. 5.16 B). Food-related calls were given only in response to the marshmallow odour presented on its own (Fig. 5.16 C).

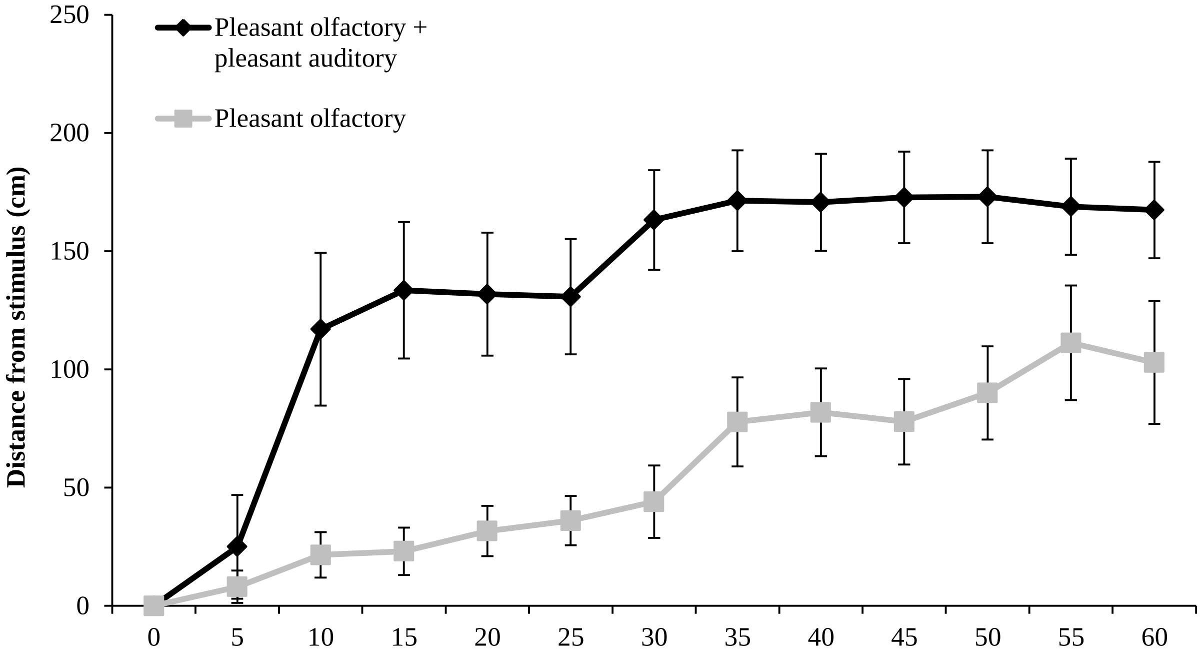


Figure 5.17. Distance (cm) over time (5-second intervals; test period) from the pleasant olfactory/auditory (marshmallow odour/marmoset food-related calls) combination and the pleasant olfactory stimulus (means ± sem). Black line (♦ symbols) shows the response to the pleasant olfactory/auditory combination. Light-grey line (□ symbols) shows the response to the marshmallow alone. There was a significant difference between the means of these two data sets.

The marmosets had a longer latency to vocalise (secs) to the combination than they did to the odour on its own ($p = 0.05$) (Fig. 5.16 D).

The number of looks downward per minute was higher in response to the combination than it was to the marshmallow odour on its own ($p = 0.03$) (Fig. 5.16 E).

5.3.2.8 Comparison of responses to the pleasant visual/olfactory/auditory combination and the stimuli presented alone

The results of the comparisons of the test periods are shown in Table 5.10.

Table 5.10. Responses to the pleasant trimodal (marshmallow/marshmallow odour/marmoset food-related calls) combination versus the individually presented stimuli. Statistical comparisons of the first minute responses (test periods).

	Main or major effect	Combination versus pleasant visual	Combination versus pleasant olfactory	Combination versus pleasant auditory
Mean distance from stimulus (cm)	–	**t = 2.52** **p = 0.03**	–	–
Closest distance to stimulus (cm)	–	Z = -0.11 p = 0.92	–	–
Latency to approach (secs)	–	Z = -1.24 p = 0.21	–	–
Activity per min	X^2 = 3.50 p = 0.32	–	–	–
Number of contact calls per min	X^2 = 1.18 p = 0.76	–	–	–
Number of mobbing/alarm calls per min	**X^2 = 15.23** **p = 0.002**	**Z = -2.08** **p = 0.04**	Z = 0.00 p = 1.00	Z = -1.83 p = 0.07
Number of food-related calls per min	**X^2 = 11.06** **p = 0.01**	Z = -1.82 p = 0.07	Z = -0.09 p = 0.93	Z = -1.60 p = 0.11
Latency to vocalise (secs)	X^2 = 6.09 p = 0.11	–	–	–
Number of looks upward per min	X^2 = 3.19 p = 0.36	–	–	–
Number of looks downward per min	X^2 = 4.44 p = 0.22	–	–	–
Number of looks at the stimulus per min	–	t = -0.50 p = 0.63	–	–

Significant differences were found only between the response to the pleasant trimodal combination and the response to the marshmallow on its own.

The marmosets' mean distance (cm) was significantly greater from the visual stimulus in the pleasant trimodal test period than it was when only the marshmallow was presented (p = 0.03) (Fig. 5.18 A), although the closest distance (cm) and the latency to approach were not statistically different. Mean distance (cm) over time (5-second intervals) is shown in Figure 5.19.

There were fewer mobbing/alarm calls per minute in the test period of the trimodal stimulus than there were in response to the marshmallow alone (p = 0.04) (Fig. 5.18 B). Although there was a significant heterogeneity across the four stimuli for the number of food-related calls per minute

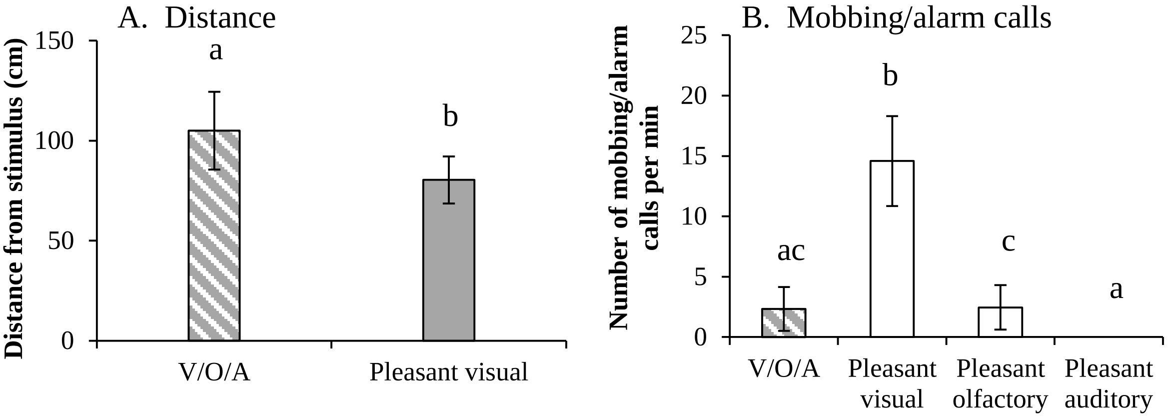


Figure 5.18. Comparison of responses during the test period: pleasant trimodal (marshmallow/marshmallow odour/marmoset food-related calls) combination (V/O/A) and individually presented stimuli (1 min). A – distance from stimulus (cm), B – mobbing/alarm calls (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’, and ‘c’ is significantly different from both ‘a’ and ‘b’; ‘ac’ is not significantly different from either ‘a’ or ‘c’, but it is from ‘b’. Mean distance was greater from the trimodal combination and marmosets made fewer mobbing/alarm calls than to the marshmallow.

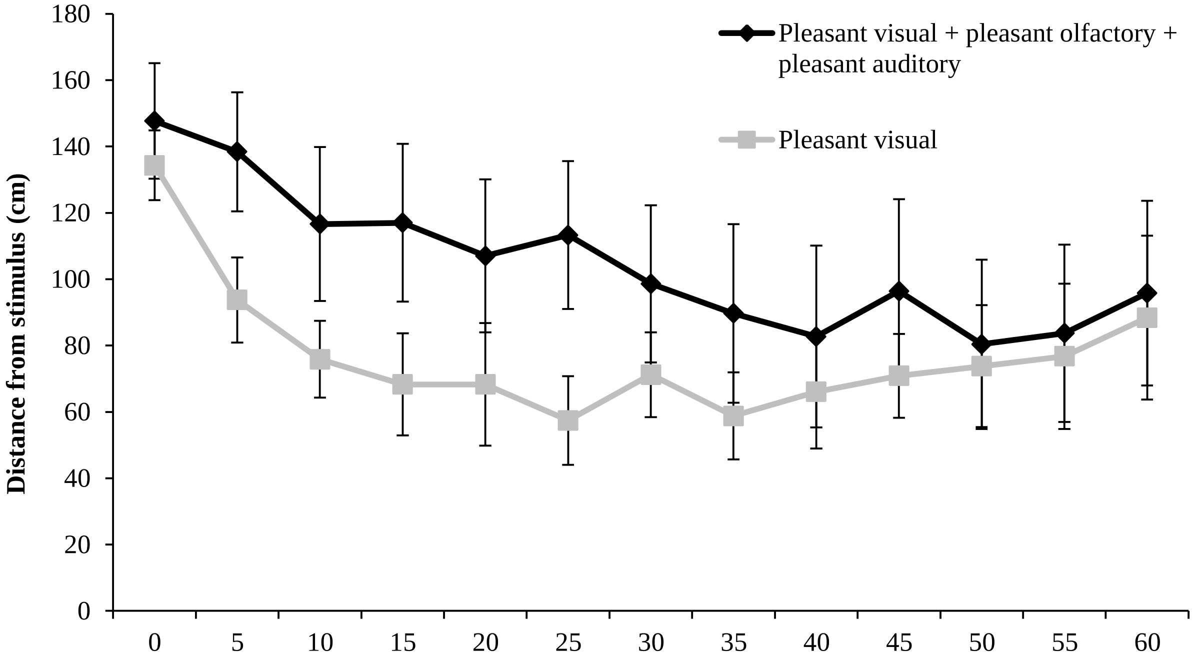


Figure 5.19. Distance (cm) over time (5-second intervals; test period) from the pleasant trimodal (marshmallow/marshmallow odour/marmoset food-related calls) combination and the pleasant visual stimulus (means ± sem). Black line (♦ symbols) shows the response to the trimodal combination. Light-grey line (□ symbols) shows the response to the marshmallow alone. There was a significant difference between the means of these two data sets. The mean distance never reaches 0 cm because not all marmosets were at the stimulus location at the same time.

(p = 0.01), *post hoc* tests revealed the significant differences were between only the three individual stimuli, as reported in Chapter 4. Additionally, two marmosets did not retrieve the marshmallow.

5.3.3 Comparison of responses to the combinations

The combinations were compared within each type (aversive and pleasant) grouping, i.e. aversive visual/olfactory was compared with aversive visual/auditory, aversive olfactory/auditory and aversive visual/olfactory/auditory, and the same applied to the pleasant combinations. The types of behaviour compared were mean distance (cm), mean closest distance (cm), mean latency to approach (secs), mean activity per two minutes, mean number of mobbing/alarm calls per two minutes, mean latency to vocalise (secs) and mean number of looks downward per two minutes. Pre-test, test and post-test periods were examined for statistical main effects. Closest distance, latency to approach/vocalise and looks at the visual stimulus were analysed only for the test periods. Mean distance, closest distance, latency to approach and looks at the stimulus did not apply to comparisons made with combinations involving olfactory/auditory-only stimuli.

The pre- and post-test comparisons found no significant differences (repeated measures ANOVA $F_{(3,33)}$ values ranged from 0.16 to 1.48 with corresponding p values ranging from 0.92 to 0.24; Friedman's test X^2 values ranged from 1.08 to 6.00 with corresponding p values ranging from 0.78 to 0.11).

5.3.3.1 Aversive combinations

The statistical results of the comparisons of responses during the test-periods of the aversive combinations are shown in Table 5.11.

Statistically significant differences in the test period were found for number of mobbing/alarm calls and the number of looks downward (Table 5.11). The number of mobbing/alarm calls, latency to vocalise (secs) and the number of looks downward showed significant differences between combinations. The marmosets gave more mobbing/alarm calls to the aversive visual/olfactory combination than they did to the aversive olfactory/auditory ($p = 0.003$) and the aversive trimodal combinations ($p = 0.01$). Additionally, the number of mobbing/alarm calls was lower in the aversive olfactory/auditory combination test period than it was in the test period of the aversive visual/auditory ($p = 0.01$) and aversive trimodal combination ($p = 0.02$) (Fig. 5.20 A). Latency to vocalise (seconds) was significantly shorter when the marmosets were presented with the aversive visual/olfactory combination than the trimodal combination ($p = 0.02$) (Fig. 5.20 B).

The marmosets looked down more often during the presentation of the aversive olfactory/auditory combination than they did for any other combination (quoll/odour of cat faeces: $p = 0.003$; quoll/leopard growl: p = 0.04; quoll/odour of cat faeces/leopard growl: $p = 0.01$) (Fig. 5.20 C).

Table 5.11. Comparison of the aversive combinations. Statistical comparisons of the responses during the test-period. 'n/a' denotes when statistical analysis was not applicable.

	Main or major effect	Visual/olfactory versus visual/auditory	Visual/olfactory versus olfactory/auditory	Visual/olfactory versus visual/olfactory/ auditory	Visual/auditory versus olfactory/auditory	Visual/auditory versus visual/olfactory/ auditory	Olfactory/auditory versus visual/olfactory/ auditory
Mean distance from stimulus (cm)	$X^2 = 5.00$ $p = 0.08$	–	n/a	–	n/a	–	n/a
Closest distance to stimulus (cm)	$F_{(2,22)} = 1.61$ $p = 0.23$	–	n/a	–	n/a	–	n/a
Latency to approach (secs)	$F_{(2,22)} = 0.57$ $p = 0.58$	–	n/a	–	n/a	–	n/a
Activity per 2 mins	$X^2 = 2.51$ $p = 0.47$	–	–	–	–	–	–
Number of mobbing/alarm calls per 2 mins	**$X^2 = 21.27$** **$p \leq 0.001$**	$Z = -1.07$ $p = 0.29$	**$Z = -2.93$** **$p = 0.003$**	**$Z = -2.75$** **$p = 0.01$**	**$Z = -2.80$** **$p = 0.01$**	$Z = -1.57$ $p = 0.12$	**$Z = -2.39$** **$p = 0.02$**
Latency to vocalise (secs)	**$X^2 = 9.63$** **$p = 0.02$**	$Z = -1.84$ $p = 0.07$	$Z = -1.81$ $p = 0.07$	**$Z = -2.40$** **$p = 0.02$**	$Z = -1.10$ $p = 0.27$	$Z = -1.10$ $p = 0.27$	$Z = -0.09$ $p = 0.93$
Number of looks downward per 2 mins	**$F_{(3,33)} = 10.83$** **$p \leq 0.001$**	$p = 1.00$	**$p = 0.003$**	$p = 1.00$	**$p = 0.04$**	$p = 1.00$	**$p = 0.01$**
Number of looks at the visual stimulus per 2 mins	$F_{(2,22)} = 2.09$ $p = 0.15$	–	n/a	–	n/a	–	n/a

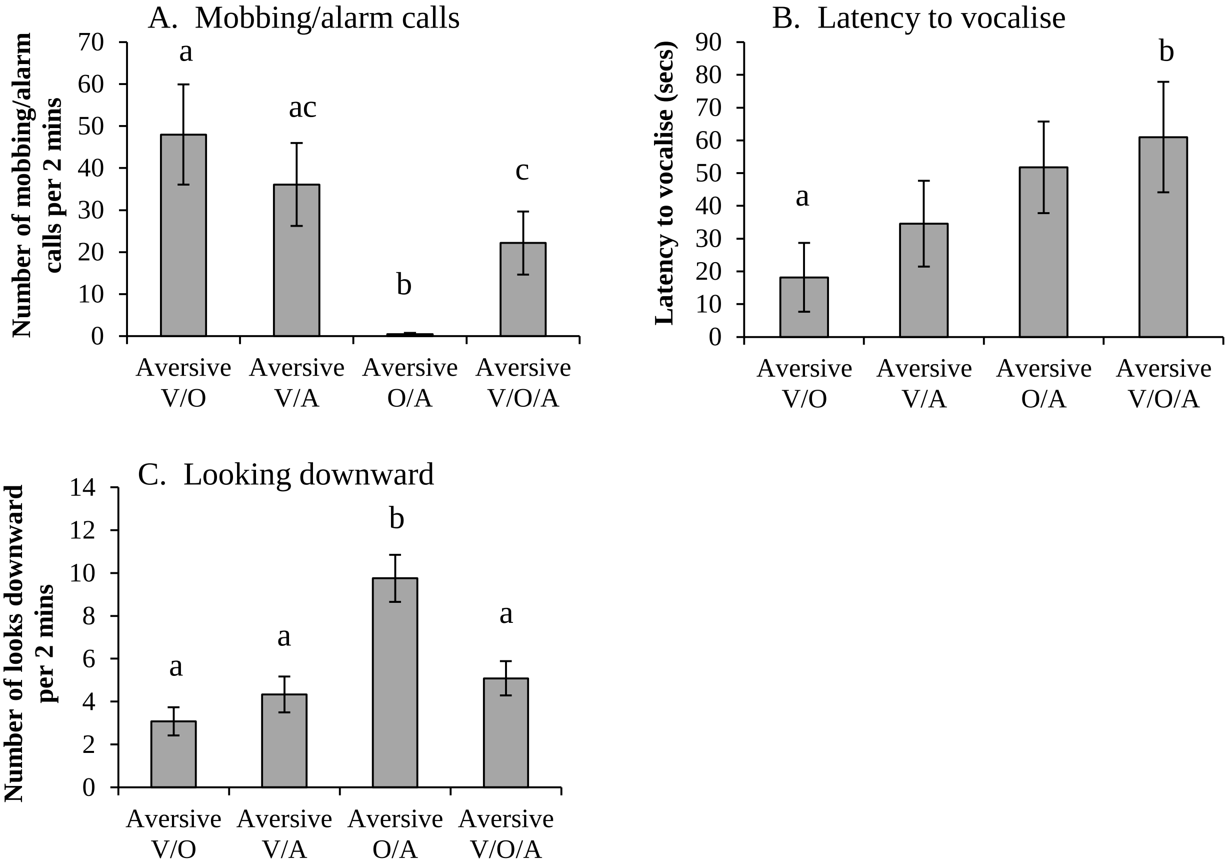


Figure 5.20. Comparison of responses during the test period of the aversive combinations: aversive visual/olfactory (V/O), aversive visual/auditory (V/A), aversive olfactory/auditory (O/A) and aversive trimodal (V/O/A) combinations (2 mins). A – mobbing/alarm calls, B – latency to vocalise (secs), C – looks downward (means ± sem). Bars marked 'a' are significantly different from those marked 'b', and 'c' is significantly different from 'a' and 'b', and 'c' is significantly different from both; 'ac' is not significantly different from 'a' or 'c' but it is from 'b'.

5.3.3.2 Pleasant combinations

The statistical results of the comparisons of the responses to the pleasant combinations during the test-periods are shown in Table 5.12.

As is evident in Table 5.12, the marmosets responded to any of the pleasant combinations mostly in similar ways. Significant differences between the pleasant combinations were found for the number of mobbing/alarm calls per two minutes; fewer in the pleasant olfactory/auditory combination than the pleasant visual/olfactory ($p = 0.03$) and pleasant visual/auditory ($p = 0.01$)

Table 5.12. Comparison of the pleasant combinations. Statistical comparisons of the responses during the test-period. ‘n/a’ denotes when statistical analysis was not applicable.

	Main or major effect	Visual/olfactory versus visual/auditory	Visual/olfactory versus olfactory/auditory	Visual/olfactory versus visual/olfactory/auditory	Visual/auditory versus olfactory/auditory	Visual/auditory versus visual/olfactory/auditory	Olfactory/auditory versus visual/olfactory/ auditory
Mean distance from stimulus (cm)	$X^2 = 3.80$ $p = 0.15$	–	n/a	–	n/a	–	n/a
Closest distance to stimulus (cm)	$X^2 = 2.00$ $p = 0.37$	–	n/a	–	n/a	–	n/a
Latency to approach (secs)	$X^2 = 3.20$ $p = 0.20$	–	n/a	–	n/a	–	n/a
Activity per 2 mins	$X^2 = 1.97$ $p = 0.58$	–	–	–	–	–	–
Number of mobbing/alarm calls per 2 mins	**$X^2 = 11.51$** **$p = 0.01$**	$Z = -0.42$ $p = 0.68$	**$Z = -2.21$** **$p = 0.03$**	$Z = -1.40$ $p = 0.16$	**$Z = -2.53$** **$p = 0.01$**	$Z = -1.48$ $p = 0.14$	$Z = -1.83$ $p = 0.07$
Number of food-related calls per 2 mins	$X^2 = 1.93$ $p = 0.59$	–	–	–	–	–	–
Latency to vocalise (secs)	**$X^2 = 9.49$** **$p = 0.02$**	**$Z = -2.67$** **$p = 0.01$**	**$Z = -1.99$** **$p = 0.05$**	$Z = -1.27$ $p = 0.20$	$Z = -1.27$ $p = 0.20$	$Z = -0.66$ $p = 0.51$	$Z = -1.58$ $p = 0.11$
Number of looks downward per 2 mins	**$F_{(3,33)} = 5.09$** **$p = 0.001$**	$p = 0.13$	$p = 0.57$	$p = 0.07$	$p = 1.00$	$p = 1.00$	$p = 0.49$
Number of looks at the visual stimulus per 2 mins	$F_{(2,22)} = 0.12$ $p = 0.88$	–	n/a	–	n/a	–	n/a

combinations (Fig. 5.21 A). Latency to vocalise (seconds) was significantly shorter when the pleasant visual/olfactory combination was presented than the pleasant visual/auditory combinations (*p* = 0.01; Fig. 5.21 B).

Although significant heterogeneity was found for the number of looks downward per two minutes (*p* = 0.01), no significant differences were found using Bonferroni *post hoc* pairwise comparisons.

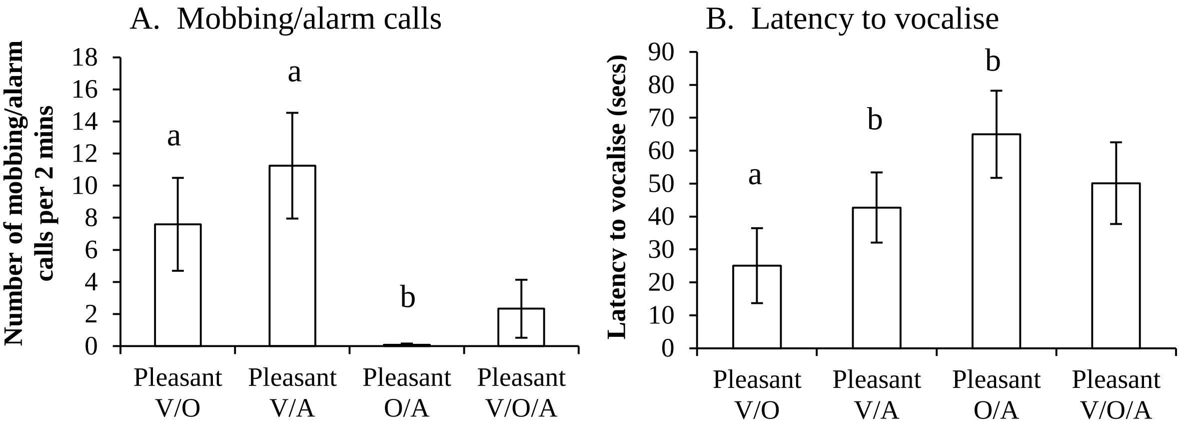


Figure 5.21. Comparison of responses during the test period of the pleasant combinations: pleasant visual/olfactory (V/O), pleasant visual/auditory (V/A), pleasant olfactory/auditory (O/A) and pleasant trimodal (V/O/A) combinations (2 mins). A – mobbing/alarm calls, B – latency to vocalise (secs) (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’.

5.4 Discussion

In Experiment 2 (Ch. 4) it was shown that the presentation of aversive and pleasant stimuli in three different modalities affected some aspects of the marmosets’ behaviour. The aim of this experiment had been to determine if combinations of related stimuli in different modalities would interact and alter both sets of responses observed to the individually presented stimuli (as reported in Ch. 4); such an effect could have been expressed as modulation. Alternatively, responding to only one component (dominance) or changing responses completely (neither *x* or *y*; emergence of a new behaviour) were alternative outcomes.

The response of the marmosets to the combination greatly depended on the modalities present and the type of stimuli (aversive or pleasant), suggesting that there was some hierarchy in responding to the modalities. A summary of these results is presented in Table 5.12. In general, responses showed that the marmosets attended to the visual component of aversive combinations more than to the other modality or modalities present; this was not as evident when presenting any of the pleasant combinations (as shown in Table 5.13). However, the visual modality did not account for the entire set of responses.

The auditory component of a combination, regardless of type, reduced the number of vocalisations produced, even when presented together with a visual stimulus to which the marmosets had responded by vocalising when presented individually (Ch. 4). The information provided in the marmoset food-related calls may suggest two things, which may make this stimulus dominant in eliciting a response: firstly, that another marmoset is nearby, and secondly, that the other marmoset has found food. The marmoset may therefore be more influenced by the food-related calls of a conspecific rather than the odour, which is not a guarantee of edible food.

The only combination in which the response indicated that the olfactory cue was important was the pleasant visual/olfactory combination. The odour may suggest the presence of a desirable food but there is no visual source. Even in the olfactory/auditory combinations, the response of the marmosets reflected more obviously the response seen for the auditory stimuli presented alone. However, this is not to say that the olfactory component of either the aversive or pleasant combinations was unimportant. A typical response to the cat faeces odour was avoidance, but when the aversive odour was coupled with the quoll, which the marmosets approached to some degree and mobbed, avoidance may not have been possible. When they were presented with the

Table 5.13. Summary of results of the related combinations. Arrows indicate the direction of change in the responses to the combination from the responses to the individual stimulus (increase or decrease). ‘-‘ indicates no change and n/a means the behaviour was not relevant for that stimulus. Closest distance, activity and number of looks upward were not included as there were no changes scored.

		Behaviour scored							
Combination tested	**Stimulus**	Mean distance	Latency to approach	Contact calls	Mobbing/ alarm calls	Food calls	Latency to vocalise	Looks down	Looks at stimulus
Visual/olfactory	Quoll	-	-	-	-	n/a	-	↑	-
	Cat faeces odour	n/a	n/a	-	↑	n/a	↑	-	n/a
Visual/auditory	Quoll	↑	↑	-	↓	n/a	-	↑	-
	Leopard growl	n/a	n/a	-	↑	n/a	↑	-	n/a
Olfactory/auditory	Cat faeces odour	↑	n/a	-	-	n/a	-	↑	n/a
	Leopard growl	n/a	n/a	-	-	n/a	-	↑	n/a
Visual/olfactory/	Quoll	↑	↑	↑	↓	n/a	↑	↑	↓
auditory	Cat faeces odour	n/a	n/a	-	↑	n/a	-	-	n/a
	Leopard growl	n/a	n/a	-	-	n/a	-	-	n/a
Visual/olfactory	Marshmallow	-	↓	-	↓	-	-	-	-
	Marshmallow odour	n/a	n/a	-	-	-	-	-	n/a
Visual/auditory	Marshmallow	-	-	-	↓	-	-	-	-
	Food-related calls	n/a	n/a	-	↑	↑	-	-	n/a
Olfactory/auditory	Marshmallow odour	↑	n/a	-	↓	↓	↑	↑	n/a
	Food-related calls	n/a	n/a	-	-	-	-	-	n/a
Visual/olfactory/	Marshmallow	↑	-	↓	-	-	-	-	-
auditory	Marshmallow odour	n/a	n/a	-	-	-	-	-	n/a
	Food-related calls	n/a	n/a	-	-	-	-	-	n/a

pleasant visual/olfactory combination, the marmosets responded quite strongly to the marshmallow odour, even manipulating and licking the tea infuser when it was accessible (visual/olfactory and trimodal combinations).

Particularly of interest in the responses to the marshmallow/marshmallow odour combination was the reduction in mobbing/alarm vocalisations and shorter latency to approach in comparison to the marshmallow-only presentation. There is no doubting the strong attraction of either of these two stimuli, but the presence of both together and simultaneously enhanced the marmosets' initial response, by significantly and markedly reducing the speed of approach (measured as latency to approach). The number of mobbing/alarm vocalisations in response to the combination was not significantly different from the number in response to the marshmallow odour alone. However, they were reduced when the sight of the marshmallow was presented together with the corresponding odour from the levels recorded in response to the marshmallow alone. This suggests that odour is important to marmosets when detecting and identifying potential food sources, and increases the attraction to the food source. It further indicates that odour is important, even dominant, in influencing vocal responses. This is interesting given that Experiment 2 had shown that the strongest vocal responses were towards the visual stimuli; it was presumed that the visual modality would continue to influence this behaviour in the combination experiments. It is likely that the original response to the marshmallow alone was born from frustration, and the arousal caused by this frustration, due to inaccessibility rather than because the marmosets saw the marshmallow as an aversive stimulus. The presence of an odour may have given the illusion of accessibility to the food source, thereby reducing frustration and the need for a high number of corresponding vocal responses.

The question of habituation, in particular to the quoll, also needs to be addressed, given the number of times the marmosets had been exposed to these stimuli. However, the number of mobbing/alarm calls only reduced when the quoll was coupled with the leopard growl. Experiment 2 had shown that the marmosets reduced vocalising when presented with auditory stimuli, regardless of type. In other words, the marmosets showed no signs of habituation to the aversive stimuli. That the marmosets only reduced mobbing towards the quoll when it was presented with the leopard growl highlights the importance of the auditory stimulus in modulating this particular behaviour.

The strongest evidence in my results to support the threat-sensitivity hypothesis (Helfman, 1989) arose in the marmosets' responses to the presentation of the aversive visual/auditory and trimodal combinations. When the visual cue was aversive (quoll) and coupled with a corresponding auditory cue (leopard growl), the marmosets' mean distance was greater than when only the quoll was presented, regardless of whether there was an olfactory cue as well. This suggests that the combination of the quoll and the leopard growl was perceived by the marmosets as an increased level of risk. When either was presented with the odour of cat faeces, the identified threat did not appear to have increased. The marmosets may not have associated the odour with either stimulus, or the level of risk the odour represented was negligible. It is important to note that once the combination was removed, the marmosets' behaviour returned to pre-test levels; that is, they did not lead to long-term changes in behaviour, as may have been expected.

Indeed, the only combination in which a pre- to post-test difference in response occurred was found in the number of contact calls in response to the pleasant visual/olfactory combination; fewer contact calls post-test than in the pre-test. However, marshmallow is very desirable to the marmosets, to the point that they will fight with cage mates to gain access to this treat rather than share. It may be that the marmosets continued to limit these vocalisations in order to reduce the possibility of competition for the marshmallow, should it be presented again.

Although the presentation of the combination of odour of cat faeces and leopard growl did not alter the behaviour of the marmosets from the pre-test, there was one particularly interesting result in regard to the number of looks downward. The marmosets looked down more often in response to this combination than they did in response to either the cat faeces odour or leopard growl presented alone. This suggests that both stimuli are required in conjunction in order for the marmosets to perceive information perhaps regarding the biological source. Although the speaker was only just above a metre from the ground the marmosets did not typically respond to any other sounds by looking down or at the speaker, and certainly the marmosets did not look down as often for just the leopard growl. In addition, the number of looks downward in response to the cat faeces odour/leopard growl combination was significantly higher than scored for any other aversive combination. The marmosets may have scanned terrestrially less often in the presence of the quoll because they had a visual point on which to fixate. The likelihood of stimuli being associated with each other may be improved when the modalities involved are visual and auditory, probably also visual and olfactory. Firstly, it is easier to present a visual stimulus with a sound or odour than it is to present an odour and sound together. Secondly, the subject animal may associate (or bind) a visual stimulus of a predator if it moves its mouth and a sound is played simultaneously (Spence and Driver, 2004). Binding of stimuli in the perception process is also likely when a visual stimulus has a particular odour. I have found no multimodal studies involving related combinations of these two stimuli. It would therefore be worth testing wild marmosets with known and related olfactory and auditory stimuli, to determine whether experience is essential for associating the two modalities in regard to a predator. It would be especially interesting if the marmosets showed a stronger reaction to the olfactory cue, given the strength of their fear response to the vocalisation of a predator.

Although this study was not focused on the type of social communication Partan and Marler (1999, 2005) used as a primary basis for their theory of multimodal responses, an attempt was made to determine whether their model would also fit responses to predators and food, rather than social or sexual contexts. As the three modalities, regardless of type, elicited different responses, the combination of these stimuli could be considered as acting as ‘non-redundant signalling’. The four possible outcomes were ‘independence’, ‘dominance’, ‘modulation’ and ‘emergence’. The first three outcomes were more likely as the same behavioural responses were scored in every situation. However, no incidents of a new (emerging) behaviour were observed.

Typically, the studies concerned with multimodal signalling have focused on one behaviour per stimulus, that is, stimulus *a* elicits behaviour *x* and stimulus *b* elicits behaviour *y*. Responses *x* and *y* may be entirely different behaviour, such as movement and vocalisations, or they may be different intensities of the same behaviour, such as no or many vocalisations. In my study I looked at a minimum of seven responses per stimulus, some of which were related, such as mean distance and closest distance, and some of which were relevant only to particular modalities. I found that no one modality appeared to completely dominate the other component or components of the combination, or across all combinations. Indeed, of the eight combinations presented, only two – the aversive visual/olfactory and pleasant visual/auditory combination – indicated modality dominance; in both cases this was the visual component. However, in both cases there was still one behaviour (aversive combination – number of looks downward, pleasant combination – number of mobbing/alarm calls) that was significantly different from the individually presented visual stimulus. Responses, when labelled as independence, dominance and modulation, were not only combination-specific but also behaviour-specific. In general, there were few responses that could be classified as ‘independence’ (i.e. in which responses elicited by all components of the combination were equal), suggesting that the components of the combinations interacted in eliciting a response.

Modulated responses were also exceedingly common, and evident when the results presented in Chapter 4 had revealed significant differences between the individual stimuli but the response to the combination varied. The trimodal combinations present a problem when trying to apply the Partan and Marler model (1999, 2005): a third component to a signal has received relatively little scientific attention and is not addressed in the model. Partan and Marler (1999, 2005) make reference to the possibility of increased complexity in a signal with more than two sensory cues and, indeed, my results seem to support this.

Predator- and food-based stimuli can provide marmosets and other animals with information regarding the predators' and food's presence, availability, location and/or activities. The marmosets can use the information to respond in particular ways, and more cues may help to improve the process of identification, determining location and appropriate response. These are all aspects of the multimodal communication model (Partan and Marler, 1999). However, when the perceiver does not have the experience to associate the individual cues with each other, the model could begin to fall apart. Furthermore, conflicting situations, in which the responses are distinctly different, also potentially fall under the non-redundant classification as outlined by Partan and Marler (1999, 2005). It would seem more likely that independent responses may occur when the marmosets are presented with predator- and food-based cues simultaneously. I test this aspect of multimodal combinations in the following chapter (Ch. 6).

CHAPTER SIX

EXPERIMENT 4: RESPONSES TO CONFLICTING MULTIMODAL COMBINATIONS

6.1 Introduction

In the previous three experiments, it was established that this group of marmosets showed consistent behaviour patterns when faced with either aversive or pleasant stimuli. No habituation occurred throughout any of the experiments. It was also established that combinations of stimuli in different modalities, but of the same type (all aversive or all pleasant), altered the response displayed first to the individual stimuli, i.e. the responses showed variations of enhancement, modulation and/or domination of the effect of one stimulus on the response. The experiment presented in this chapter investigates conflicting situations. Conflicts in motivation occur naturally when one stimulus elicits approach and investigation (e.g. a food source) while another may arouse fear (e.g. a potential predator), eliciting withdrawal or flight (Skals *et al.*, 2005). In this fourth experiment, food- and predator-based stimuli in different modalities were presented simultaneously to determine which motivation might outweigh another.

One way in which an animal can respond to two conflicting stimuli is by reducing the strength of one response so that it can also attend to the other stimulus, even if in a limited capacity. For example, Caine (1998) showed that foraging Geoffroy’s marmosets reduce, but do not stop, foraging when faced with a potential predatory threat. However, should the level of risk escalate, it is predicted that the animal would stop foraging entirely in order to focus all its attention on the immediate threat. Indeed, this was shown well by Skals and colleagues’ (2005) experiment involving a male moth being presented simultaneously with an auditory cue of a potential predator and an olfactory cue of a potential mate, as already described (Ch. 1, Section 4.3).

When the volume of the predator call was increased, simulating the closer proximity of the bat to the male moth and, hence, an increased risk, the male moth moved as though to avoid the predator and was less attentive to the olfactory cue; the opposite occurred when the concentration of the olfactory cue was strengthened (Skals *et al*., 2005). However, an argument could also be made that when two sensory cues afford conflicting or incompatible information, animals may be forced to choose on which stimulus to focus their attention (Bernays, 2001). That is, the animal may ignore one stimulus, limiting its attention, in favour of another due to constraints in information processing (Dukas, 2002; Pashler, 1998; Spence and Driver, 2004). In these cases, one would expect there to be a complete dominance of one modality or stimulus over the other.

Risk assessment and risk-taking may vary according to modality and even individual temperament (Kemp and Kaplan, 2011; Owings, 2002). For instance, a visual stimulus of a predator may imply an immediate potential threat that outweighs the presence of food, in any modality. However, the use of marshmallow as the primary food stimulus (visual and olfactory) may act as a strong incentive and the greatest risk-takers in the group may choose to ignore the risk in order to retrieve this favourite food item. Should the food stimulus be less enticing, such as a food item the marmosets receive daily instead of a rare treat, it is conceivable that motivation to retrieve the item will be low and therefore the focus of attention will be on the aversive stimulus.

It is worth noting here that this experiment is based on the assumption that food and predatory cues are of equal importance and therefore suitable for testing an approach-withdrawal effect. This is important to identify since some studies have treated the aversive cue as the affecting stimulus and the presence of food merely as a lure for measuring the response to the predator.

For example, in an experiment by Blumstein *et al*. (2002*b*), predator-naive tammar wallabies (*Macropus eugenii*) and red-necked pademelons (*Thylogale thetis*) were allowed access to two food bins, one of which had the faeces of a carnivore underneath and the other faeces of a herbivore. The food bowl from which the animal chose to eat was then analysed as a response to the predator cue ('repellency factor') rather than as a cue itself ('attractant factor'). I am arguing here that the food itself may have an attractant effect. Furthermore, some individuals may be highly food motivated; that is, they may be more willing to take risks when food, particularly favourite food, is offered. Although the prey animals in the study by Blumstein *et al*. (2002) spent significantly more time feeding at the bin with the herbivorous faeces, suggesting that the carnivore faeces were aversive and repellent, they did still spend some time eating at the bin with the carnivore faeces; this shows that the attractant value of the food could override the repellency factor of the carnivore faeces. In the experiment presented in this chapter, I treated both stimuli as having similar influence in affecting the marmosets' response.

By presenting the marmosets with food- and predator-based stimuli simultaneously in different combinations, the question could then be posed whether it was the modality (visual, olfactory or auditory) or the type of cue (aversive or pleasant) that was more important in eliciting a response or indeed the strength of a specific response. It was predicted that there would be a trade-off in behavioural response to the conflicting stimuli, and such a trade-off would reflect the perceived level of risk from the predatory stimulus, which may vary with sensory modality.

6.2 Materials and methods

Eleven marmosets (6 females/5 males, aged 24 to 161 months) were tested individually for their response to conflicting combinations of the aversive and pleasant stimuli presented in Experiments 2 and 3. Delta, a male aged 150 months as of February 2008, who had been tested for his response to the individual stimuli in Experiment 2 and the related combinations in Experiment 3, was no longer agile enough to come to the playroom and was hence excluded from further testing. For the purpose of this experiment, his scores were excluded from the results of the individually presented stimuli, which were reported in Chapter 4. Therefore, the results of the individually presented stimuli used in this chapter are slightly different from those presented in Chapter 4.

6.2.1 Combinations tested

Six combinations of the six aversive and pleasant stimuli were tested. Four of these combinations were of mixed modalities:

1. Aversive visual (quoll) + pleasant auditory (marmoset food-related calls)
2. Pleasant visual (marshmallow) + aversive auditory (leopard growl)
3. Aversive olfactory (cat faeces odour) + pleasant auditory (marmoset food-related calls)
4. Pleasant olfactory (marshmallow odour) + aversive auditory (leopard growl)

Two combinations included stimuli from the same modality:

5. Pleasant visual (marshmallow) + aversive visual (quoll)
6. Pleasant visual (marshmallow) + aversive visual (quoll) + aversive auditory (leopard growl)

Combination 5 provided an opportunity to test a situation in which responses to two visual stimuli that had been shown to have opposing spatial behavioural effects (approaching/staying away) could be measured. The addition of the aversive auditory stimulus to these two visual stimuli (combination 6) provided a means by which to test the threat-sensitivity predator-avoidance hypothesis (Helfman, 1989) in so far as the degree of aversiveness (risk) was increased during this trial.

The combination of olfactory and visual stimuli was not tested as there was no way to guarantee that the marmosets would approach the source of the olfactory stimulus closely enough to perceive the odour, particularly in the case of the visual aversive stimulus.

6.2.2 Experimental procedure

The same experimental procedure was followed as described in the General Methods (Ch. 2, Section 2.3) and used in Experiments 2 (Ch. 4, Section 4.2) and 3 (Ch. 5, Section 5.2). To reiterate, an individual marmoset was enticed into the indoor room and allowed five minutes to settle and explore. After this period, the individual was observed for two minutes pre-test, then scored for two minutes when the combination was presented before it was removed (or stopped in the case of the auditory stimuli), and then scored for a further two minutes post-test. Marmosets were tested using only one combination per day, with a minimum of one day between each combination trial. Each combination was tested once, in random order.

Again, special care was taken to make the presentations alike and simultaneous. This was especially important for conflicting stimuli. The experiment described in this chapter did not rely on the marmosets associating the two conflicting stimuli, as might have been more important to Experiment 3 (Ch. 5). Instead, the aim was to provide the marmosets with a situation in which the two stimuli presented simultaneously had been demonstrated to lead to different and, importantly, often opposite responses.

The methodology described for Experiment 3 (related combinations, Ch. 5) was used. For example, in the case of the visual/auditory combinations, the visual stimulus needed to be covered before being placed on the platform in the playroom (within arm’s reach of the door). This allowed for simultaneous presentation of the stimuli because the auditory stimulus could be played at the same time as the cover was removed from the visual stimulus. At the end of the test period the sound was stopped and the visual stimulus was removed from the room.

For the aversive visual/pleasant visual (quoll/marshmallow) and aversive visual/pleasant visual/aversive auditory (quoll/marshmallow/leopard growl) conflicting combinations, specific adaptations had to be applied to the methodology. Both visual stimuli were again covered and placed on the platform in the indoor room within arm's reach of the door. They were placed 20 cm apart with the marshmallow to the left of the quoll, and were uncovered simultaneously. In the triple conflicting combination, the auditory stimulus was played once the covers were removed. At the end of the testing period, the visual stimuli were removed from the room and the auditory stimulus was then stopped.

6.2.3 Behaviour scored

The types of behaviour scored were the same as listed in Chapter 4 (Section 4.2.3) and Chapter 5 (Section 5.2.3). Detailed definitions of these behavioural responses have been provided in the General Methods (Section 2.4). In the combinations involving two visual stimuli (20 cm apart), distance was scored from the position of the aversive visual stimulus.

6.2.4 Statistical analysis

The statistical analyses used for this Experiment are the same as those detailed in Chapter 5 (Section 5.2.4). Again, as the test period of the combinations were conducted for two minutes but the test period of the individually presented stimuli was one minute, only the first minute was used for comparisons of the responses in the test period to these presentations. The full two minutes were used in comparisons of the pre-test, test and post-test periods for each combination.

6.3 Results

6.3.1 Comparison of pre-test, test and post-test results, within each combination

The statistical results for all combinations are reported in Table 6.1. The data used in these analyses are shown in Appendix VIII.

Table 6.1. Statistical comparisons of the responses in the pre-test, test and post-test periods of each conflicting combination. Tests of heterogeneity were first performed using a Friedman's test for non-parametric data; *post hoc* Wilcoxon signed-rank tests are shown where applicable. Pairwise comparisons were made using two-tailed t-tests for normal data and Wilcoxon signed-rank tests for non-parametric data. Significant results are bolded. The '–' indicates that statistical tests were not applicable.

	Main or major effect	Pre-test versus test	Test versus post-test	Pre-test versus post-test
Aversive visual/pleasant auditory combination				
Mean distance from stimulus (cm)	$X^2 = 1.64$ $p = 0.44$	–	–	–
Activity per 2 mins	**F = 4.58** **$p = 0.02$**	$p = 0.13$	$p = 0.06$	$p = 1.00$
Number of contact calls per 2 mins	**$X^2 = 7.95$** **$p = 0.02$**	$Z = -1.85$ $p = 0.07$	**$Z = -2.50$** **$p = 0.01$**	$Z = -0.21$ $p = 0.84$
Number of mobbing/alarm calls per 2 mins	**$X^2 = 15.70$** **$p \leq 0.001$**	**$Z = -2.70$** **$p = 0.01$**	**$Z = -2.80$** **$p = 0.01$**	Z = -1.60 $p = 0.11$
Number of looks upward per 2 mins	$X^2 = 2.53$ $p = 0.28$	–	–	–
Number of looks downward per 2 mins	$X^2 = 5.42$ $p = 0.07$	–	–	–
Pleasant visual/aversive auditory combination				
Mean distance from stimulus (cm)	**$X^2 = 11.09$** **$p = 0.004$**	**$Z = -2.85$** **$p = 0.004$**	**$Z = -2.85$** **$p = 0.004$**	$Z = -0.45$ $p = 0.66$
Activity per 2 mins	$F = 2.80$ $p = 0.09$	–	–	–
Number of contact calls per 2 mins	**$X^2 = 12.98$** **p = 0.002**	**$Z = -2.95$** **$p = 0.003$**	**$Z = -2.68$** **$p = 0.01$**	$Z = -1.66$ $p = 0.10$
Number of mobbing/alarm calls per 2 mins	**$X^2 = 12.78$** **$p = 0.002$**	**$Z = -2.37$** **$p = 0.02$**	**$Z = -2.37$** **$p = 0.02$**	$Z = -0.45$ $p = 0.66$
Number of food-related calls per 2 mins	**$X^2 = 7.54$** **$p = 0.02$**	$Z = -1.83$ $p = 0.07$	$Z = -1.83$ $p = 0.07$	$Z = -1.00$ $p = 0.32$
Number of looks upward per 2 mins	$F = 4.55$ $p = 0.10$	–	–	–
Number of looks downward per 2 mins	$F = 0.25$ $p = 0.78$	–	–	–
Aversive olfactory/pleasant auditory combination				
Mean distance from stimulus (cm)	–	–	–	$t = -0.86$ $p = 0.41$
Activity per 2 mins	$F = 1.47$ $p = 0.26$	–	–	–
Number of contact calls per 2 mins	**$X^2 = 10.89$** **$p = 0.004$**	**$Z = -2.53$** **$p = 0.01$**	**$Z = -2.62$** **$p = 0.01$**	$Z = -0.28$ $p = 0.78$
Number of mobbing/alarm calls per 2 mins	$X^2 = 1.40$ $p = 0.50$	–	–	–

Continued from previous page				
	Main or major effect	Pre-test versus test	Test versus post-test	Pre-test versus post-test
Number of looks upward per 2 mins	$X^2 = 0.05$ $p = 0.98$	–	–	–
Number of looks downward per 2 mins	$F = 1.69$ $p = 0.21$	–	–	–
Pleasant olfactory/aversive auditory combination				
Mean distance from stimulus (cm)	–	–	–	$t = -1.31$ $p = 0.22$
Activity per 2 mins	$F = 2.09$ $p = 0.15$	–	–	–
Number of contact calls per 2 mins	**$F = 4.37$** **$p = 0.03$**	$p = 0.33$	**$p = 0.03$**	$p = 0.96$
Number of mobbing/alarm calls per 2 mins	$X^2 = 5.47$ $p = 0.07$	–	–	–
Number of food-related calls per 2 mins	$X^2 = 2.00$ $p = 0.37$	–	–	–
Number of looks upward per 2 mins	$X^2 = 0.60$ $p = 0.74$	–	–	–
Number of looks downward per 2 mins	$F = 0.32$ $p = 0.73$	–	–	–
Aversive visual/pleasant visual combination				
Mean distance from stimulus (cm)	**$X^2 = 6.73$** **$p = 0.04$**	**$Z = -2.67$** **$p = 0.01$**	**$Z = -2.49$** **$p = 0.01$**	$Z = -0.09$ $p = 0.93$
Activity per 2 mins	**$F = 4.62$** **$p = 0.02$**	$p = 0.11$	$p = 0.11$	$p = 1.00$
Number of contact calls per 2 mins	**$X^2 = 15.76$** **$p \leq 0.001$**	**$Z = -2.94$** **$p = 0.003$**	**$Z = -2.81$** **$p = 0.01$**	$Z = -0.56$ $p = 0.57$
Number of mobbing/alarm calls per 2 mins	**$X^2 = 13.27$** **$p = 0.001$**	**$Z = -2.67$** **$p = 0.01$**	**$Z = -2.70$** **$p = 0.01$**	$Z = -129$ $p = 0.20$
Number of food-related calls per 2 mins	$X^2 = 2.00$ $p = 0.37$	–	–	–
Number of looks upward per 2 mins	$X^2 = 3.94$ $p = 0.14$	–	–	–
Number of looks downward per 2 mins	**$X^2 = 9.14$** **$p = 0.01$**	**$Z = -2.39$** **$p = 0.02$**	**$Z = -2.68$** **$p = 0.01$**	$Z = 0.00$ $p = 1.00$
Aversive visual/pleasant visual/aversive auditory combination				
Mean distance from stimulus (cm)	**$X^2 = 14.36$** **$p = 0.001$**	**$Z = -2.93$** **$p = 0.003$**	**$Z = -2.76$** **$p = 0.01$**	$Z = 0.00$ $p = 1.00$
Activity per 2 mins	**$F = 15.75$** **$p \leq 0.001$**	**$p = 0.001$**	**$p = 0.004$**	$p = 1.00$
Number of contact calls per 2 mins	**$X^2 = 18.49$** **$p \leq 0.001$**	**$Z = -2.94$** **$p = 0.003$**	**$Z = -2.94$** **$p = 0.003$**	$Z = -1.41$ $p = 0.16$
Number of mobbing/alarm calls per 2 mins	**$X^2 = 12.78$** **$p = 0.002$**	**$Z = -2.37$** **$p = 0.02$**	**$Z = -2.37$** **$p = 0.02$**	$Z = -0.45$ $p = 0.66$
Number of food-related calls per 2 mins	$X^2 = 2.00$ $p = 0.37$	–	–	–
Number of looks upward per 2 mins	$X^2 = 0.28$ $p = 0.87$	–	–	–
Number of looks downward per 2 mins	**$X^2 = 11.15$** **$p = 0.004$**	**$Z = -2.55$** **$p = 0.01$**	**$Z = -2.81$** **$p = 0.01$**	$Z = -0.66$ $p = 0.51$

6.3.1.1 Aversive visual/pleasant auditory combination

As shown in Table 6.1 above and Figure 6.1 A below, there were significantly fewer contact calls in the test period than in the post-test period (*p* = 0.01) and significantly more mobbing/alarm calls (Fig. 6.1 B) in the test period than in the pre- (*p* = 0.01) and post-test (*p* = 0.01) period. Significant heterogeneity was found for activity (*p* = 0.02), but *post hoc* tests showed only a trend for a greater rate of activity in the test period than in the post-test.

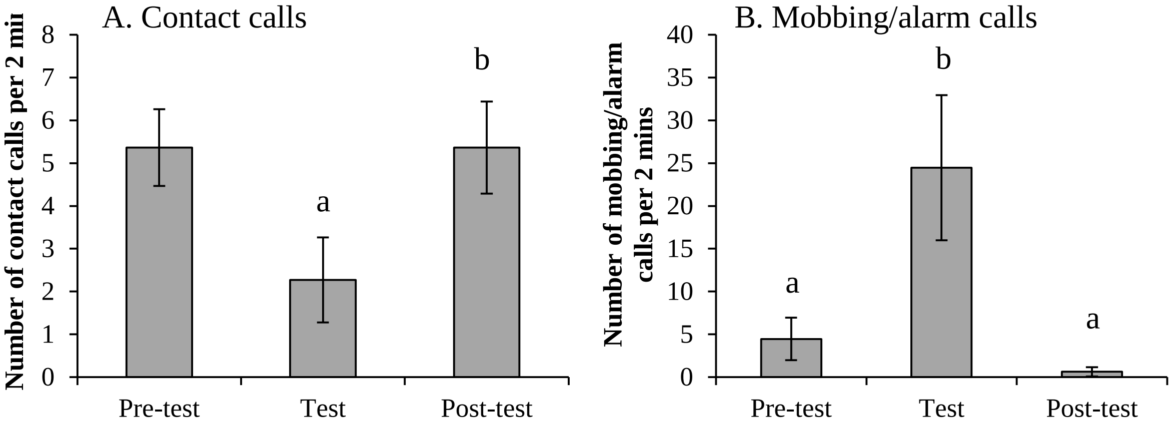


Figure 6.1. Comparison of responses in the pre-test, test and post-test periods: aversive visual/pleasant auditory (quoll/marmoset food-related calls) combination (2 mins). A – contact calls, B – mobbing/alarm calls (means ± sem). Bars marked ‘b’ are significantly different from those marked ‘a’.

6.3.1.2 Pleasant visual/aversive auditory combination

As shown in Figure 6.2 A, the marmosets came significantly closer (Table 6.1) to the visual stimulus in comparison with their pre- (*p* = 0.004) or post-test (*p* = 0.004) distance. They produced fewer contact calls (Fig. 6.2 B) and more mobbing/alarm calls (Fig. 6.2 C) than in either the pre- (*p* = 0.003 and *p* = 0.02, respectively) or post-test period (*p* = 0.01 and *p* = 0.02, respectively). Significant heterogeneity (*p* = 0.02) was found for the number of food-related calls, but *post hoc* analysis found only a trend for more food-related calls given in the test period than in the pre- or post-test period.

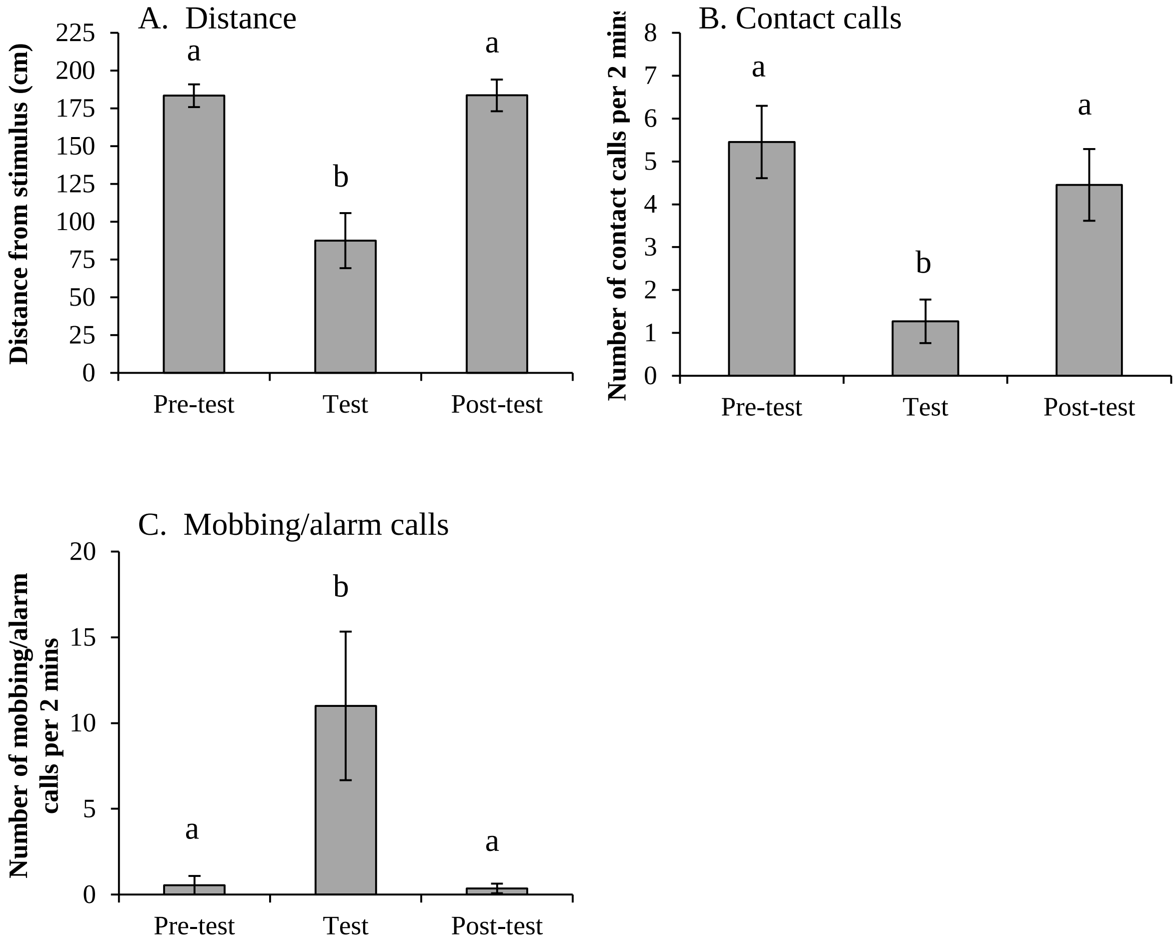


Figure 6.2. Comparison of responses in the pre-test, test and post-test periods: pleasant visual/aversive auditory (marshmallow/leopard growl) combination (2 mins). A – distance from the stimulus (cm), B – contact, C – mobbing/alarm calls (means ± sem). Bars marked 'b' are significantly different from those marked 'a'.

All but one of the marmosets retrieved the marshmallow and did so within the first minute of presentation.

6.3.1.3 Aversive olfactory/pleasant auditory combination

As also shown in Table 6.1, significant differences were found only for the number of contact calls made, with Wilcoxon signed-rank *post hoc* tests showing that the marmosets gave significantly fewer of these vocalisations in the test period than in the pre- ($p = 0.01$) or post-test ($p = 0.01$) period (Fig. 6.3).

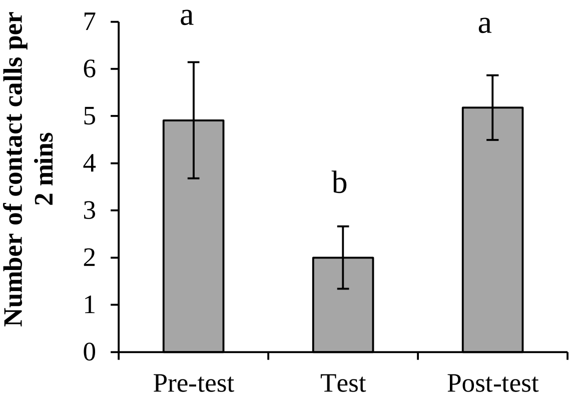


Figure 6.3. Comparison of responses in the pre-test, test and post-test periods: aversive olfactory/pleasant auditory (odour of cat faeces/marmoset food-related calls) combination (2 mins). Bar marked 'b' is significantly different from bar marked 'a'.

6.3.1.4 Pleasant olfactory/aversive auditory combination

As shown further in Table 6.1, significant differences were found only in regard to the number of contact calls (Fig. 6.4): the marmosets produced fewer contact calls in the test period than in the post-test period ($p = 0.03$).

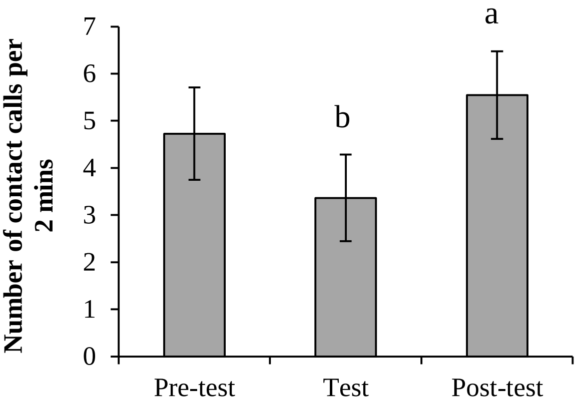


Figure 6.4. Comparison of responses in the pre-test, test and post-test periods: pleasant olfactory/aversive auditory (marshmallow/leopard growl) combination (2 mins) – number of contact calls (means ± sem) Bar marked 'b' is significantly different from bar marked 'a'.

6.3.1.5 Aversive visual/pleasant visual combination

As shown in Table 6.1, there was a significantly reduced distance from the stimulus location during the presentation of the quoll/marshmallow combination than in the pre- ($p = 0.01$) or post-test (*p* = 0.01) period (Fig. 6.5 A). While significant heterogeneity was found for activity (*p* = 0.02), no significant differences were found in the *post hoc* tests. The marmosets gave significantly fewer contact calls per two minutes (Fig. 6.5 B), but more mobbing/alarm calls (Fig. 6.5 C), in the test period than in the pre- (*p* = 0.003 and *p* = 0.01, respectively) and post-test (*p* = 0.01 and *p* = 0.01, respectively) period. The marmosets looked down significantly less frequently during the test period than the pre- (*p* = 0.02) and post-test (*p* = 0.01) period (Fig. 6.5 D).

Five of the 11 marmosets did not retrieve the marshmallow. A sixth individual took over a minute (61.75 secs) to retrieve the food.

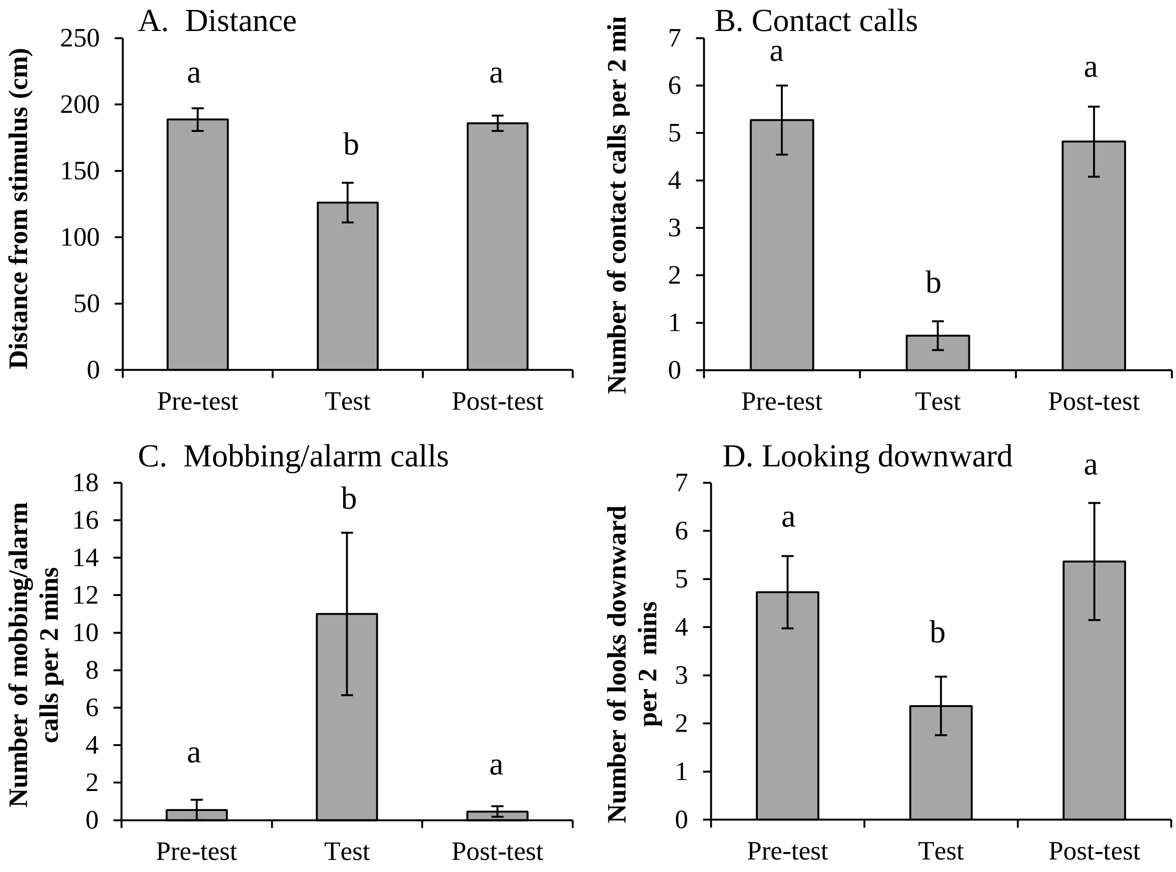


Figure 6.5. Comparison of responses in the pre-test, test and post-test periods: aversive visual/pleasant visual (quoll/marshmallow) combination (2 mins). A – distance from the stimulus (cm), B – contact calls, C – mobbing/alarm calls, D – looks downward (means ± sem). Bars marked 'b' are significantly different from those marked 'a'.

6.3.1.6 Aversive visual/pleasant visual/aversive auditory combination

As shown in Figure 6.6 A, the marmosets had a significantly closer mean distance from the quoll position in the test period than either the pre- (p = 0.01) or post-test (p = 0.01) period.

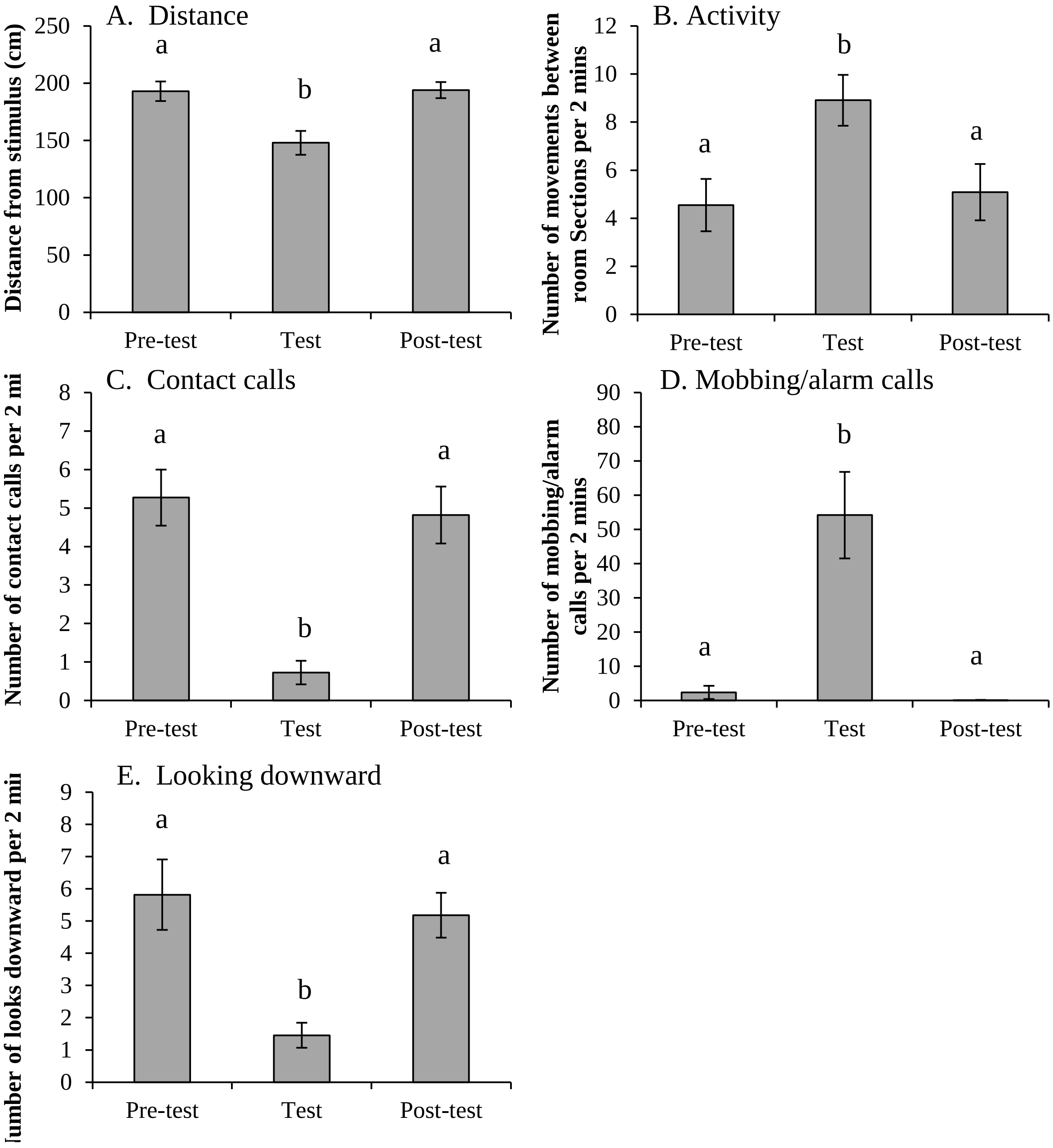


Figure 6.6. Comparison of responses in the pre-test, test and post-test periods: aversive visual/pleasant visual/aversive auditory (quoll/marshmallow/leopard growl) combination (2 mins). A – distance from the stimulus (cm), B – activity , C – contact calls, D – mobbing/alarm calls, E – looks downward (means ± sem). Bars marked 'b' are significantly different from those marked 'a'.

Mean activity was higher in the test period than in the pre- (p = 0.001) or post-test (p = 0.004) period (Fig. 6.6 B, above). The number of contact calls per two minutes was lower, but the mean number of mobbing/alarm calls per two minutes was higher, in the test period than in the pre- (p = 0.003 and p = 0.02, respectively) or post-test (p = 0.003 and p = 0.02, respectively) period (Fig. 6.6 C and D, respectively). The marmosets also looked down less often during the presentation of the combination than they did in the pre- (p = 0.01) and post-test (p = 0.01) period (Fig. 6.6 E).

Four of the five marmosets that did not retrieve the marshmallow during the aversive visual/pleasant visual combination again did not retrieve it. A fifth marmoset took well over a minute (114.81 secs) to retrieve the food.

6.3.2 Comparison of responses to the conflicting combinations and the individually presented stimuli

First-minute results of combination trials were compared with results of respective individually presented stimuli and are reported below (Sections 6.3.2.1 to 6.3.2.6). The first and second minutes of the test period of each combination were also compared; these results are shown in Appendix IX. To summarise, six significant differences were found: distance from the marshmallow/leopard growl combination increased in the second minute (p = 0.01), looking down during the presentation of the marshmallow odour/leopard growl combination increased in the second minute (p = 0.01), looking at the quoll stimulus (p = 0.01) and the number of mobbing/alarm calls made (p = 0.01) during the presentation of the quoll/marshmallow combination decreased in the second minute, and in response to the quoll/marshmallow/leopard growl combination distance from the combination increased (p = 0.04) but mobbing/alarm calls decreased in the second minute (p = 0.01).

The pre- and post-test results were compared between combinations and respective individually presented stimuli; these are reported in Appendix X. No significant differences were found in the pre-test comparisons. Only one significant result was found in the post-test comparisons: mean distance between the quoll/marshmallow/leopard growl combination and the combination of the two conflicting visual stimuli (repeated measures ANOVA, $F = 4.84$, $p = 0.02$). Bonferroni pairwise *post hoc* comparison tests found that mean distance in the post-test of the combination was significantly greater than after the presentation of the quoll alone ($p = 0.05$).

The comparison of the responses to the individually presented stimuli relevant to each combination are also shown in the tables in this section as these results may be slightly different to those presented in Chapter 4 due to the removal of one marmoset's responses from the data set. These results also provide a reference point when the response to the combination is not significantly different from the response to either stimulus presented alone, but the responses to the individual stimuli are significantly different.

6.3.2.1 Comparison of responses to the aversive visual/pleasant auditory combination and the stimuli presented alone

The results of the test-period comparisons between the aversive visual/pleasant auditory (quoll/marmoset food-related calls) combination and the aversive visual (quoll) and pleasant auditory (marmoset food-related calls) presented individually shown in Table 6.2. Mean distance (Fig. 6.7A), closest distance, latency to approach (Fig. 6.7B) and number of looks at the stimulus (Fig. 6.7E) were compared only between the combination and the visual stimulus, as these behavioural responses could not be scored for the auditory stimulus.

Table 6.2. Test-period comparison of the responses to the aversive visual/pleasant auditory (quoll/marmoset food-related calls) combination and the individually presented stimuli.

	Main or major effect	Combination versus aversive visual	Combination versus pleasant auditory	Aversive visual versus pleasant auditory
Mean distance from stimulus (cm)	–	**t = 3.62** **p = 0.01**	–	–
Closest distance to stimulus (cm)	–	t = -0.03 p = 0.98	–	–
Latency to approach (secs)	–	**Z = -2.40** **p = 0.02**	–	–
Activity per min	X^2 = 0.63 p = 0.73	–	–	–
Number of contact calls per min	X^2 = 2.89 p = 0.24	–	–	–
Number of mobbing/alarm calls per min	**X^2 = 20.60** **$p \leq 0.001$**	**Z = -2.94** **p = 0.003**	**Z = -2.37** **p = 0.02**	**Z = -2.93** **p = 0.003**
Latency to vocalise (secs)	**X^2 = 17.02** **$p \leq 0.001$**	**Z = -2.29** **p = 0.02**	**Z = -2.67** **p = 0.01**	**Z = -2.93** **p = 0.003**
Number of looks upward per min	X^2 = 0.21 p = 0.90	–	–	–
Number of looks downward per min	**X^2 = 12.05** **p = 0.002**	Z = -1.58 p = 0.11	Z = -1.43 p = 0.15	**Z = -2.95** **p = 0.003**
Number of looks at the stimulus per min	–	**Z = -2.32** **p = 0.02**	–	–

As shown in Table 6.2, the mean distance (cm) (Fig. 6.7 A) from the aversive visual/pleasant auditory combination was significantly different (staying further away) from the mean distance from the quoll presented on its own (p = 0.01). Figure 6.8 tracks the marmosets' distance (cm) over time (5-second intervals) and shows that, for the entire test minute the marmosets maintained a greater distance from the combined stimuli than from the quoll alone, even though the auditory stimulus referred to a pleasant context. The addition of the marmoset food-related calls increased the latency to approach (seconds) (Fig. 6.7 B) in comparison with the quoll presented alone (p = 0.02).

The number of mobbing/alarm calls per minute was lower during the presentation of the conflicting combination than of the quoll alone (p = 0.003), but higher than the marmoset food-related calls alone (p = 0.02) (Fig. 6.7 C).

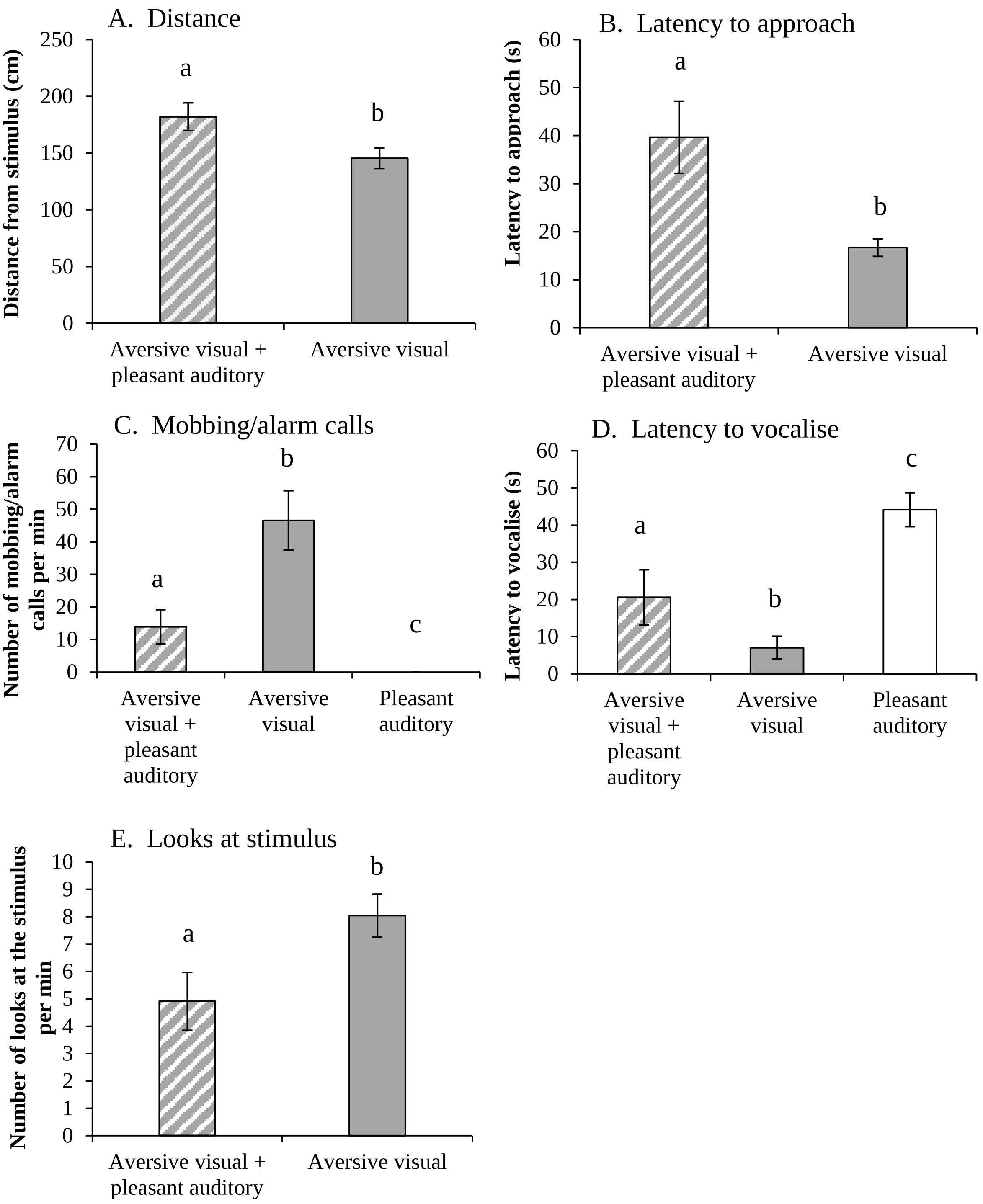


Figure 6.7. Comparison of responses during the test period: aversive visual/pleasant auditory (quoll/marmoset food-related calls) combination and individually presented stimuli (1 min). A – distance from the stimulus (cm), B – latency to approach (seconds), C – mobbing/alarm calls, D – latency to vocalise (secs), E – looks at the visual stimulus (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’, and ‘c’ is significantly different from both ‘a’ and ‘b’. The marmoset food-related calls were not relevant for the distance, latency to approach and looks at stimulus measurements and were thus not scored.

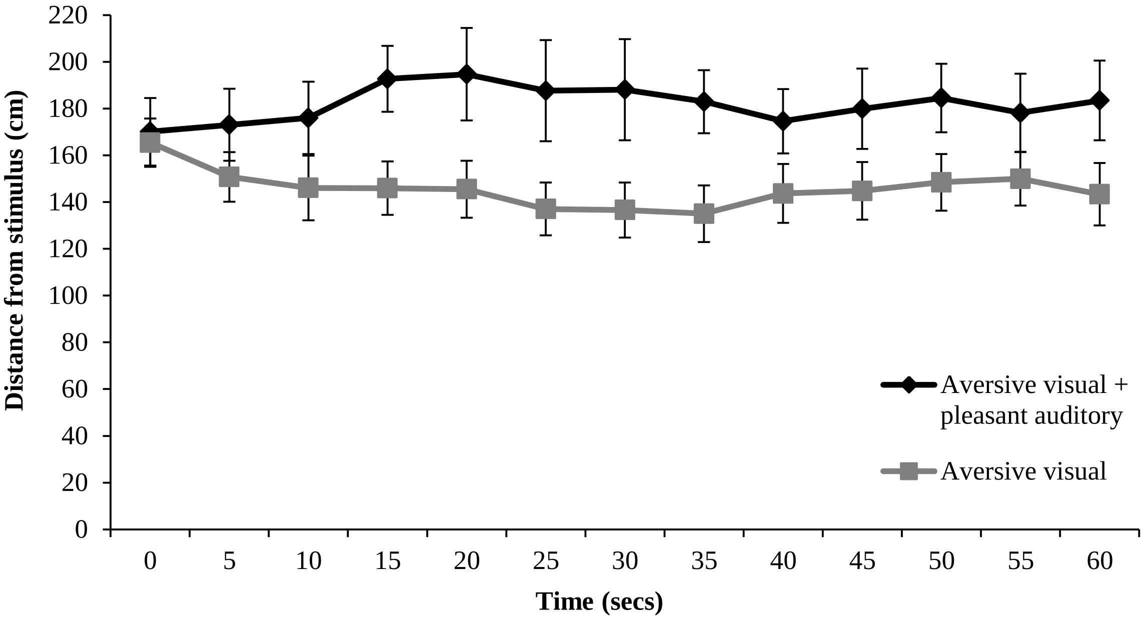


Figure 6.8. Distance (cm) over time (5-second intervals; test period) from the aversive visual/pleasant auditory (quoll/marmoset food-related calls) combination and the quoll alone (means ± sem). Black line (♦ symbols) – mean distance from the combination. Dark-grey line (□ symbols) – mean distance from the quoll alone.

Results for latency to vocalise (Fig. 6.7 D) in response to the two combined stimuli were significantly different from latency to vocalise when wither stimulus was presented alone: the marmosets took longer to vocalise to the combination than in response to the quoll (*p* = 0.02) or to the marmoset food-related calls alone (*p* = 0.01).

The marmosets looked at the quoll less often when it was presented together with the food-related calls (*p* = 0.02) (Fig. 6.7 E) than when it was presented alone. Although significant treatment effects were found for the number of looks downward (*p* = 0.002), *post hoc* analysis found no significant difference between the combination and either of the two stimuli presented alone; only the aversive visual and pleasant auditory stimuli were significantly different from each other (Table 6.2) as reported in Chapter 4.

6.3.2.2 Comparison of responses to the pleasant visual/aversive auditory combination and the stimuli presented alone

Table 6.3 shows the results of the comparisons of the test period of the marshmallow/leopard growl combination and the marshmallow and leopard growl presented alone.

Table 6.3. Test-period comparison of the responses to the pleasant visual/aversive auditory (marshmallow/leopard growl) combination and the individually presented stimuli.

	Main or major effect	Combination versus pleasant visual	Combination versus aversive auditory	Pleasant visual versus aversive auditory
Mean distance from stimulus (cm)	–	$t = -0.55$ $p = 0.59$	–	–
Closest distance to stimulus (cm)	–	$Z = -0.37$ $p = 0.72$	–	–
Latency to approach (secs)	–	$Z = -1.42$ $p = 0.16$	–	–
Activity per min	**$F_{(2,20)} = 3.50$** **$p = 0.05$**	$p = 1.00$	$p = 0.07$	$p = 0.20$
Number of contact calls per min	$X^2 = 3.83$ $p = 0.15$	–	–	–
Number of mobbing/alarm calls per min	**$X^2 = 11.23$** **$p = 0.004$**	**$Z = -2.70$** **$p = 0.01$**	$Z = -0.68$ $p = 0.50$	**$Z = -2.05$** **$p = 0.04$**
Number of food-related calls per min	**$X^2 = 9.85$** **$p = 0.01$**	$Z = -1.35$ $p = 0.18$	$Z = -1.83$ $p = 0.07$	**$Z = -2.52$** **$p = 0.01$**
Latency to vocalise (secs)	$F_{(2,20)} = 0.94$ $p = 0.41$	–	–	–
Number of looks upward per min	$X^2 = 2.25$ $p = 0.33$	–	–	–
Number of looks downward per min	$X^2 = 2.92$ $p = 0.23$	–	–	–
Number of looks at the stimulus per min	–	$t = -1.57$ $p = 0.15$	–	–

Overall, responses to the marshmallow/leopard growl combination appeared to be largely similar to responses to either stimulus presented alone (Table 6.3). However, the marmosets gave fewer mobbing/alarm calls in response to the combined stimuli than to the marshmallow alone ($p = 0.01$) (Fig. 6.9). Significant treatment difference was found for activity scores and number of food-related calls produced per minute, but *post hoc* differences were found only between the stimuli presented alone.

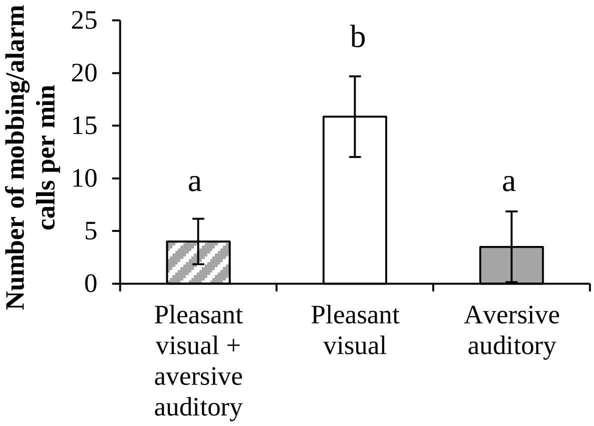


Figure 6.9. Comparison of responses during the test period: pleasant visual/aversive auditory (marshmallow/leopard growl) combination and individually presented stimuli (1 min) – mobbing/alarm calls (means ± sem). Bars marked ‘a’ are significantly different from bars marked ‘b’.

6.3.2.3 Comparison of responses to the aversive olfactory/pleasant auditory combination and the stimuli presented alone

The results comparing test periods of the aversive olfactory/pleasant auditory (odour of cat faeces/marmoset food-related calls) combination with the stimuli presented separately, aversive olfactory (odour of cat faeces) and pleasant auditory (marmoset food-related calls), are shown in Table 6.4. Closest distance, latency to approach and number of looks by the marmosets at the stimulus were not scored for either the combined or individually presented stimuli as these scores did not apply to these stimuli. Furthermore, mean distance was relevant only for the olfactory stimuli.

The only significant difference found was in the number of mobbing/alarm calls (Table 6.4). The marmosets gave fewer mobbing/alarm calls per minute during the presentation of the aversive olfactory/pleasant auditory combination than they did in response to the faecal odour alone (p = 0.04) (Fig. 6.10).

Table 6.4. Test-period comparison of the responses to the aversive olfactory/pleasant auditory (odour of cat faeces/marmoset food-related calls) combination with the individually presented stimuli.

	Main or major effect	Combination versus aversive olfactory	Combination versus pleasant auditory	Aversive olfactory versus pleasant auditory
Mean distance from stimulus (cm)	–	$t = 0.80$ $p = 0.44$	–	–
Activity per min	$F_{(2,20)} = 0.28$ $p = 0.76$	–	–	–
Number of contact calls per min	$X^2 = 4.47$ $p = 0.11$	–	–	–
Number of mobbing/alarm calls per min	**$X^2 = 9.50$** **$p = 0.01$**	**$Z = -2.03$** **$p = 0.04$**	$Z = -1.00$ $p = 0.32$	**$Z = -2.03$** **$p = 0.04$**
Latency to vocalise (secs)	$F_{(2,20)} = 1.52$ $p = 0.24$	–	–	–
Number of looks upward per min	$X^2 = 1.56$ $p = 0.46$	–	–	–
Number of looks downward per min	$X^2 = 1.85$ $p = 0.40$	–	–	–

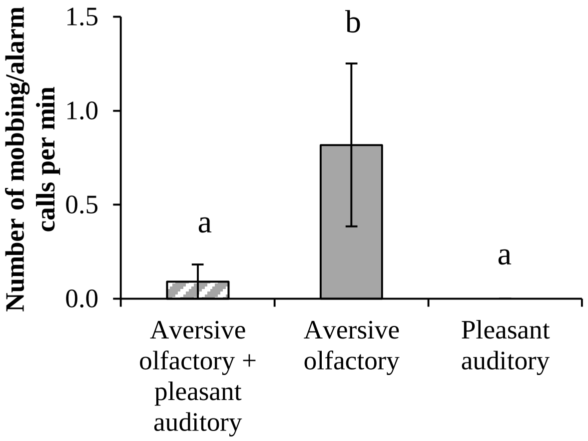


Figure 6.10. Comparison of responses during the test period: aversive olfactory/pleasant auditory (odour of cat faeces/marmoset food-related calls) combination and individually presented stimuli (1 min) – mobbing/alarm calls (means ± sem). Bars marked 'a' are significantly different from bars marked 'b'.

It is also worth noting that mean distance (cm) from the olfactory component of the combination over time (5-second intervals) closely matched their distance at every point from that recorded in response to the faecal odour alone.

6.3.2.4 Comparison of responses to the pleasant olfactory/aversive auditory combination and the stimuli presented alone

The results of the comparisons of the test periods are presented in Table 6.5.

Table 6.5. Test-period comparison of the responses to the pleasant olfactory/aversive auditory (marshmallow odour/leopard growl) combination and the individually presented stimuli.

	Main or major effect	Combination versus pleasant olfactory	Combination versus aversive auditory	Pleasant olfactory versus aversive auditory
Mean distance from stimulus (cm)	–	$t = 1.82$ $p = 0.10$	–	–
Activity per min	**$F_{(2,20)} = 5.92$** **$p = 0.01$**	**$p = 0.01$**	$p = 0.06$	$p = 1.00$
Number of contact calls per min	$X^2 = 0.05$ $p = 0.98$	–	–	–
Number of mobbing/alarm calls per min	$X^2 = 1.88$ $p = 0.39$	–	–	–
Number of food-related calls per min	**$X^2 = 6.40$** **$p = 0.04$**	$Z = -1.16$ $p = 0.25$	$Z = -1.34$ $p = 0.18$	**$Z = -2.21$** **$p = 0.03$**
Latency to vocalise (secs)	$F_{(2,20)} = 1.52$ $p = 0.24$	–	–	–
Number of looks upward per min	$X^2 = 1.72$ $p = 0.42$	–	–	–
Number of looks downward per min	$F_{(2,20)} = 2.23$ $p = 0.13$	–	–	–

As shown in Table 6.5, the marmosets had a significantly higher activity score per minute (Fig. 6.11) during the presentation of this combination than they did during the presentation of the pleasant olfactory stimulus alone ($p = 0.01$). There was a strong trend for higher activity in response to the combination than in response to the leopard growl alone (Table 6.5). Significant heterogeneity was found for the number of food-related calls per minute, but *post hoc* tests revealed that the significant difference was between the individually presented stimuli rather than the combination.

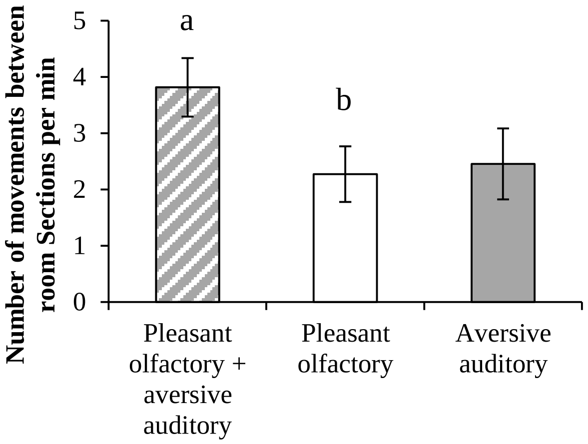


Figure 6.11. Comparison of responses during the test period: pleasant olfactory/aversive auditory (marshmallow odour/leopard growl) combination and individually presented stimuli (1 min) – activity (means ± sem). Bar marked ‘a’ is significantly different from bar marked ‘b’.

6.3.2.5 Comparison of responses to the aversive visual/pleasant visual combination and the stimuli presented alone

The results of the comparisons of the combined and individually presented visual stimuli (aversive visual – quoll; pleasant visual – marshmallow) are shown in Table 6.6.

Number of looks at stimulus during the combination presentation was separated by analysing specifically the looks at the aversive visual and the looks at the pleasant visual stimuli. These scores were then compared only to the responses to the relevant visual stimulus presented alone.

As shown in Table 6.6, significant differences were found only between the responses to the combination and the marshmallow on its own: number of mobbing/alarm calls (p = 0.02), number of food-related calls (p = 0.02) and number of looks at the stimulus (p = 0.003) per minute, as discussed below (Fig. 6.12).

Table 6.6. Test-period comparison of the responses to the aversive visual/pleasant visual (quoll/marshmallow) combination and the individually presented stimuli.

	Main or major effect	Combination versus aversive visual	Combination versus pleasant visual	Aversive visual versus pleasant visual
Mean distance from stimulus (cm)	**X^2 = 11.64** **p = 0.003**	Z = -1.69 p = 0.09	Z = -1.33 p = 0.18	**Z = -2.93** **p = 0.003**
Closest distance to stimulus (cm)	**X^2 = 14.73** **p = 0.001**	Z = -1.87 p = 0.06	Z = -1.60 p = 0.11	**Z = -2.93** **p = 0.003**
Latency to approach (secs)	X^2 = 5.09 p = 0.08	–	–	–
Activity per min	$F_{(2,20)}$ = 0.93 p = 0.41	–	–	–
Number of contact calls per min	**X^2 = 7.18** **p = 0.03**	Z = 0.00 p = 1.00	Z = -1.38 p = 0.17	**Z = -2.23** **p = 0.03**
Number of mobbing/alarm calls per min	**X^2 = 12.18** **p = 0.002**	Z = -1.78 p = 0.08	**Z = -2.27** **p = 0.02**	**Z = -2.93** **p = 0.003**
Number of food-related calls per min	**X^2 = 12.67** **p = 0.002**	Z = -1.00 p = 0.32	**Z = -2.31** **p = 0.02**	**Z = -2.52** **p = 0.01**
Latency to vocalise (secs)	X^2 = 4.23 p = 0.12	–	–	–
Number of looks upward per min	X^2 = 5.62 p = 0.06	–	–	–
Number of looks downward per min	**X^2 = 6.40** **p = 0.04**	Z = -1.27 p = 0.21	Z = -1.13 p = 0.26	**Z = -2.38** **p = 0.02**
Number of looks at the stimulus per min	**X^2 = 18.82** **$p \leq 0.001$**	Z = -1.34 p = 0.18	**Z = -2.94** **p = 0.003**	**Z = -2.59** **p = 0.01**

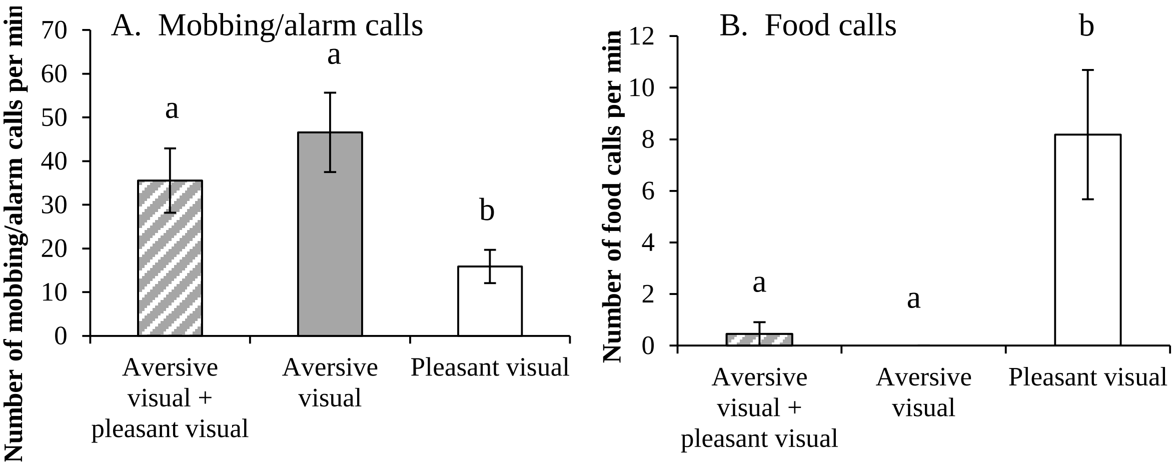


Figure 6.12. Comparison of responses during the test period: aversive visual/pleasant visual (quoll/marshmallow) combination and individually presented stimuli (1 min). A – mobbing/alarm calls, B – food-related calls (means ± sem). Bars marked ‘a’ are significantly different from bars marked ‘b’.

6.3.3.5.1 Vocalisations: The marmosets made more mobbing/alarm calls (Fig. 6.12 A) but fewer food-related calls (Fig. 6.12 B) in response to the combination than they did to the marshmallow presented on its own.

6.3.3.5.2 Looks at stimulus: The marmosets looked at the quoll during the presentation of the combination a mean of 6.09 (± 0.80) times per min; this was not significantly different from the presentation of this stimulus on its own (8.05 ± 0.78 times per min) (Table 6.6). However, they looked at the marshmallow less often when it was presented together with the quoll (1.00 ± 0.40 times per min) than they did when it was presented alone (5.59 ± 0.55 times per min) ($p \leq 0.001$). During the combination presentation the marmosets looked at the aversive visual component more often than they did the pleasant visual component ($p = 0.003$).

6.3.3.5.3 Distance: Mean distance did not differ significantly between the combined and individually presented visual stimuli, even though the two stimuli presented alone were significantly different ($p = 0.003$; as reported in Chapter 4 the mean distance from the quoll was 145.36 ± 8.24 cm and from the marshmallow was 80.36 ± 11.77 cm). The mean distance scored in response to the presentation of the combined stimuli was about the midpoint of the mean distances scored for the quoll and marshmallow. This is shown clearly in Figure 6.13 below.

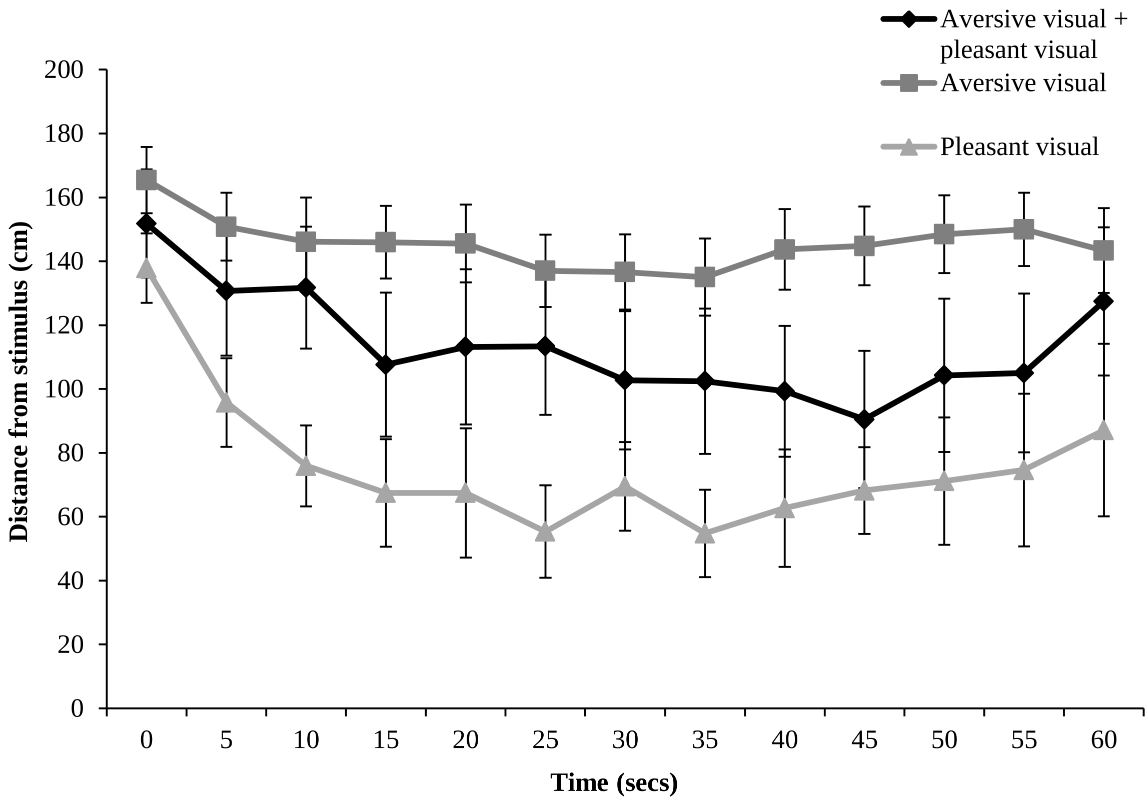


Figure 6.13. Distance (cm) over time (5-second intervals; test period) from the aversive visual/pleasant visual (quoll/marshmallow) combination and the visual stimuli presented alone (means ± sem). Black line (♦ symbols) – mean distance from the combined conflicting visual stimuli; dark-grey line (□ symbols) – mean distance from the quoll alone; light-grey line (Δ symbols) – mean distance from the marshmallow alone.

6.3.2.6 Comparison of responses to the aversive visual/pleasant visual combination and the stimuli presented alone

Table 6.7 shows the results of the statistical comparisons between the triple combination and the individually presented stimuli.

Again, the number of looks at the stimulus was separated into scores for looking at the quoll and the marshmallow and compared only with the relevant individually presented stimuli. Statistical comparisons of the individual stimuli are not included here (they are shown in Tables 6.2 and 6.5).

Table 6.7. Test-period comparisons of the responses to the aversive visual/pleasant visual/aversive auditory (quoll/marshmallow/leopard growl) combination and the individually presented stimuli.

	Main or major effect	Combination versus aversive visual	Combination versus pleasant visual	Combination versus aversive auditory
Mean distance from stimulus (cm)	**$F_{(2,20)} = 12.48$** **$p \leq 0.001$**	$p = 1.00$	**$p = 0.04$**	–
Closest distance to stimulus (cm)	**$X^2 = 14.28$** **$p = 0.001$**	**$Z = -1.91$** **$p = 0.05$**	$Z = -1.48$ $p = 0.14$	–
Latency to approach (secs)	$X^2 = 2.18$ $p = 0.34$	–	–	–
Activity per min	**$F = 3.57$** **$p = 0.03$**	$p = 1.00$	$p = 1.00$	$p = 0.12$
Number of contact calls per min	**$X^2 = 9.35$** **$p = 0.03$**	$Z = -0.96$ $p = 0.34$	$Z = -0.34$ $p = 0.73$	$Z = -1.49$ $p = 0.14$
Number of mobbing/alarm calls per min	**$X^2 = 19.47$** **$p \leq 0.001$**	**$Z = -2.67$** **$p = 0.01$**	$Z = -1.82$ $p = 0.07$	**$Z = -2.05$** **$p = 0.04$**
Number of food-related calls per min	**$X^2 = 19.89$** **$p \leq 0.001$**	$Z = -1.00$ $p = 0.32$	**$Z = -2.43$** **$p = 0.02$**	$Z = -1.00$ $p = 0.32$
Latency to vocalise (secs)	**$X^2 = 13.69$** **$p = 0.003$**	$Z = -1.42$ $p = 0.16$	$Z = -1.78$ $p = 0.08$	**$Z = -2.67$** **$p = 0.01$**
Number of looks upward per min	$X^2 = 2.87$ $p = 0.41$	–	–	–
Number of looks downward per min	**$X^2 = 13.93$** **$p = 0.003$**	$Z = 0.00$ $p = 1.00$	**$Z = -1.97$** **$p = 0.05$**	**$Z = -2.50$** **$p = 0.01$**
Number of looks at the stimulus per min	**–**	$Z = -1.78$ $p = 0.08$	**$Z = -2.96$** **$p = 0.003$**	**–**

6.3.3.6.1 Distance: Mean distance (cm) from the triple combination was significantly greater than mean distance scored in response to the marshmallow ($p = 0.04$) (Fig. 6.14 A). Figure 6.15 shows mean distance over time. However, the closest distance (cm) of approach was significantly closer in response to the combination than to the quoll alone ($p = 0.05$) (Fig. 6.14 B).

6.3.3.6.2 Vocalisations: As Figure 6.14 C (below) shows, the marmosets gave fewer mobbing/alarm calls during the presentation of the triple combination than during the presentation of the quoll ($p = 0.01$), but more than to the leopard growl ($p = 0.04$). Similarly, the marmosets gave fewer food-related calls in response to the combination than they did to the marshmallow ($p = 0.02$) (Fig. 6.14 D).

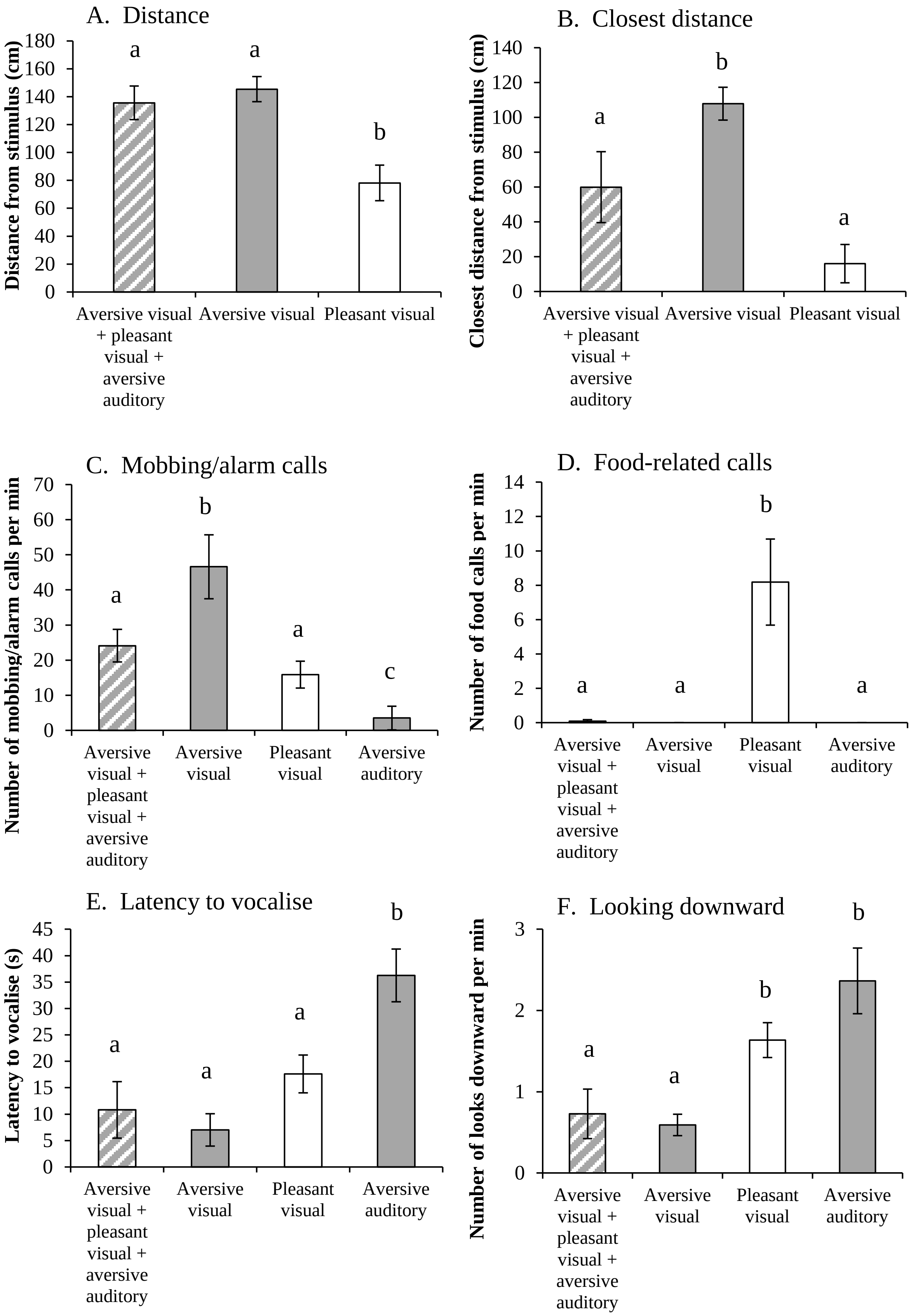


Figure 6.14. Comparison of responses during the test period: triple combination (quoll/marshmallow/leopard growl) and individually presented stimuli. A – distance from the stimulus (cm), B – closest distance (cm), C – mobbing/alarm calls, D – food-related calls, E – latency to vocalise (secs), F – looks downward. Bars marked ‘a’ are significantly different from those marked ‘b’, and ‘c’ is significantly different from both ‘a’ and ‘b’.

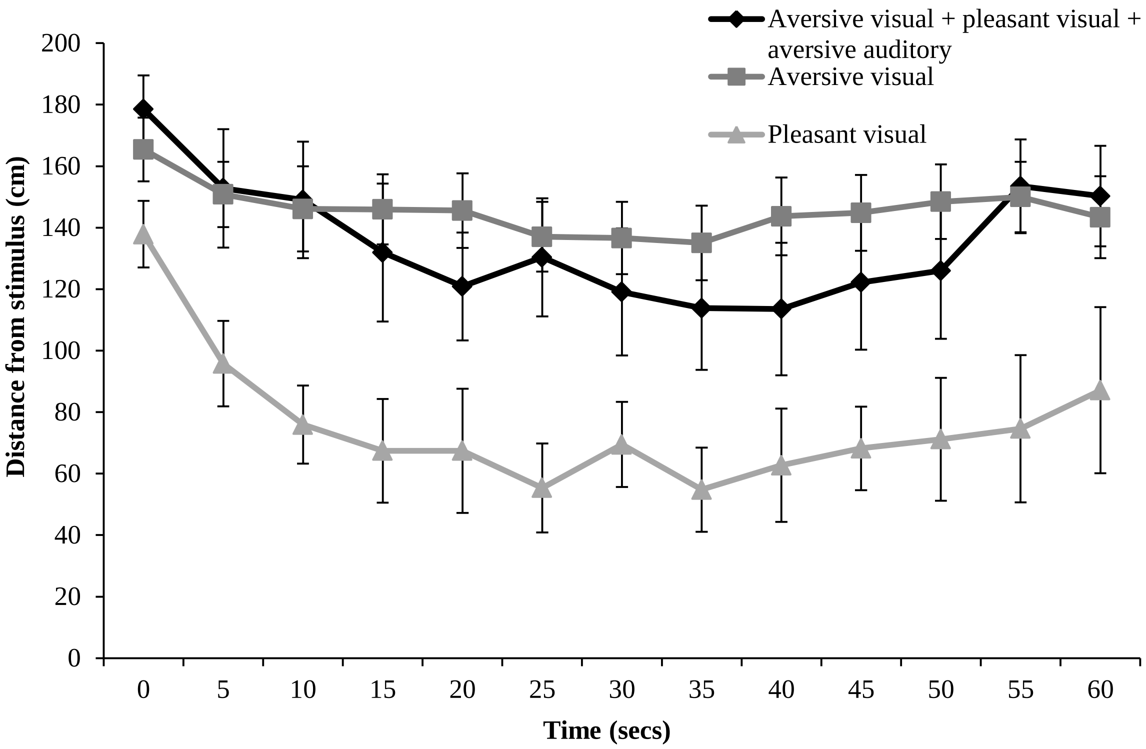


Figure 6.15. Distance (cm) over time (5-second intervals; test period) from the triple combination (quoll/marshmallow/leopard growl) and the visual stimuli presented alone (means ± sem). Black line (♦ symbols) represents results obtained from the triple combination (including the leopard growl). Dark-grey line (□ symbols) shows distances from the quoll alone. Light-grey line (Δ symbols) shows distances to the marshmallow alone.

The latency to vocalise when the marmosets were presented with the combination was significantly shorter than the latency to vocalise in response to the leopard growl alone ($p = 0.01$) (Fig. 6.14 E).

<ins>6.3.3.6.3 Direction of looking</ins>: The marmosets looked down less frequently during the presentation of the triple combination than to the marshmallow ($p = 0.05$) and leopard growl ($p = 0.01$) alone (Fig. 6.14 F). The marmosets looked at the marshmallow less often (0.36 ± 0.20 times per min) when it was in combination with the aversive stimuli than when it was presented individually (5.59 ± 0.55 times per min) ($p = 0.003$). During the combination presentation the marmosets looked at the quoll more often than the marshmallow ($p = 0.003$).

6.3.3 Comparison of responses to the combinations

The combinations tested were compared for mean distance (cm), closest distance (cm), latency to approach (seconds), activity per minute, number of mobbing/alarm calls per minute, latency to vocalise (seconds) and number of looks downward per minute across the pre-test, test and post-test periods where applicable. The pre- and post-test comparisons found no significant differences (repeated measures ANOVA $F_{(5,50)}$ values ranged from 1.12 to 2.22 with corresponding p values ranging from 0.36 to 0.07; Friedman's test X^2 values ranged from 0.65 to 7.39 with corresponding p values ranging from 0.97 to 0.19). The statistical results of the test-period comparisons are shown in Table 6.8.

6.3.3.1 Distance and approach

As can be seen in Table 6.8, significant treatment difference was found for mean distance and closest distance. All conflicting combinations compared were significantly different from one another for mean distance (cm). Only the comparison of the combined visual stimuli with the triple combination was not significantly different for mean closest distance. Figure 6.16 shows distance (cm) over time (5-second intervals) for the four conflicting combinations involving a visual stimulus. The mean distance from the aversive visual + aversive auditory (Experiment 3) is also included in Figure 6.16, as a reference point for a strong avoidance response. Mean distance (cm) from the related aversive combination (quoll/leopard growl) was compared to the conflicting stimuli (heterogeneity: Friedman's test, $X^2 = 28.44$, $p \leq 0.001$); it was significantly greater than the distance from the marshmallow/leopard growl combination (Wilcoxon signed-rank, $Z = -2.58$, $p = 0.01$) and the combined visual stimuli (quoll/marshmallow) (Wilcoxon signed-rank, $Z = -2.05$, $p = 0.04$). It was not significantly different from the quoll/marmoset food-related calls combination (Wilcoxon signed-rank, $Z = -0.89$, $p = 0.37$) or the triple combination (Wilcoxon signed-rank, $Z = -1.42$, $p = 0.16$).

Table 6.8. Test-period comparisons of the conflicting combinations. '-' indicates that statistical tests were not applicable.

	Main or major effect	Aversive visual/pleasant auditory versus aversive olfactory/pleasant auditory	Aversive visual/pleasant auditory versus aversive visual/pleasant visual	Pleasant visual/aversive auditory versus pleasant olfactory/aversive auditory	Pleasant visual/aversive auditory versus aversive visual/pleasant visual	Pleasant visual/aversive auditory versus aversive visual/pleasant visual/aversive auditory	Aversive visual/pleasant visual versus aversive visual/pleasant visual/aversive auditory
Mean distance from stimulus (cm)	**X^2 = 24.27** **$p \leq 0.001$**	–	**Z= -2.67** **p = 0.01**	–	**Z = -1.96** **p = 0.05**	**Z = -2.93** **p = 0.003**	**Z = -2.31** **p = 0.02**
Closest distance to stimulus (cm)	**X^2 = 18.50** **$p \leq 0.001$**	–	**Z = -2.55** **p = 0.01**	–	**Z = -2.71** **p = 0.01**	**Z = -2.12** **p = 0.03**	Z = -0.42 p = 0.67
Latency to approach (secs)	$F_{(5,50)}$ = 0.64 p = 0.67	–	–	–	–	–	–
Activity per 2 mins	X^2 = 7.35 p = 0.06	–	–	–	–	–	–
Number of mobbing/alarm calls per 2 mins	**X^2 = 35.13** **$p \leq 0.001$**	**Z = -2.38** **p = 0.02**	**Z = -2.43** **p = 0.02**	Z = -1.54 p = 0.12	**Z = -2.67** **p = 0.01**	**Z = -2.67** **p = 0.01**	**Z = -1.99** **p = 0.05**
Latency to vocalise (secs)	**X^2 = 14.28** **$p \leq 0.001$**	Z = -1.84 p = 0.07	Z = -1.48 p = 0.14	Z = -0.30 p = 0.77	**Z = -2.55** **p = 0.01**	**Z = -2.50** **p = 0.01**	Z = -0.46 p = 0.65
Number of looks downward per 2 mins	**X^2 = 29.95** **$p \leq 0.001$**	**Z = -2.50** **p = 0.01**	Z = -1.16 p = 0.25	Z= -1.67 p = 0.10	**Z = -2.59** **p = 0.01**	**Z = -2.82** **p = 0.01**	Z = -1.63 p = 0.10
Number of looks at the aversive visual stimulus per 2 mins	$F_{(2,20)}$ = 0.21 p = 0.65	–	–	–	–	–	–
Number of looks at the pleasant visual stimulus per 2 mins	**X^2 = 16.67** **$p \leq 0.001$**	–	–	–	**Z = -2.77** **p = 0.01**	**Z = -2.94** **p = 0.003**	Z = -1.80 p = 0.07

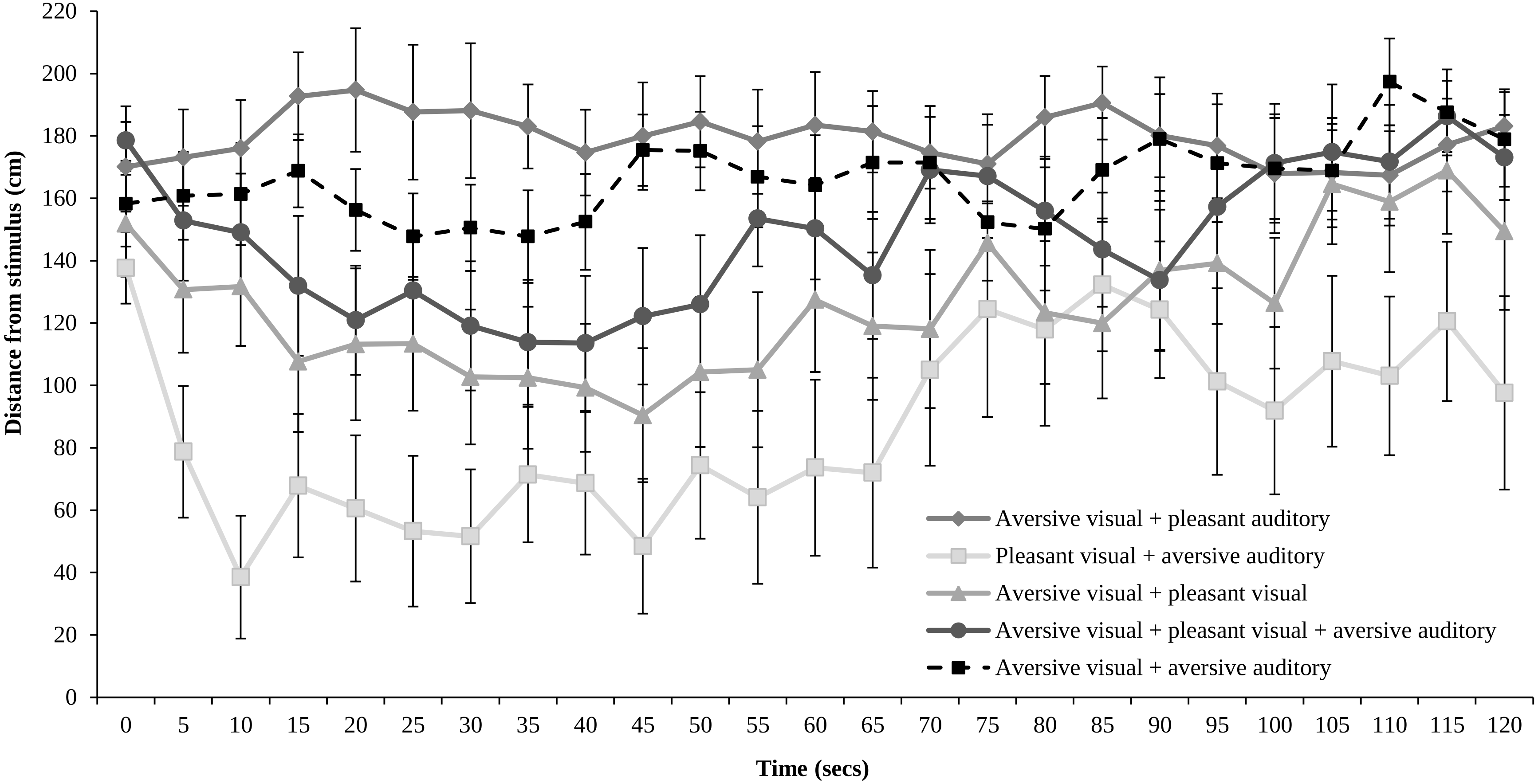


Figure 6.16. Distance (cm) over time (5-second intervals) from the four conflicting combinations with a visual component (aversive visual = quoll, pleasant visual = marshmallow, aversive auditory = leopard growl, pleasant auditory = marmoset food-related calls) (means ± sem). The results of the aversive visual/aversive auditory combination (Ch. 5), shown by the black dotted line, have also been included as reference point to show how this exclusively aversive combination scored. Mean distance was significantly different between all conflicting combinations (Table 6.8). The aversive combination (quoll/leopard growl) was significantly different from the pleasant visual/aversive auditory (marshmallow/leopard growl) (*p* = 0.01) combination and combined visual stimuli (quoll/marshmallow) (*p* = 0.04).

6.3.3.2 Vocalisations

Table 6.8 shows the statistical results of the comparisons made between the vocal responses to the conflicting combinations. Comparisons made between combinations for number of mobbing/alarm calls were significantly different except when the marshmallow/leopard growls and marshmallow odour/leopard growl combinations were compared. The number of mobbing/alarm calls was typically higher when a visual stimulus was present, particularly the quoll, than when a combination consisted of only olfactory and auditory stimuli.

Latency to vocalise was significant different when the marshmallow/leopard growl combination was compared to the combined visual stimuli and the triple combination (p = 0.01 and p = 0.01, respectively); the marmosets vocalised sooner when the quoll was present.

6.3.3.3 Direction of looking

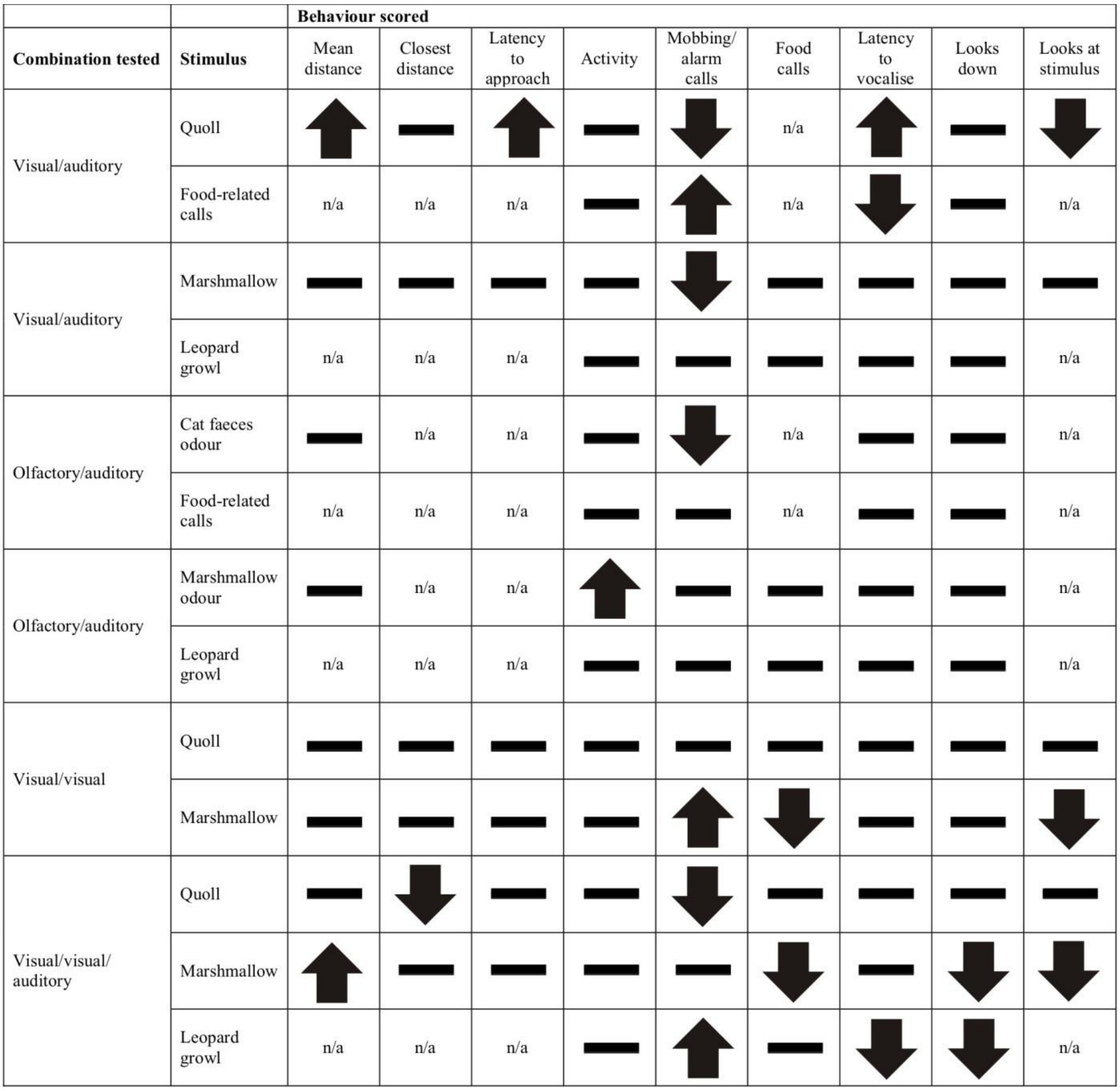
The marmosets looked down less often during the presentation of the quoll/marmoset food-related calls combination than during the presentation of the cat faeces/marmoset food-related calls (p = 0.01). They also looked down more often during the presentation of the marshmallow/leopard growl combination than during the presentation of either the combined visual stimuli (p = 0.01) or the triple combination (p = 0.01) (Table 6.8). There was no difference in the mean number of looks at the quoll when presented in a combination, regardless of other added stimuli (p = 0.65). Results for the pleasant visual stimulus were variable. When the pleasant visual stimulus was presented together with the aversive auditory stimulus, the marmosets looked at it more often than they did when they were in the presence of the aversive visual stimulus, with or without the aversive auditory stimulus (p = 0.003 and p = 0.01, respectively).

6.4 Discussion

The aim of this experiment was to determine whether modality or type was more important in eliciting a response in a conflicting situation. In the previous experiment (Ch. 5), only sensory modality was a factor: the combinations presented were all of the same type (aversive or pleasant). Whether a particular modality was more influential or dominant in eliciting a response changed depending on the modality with which it was presented (e.g. auditory was the stronger influence on behaviour when paired with an olfactory cue, but not when paired with a visual cue), the behavioural response scored (e.g. distance was affected by the visual cue, but vocalisations were affected by the auditory cue) and the type of combination (aversive or pleasant). The experiment presented in this chapter tested a mix of both modalities and type, except in one conflicting combination of visual stimuli in which only type was a factor (quoll/marshmallow). The results show that the marmosets typically responded to both the aversive and pleasant cue within the combination, but which stimulus was dominant in eliciting a response depended on the behaviour being scored. Furthermore, when two equally dominant stimuli were presented (i.e. the combined visual stimuli), the response of the marmosets appeared to be a ‘trade-off’, in which they alternated their response so as to attend to both stimuli. A summary of the findings of the comparisons between the responses to the combination and the stimuli presented alone are presented in Table 6.9.

The results suggest that sensory modality may become more important when conflicting stimuli arise than when related stimuli in different modalities are presented. This further supports the idea that different sensory modalities may convey different information or levels of intensity. For example, when the leopard growl was presented together with the marshmallow, the marmosets responded more to the marshmallow than to the leopard growl (Table 6.2). However, when the same leopard growl was presented together with the marshmallow odour, the marmosets’ response reverted to the fearful behaviour that had been seen when the leopard growl was presented alone (Table 6.4). These findings further support the theory that there may be a hierarchy of sensory modalities influencing a response. In the specific instances described, impact, from strongest to weakest was: visual > auditory > olfactory. However, this potential ranking did not apply to responses to the conflicting triple combination.

Table 6.9. Summary of results of the conflicting combinations. Arrows indicate the direction of change in the responses to the combination from the responses to the individual stimulus (increase or decrease). '-' indicates no change and n/a means the behaviour was not relevant for that stimulus. Number of contact calls and looks upward were not included as there were no changes scored.



		Behaviour scored								
Combination tested	**Stimulus**	Mean distance	Closest distance	Latency to approach	Activity	Mobbing/ alarm calls	Food calls	Latency to vocalise	Looks down	Looks at stimulus
Visual/auditory	Quoll	↑	—	↑	—	↓	n/a	↑	—	↓
	Food-related calls	n/a	n/a	n/a	—	↑	n/a	↓	—	n/a
Visual/auditory	Marshmallow	—	—	—	—	↓	—	—	—	—
	Leopard growl	n/a	n/a	n/a	—	—	—	—	—	n/a
Olfactory/auditory	Cat faeces odour	—	n/a	n/a	—	↓	n/a	—	—	n/a
	Food-related calls	n/a	n/a	n/a	—	—	n/a	—	—	n/a
Olfactory/auditory	Marshmallow odour	—	n/a	n/a	↑	—	—	—	—	n/a
	Leopard growl	n/a	n/a	n/a	—	—	—	—	—	n/a
Visual/visual	Quoll	—	—	—	—	—	—	—	—	—
	Marshmallow	—	—	—	—	↑	↓	—	—	↓
Visual/visual/ auditory	Quoll	—	↓	—	—	↓	—	—	—	—
	Marshmallow	↑	—	—	—	—	↓	—	↓	↓
	Leopard growl	n/a	n/a	n/a	—	↑	—	↓	↓	n/a

The conflicting triple combination was unique in that it involved two aversive stimuli (quoll and leopard growl) and a stimulus that provided elicited an opposing reaction (marshmallow). This combination tested several points: the increased risk perceived when the two aversive stimuli were presented (Ch. 5), the approach-withdrawal effect of the two conflicting visual stimuli, and the seemingly reduced risk of the leopard growl when presented with the marshmallow (as discussed in the previous paragraph). All three stimuli had been shown to affect behaviour strongly, both in previous experiments and in other conflicting combinations tested in this experiment; therefore, it was possible that any of them could dominate in eliciting a response. Indeed, there was no evidence in the responses scored to suggest that there was a hierarchy of these stimuli or modalities. The marmosets' mean distance from the stimulus during the simultaneous presentation of all three stimuli was not significantly different from the mean distance from either the quoll presented alone or the quoll and the leopard growl presented together; however, the closest approach was statistically the same as that seen in response to the marshmallow alone. Furthermore, mean distance from the triple combination was significantly greater than when the two visual stimuli were presented together. This shows that the quoll and leopard growl again modulated the response of the marmosets by indicating an increased threat, although the marshmallow still acted as a strong attractant and its presence encouraged the marmosets to approach, even though they did so very briefly.

The vocalisation results also provided evidence that the three stimuli modulated the responses observed to individually presented stimuli. The marmosets gave fewer mobbing/alarm calls to the triple combination than they did to the quoll alone, but more than they did to the leopard growl alone. There were also fewer mobbing/alarm calls recorded during the conflicting triple combination than when only the two visual stimuli were presented together (quoll/marshmallow combination). Furthermore, the marmosets gave more mobbing/alarm calls to the quoll alone than they did to the marshmallow or leopard growl alone (Ch. 4, Tables 4.4 and 4.11); there were also more mobbing/alarm calls in response to the combined visual stimuli than to the marshmallow/leopard growl combination. The number of food-related calls was significantly lower during the presentation of the triple combination – even though the marshmallow was visible – than in response to the marshmallow alone. The auditory stimulus has been shown throughout this research to reduce the number of vocalisations produced in response. Therefore, these vocalisation findings indicate that all three stimuli (quoll, marshmallow and leopard growl) modulated the response of the marmosets, rather than the stimuli acting in a hierarchy. That is, in the triple combination the quoll still elicited mobbing/alarm vocalisations, the marshmallow still elicited food-related calls, but the presence of the leopard growl reduced the number of these vocalisations from the scores originally produced when the stimuli were presented alone (Ch. 4).

To my knowledge, results reported here may be the first example of a triple combination to test Helfman’s (1989) threat-sensitivity predator-avoidance (TSPA) hypothesis in a conflicting situation. Typically the TSPA is tested using only predatory or aversive stimuli (e.g. Amo *et al*., 2006; Ferrari *et al*., 2008; Smith and Belk, 2001; Zhao *et al*., 2006). In my experiments a range of stimuli were tested, showing that risk perception is lowest when stimuli are presented individually and higher when some of the stimuli are combined. I have confirmed these results by presenting a highly desirable food item, a conflicting stimulus, together with aversive stimuli which may represent different levels of threat. The marmosets responded to both the quoll and leopard growl as threats, but once these stimuli were combined they seemed to represent a higher-level threat. That is, they found the quoll more aversive (measured as distance) when presented with the leopard growl (Ch. 5) than when it was on its own (Ch. 4), even when the marshmallow was also present (this Chapter). The threat that the quoll represented was somewhat dampened when presented together with just the marshmallow. This finding is important also when testing predator recognition in any modality. It highlights the importance of the role of food, if used as enticement, as a factor contributing to and shaping overall responses to any predatory presence.

The degree of risk perceived was particularly evident when comparing the results of mean distances in response to each combination; in order of risk (from least to worst) ranking was: 1) marshmallow alone and, interestingly, marshmallow presented together with the leopard growl, 2) quoll presented together with marshmallow, 3) quoll alone, 4) conflicting triple combination, 5) quoll presented together with the leopard growl, 6) quoll presented together with the marmoset food-related calls. This ranking highlights the attractant value of the marshmallow and the repellent qualities of the combined quoll and leopard growl. However, it was unexpected that a combination of the quoll and marmoset food-related calls would generate the greatest mean distance scored and, by implication, caution. It had been expected that the marmosets would be more inclined to investigate the quoll when the pleasant auditory stimulus was played.

It had been hypothesised that, as perceived risk increased, the marmosets would forgo foraging altogether in order to attend to the threat. The particularly interesting outcome of this experiment was that the marmosets were willing to take seemingly high risks in order to obtain the food item, despite the presence of aversive stimuli – the quoll and the leopard growl – that had been shown to be consistently aversive and fear-inducing throughout all experiments. This behaviour was particularly evident when both stimuli were visual (i.e. the quoll/marshmallow combination), but less evident when the food-based stimulus was an odour. Of the 11 marmosets tested, six retrieved the marshmallow when it was presented together with the quoll, both with and without the addition of the leopard growl, and five did not. That is, six marmosets moved as close as 20 cm towards the quoll (to reiterate, the marshmallow was placed 20 cm away from the quoll) – an animal substantially larger than the marmoset – just in order to retrieve the food. When the quoll was presented individually (Experiment 2, Ch. 4), most marmosets did not come within 100 cm of the quoll, and those that did, did so only very briefly. Of the five marmosets that did not retrieve the marshmallow in the presence of the quoll, three still approached to within 100 cm of the quoll's location. However, they approached the platform from the side that was closer to the marshmallow (showing that they were attracted by the pleasant visual stimulus) as if they wanted to retrieve it but were too anxious about the presence of the quoll. Indeed, even the six marmosets that retrieved the piece of marshmallow showed extreme caution while doing so: they approached and retreated several times, moving in a wide semi-circle in front of the quoll before jumping onto the side of the platform closest to the marshmallow. As they then approached the marshmallow they moved slowly, looking at the quoll repeatedly, with quick glances in between at the marshmallow. When they were finally within touching distance of the marshmallow they continued to move their gaze quickly between the two visual stimuli; after they had retrieved the marshmallow they immediately retreated into the branches. This, again, highlights the approach-withdrawal effect of the two conflicting stimuli, but it does not support my prediction, at least not uniformly, that high risk resulted in full attention to the predator. This was only true in less than half of all marmosets. It may be that the marmosets assessed the level of risk through other cues, such as movement, or lack thereof in this case, as low and were willing to approach closely as the quoll did not, nor ever, move. Other species have been shown to use the predator's behaviour to assess the actual risk of predation (e.g. Columbian black-tailed deer, *Odocoileus hemionus,* Stankowich and Coss, 2006). It is possible that after so many repeat exposures to the quoll, in which nothing adverse had actually happened (i.e. no movement or attack), the marmosets now considered this stimulus to be of lower threat than originally assessed (Experiment 2) and risked approaching. However, not all marmosets retrieved the marshmallow. Furthermore, the cautiousness with which some approached, the speed of retrieval and withdrawal, and the repeated glances at the quoll during approach and retrieval, suggest that the marmosets were still very wary of this aversive visual stimulus.

Many responses to combinations fell about halfway between the scores for response to individual stimuli. For example, mean distance to the quoll and the marshmallow presented together was not significantly different from mean distance to either the quoll or marshmallow presented alone, despite the response to the quoll and marshmallow when presented individually being significantly different (Ch.4). Another example of this type of response was the number of food-related calls given in response to the marshmallow/leopard growl combination: the marmosets gave significantly more food-related calls when the marshmallow was presented on its own than when the leopard growl was presented on its own, but the response to the combination was not significantly different from either individual response. This was also the case when the leopard growl was presented with the marshmallow odour. It suggests that the two conflicting stimuli had a push–pull effect, in which the marmosets were influenced by both. By trying to respond to both stimuli, the marmosets were unable to attend fully to either. These instances could be considered as examples of non-redundant, modulated signalling. However, it is important to note that the modulated classification applies only to these specific examples in the entire suite of responses.

Most multimodal signalling research has focused on only one behavioural context (Partan and Marler, 2005). When only one behaviour is considered, it is easier to determine the classification of a multimodal signal. Multiple behavioural responses, especially in a count of five or more behavioural scores, as shown in my research, may defy signal classification as each behaviour may show a different type of response, e.g. modulation, dominance or independence. For example, as shown in Chapter 4, the marmosets approached both the quoll and the marshmallow when the stimuli were presented individually, but they approached the marshmallow more closely. Therefore, the response to the quoll (stimulus *c*, using the terminology for the different signalling types used in Table 1.1) is *x* and the response to the marshmallow (stimulus *d*) is *y*. However, when the visual stimuli were presented simultaneously, the marmosets approached within a distance that was statistically between both responses. If only distance was considered, it would be assumed that the signal classification was non-redundant and modulated. Typically, modulation of only one response occurs, but in this example both responses were modulated to some degree. However, if the number of mobbing/alarm calls is also considered, the marmosets made the same number of these calls in response to the combination as they did to the quoll presented on its own – an example of dominance. The mixture in types of response (modulation, dominance, etc.) to any one combination was also evident in the results of Experiment 3. Therefore, relying on only one behavioural response to classify a signal (or combination of stimuli) may result in an incorrect classification or underestimating the complexity of possible outcomes. Scoring multiple behavioural responses resulted in a mixture of classifications, and therefore the concept presented by Partan and Marler (1999, 2005) may be usefully applied when limited to only one or a few behavioural responses, although the authors encouraged the use of multiple responses when testing their model.

CHAPTER SEVEN

EXPERIMENT 5: RESPONSES TO AUDITORY CUES FROM THREE DIFFERENT PREDATORS

7.1 Introduction

It has been mentioned in the introductory chapter that the use of vocalisations has been argued to be of little value in testing responses to predatory (aversive) stimuli. Firstly, as Blumstein *et al.* (2008) argued, predator vocalisations are irrelevant in so far as most predators tend to be silent when they hunt. However, as pointed out previously, this is not true of all predators; some especially announce their whereabouts (e.g. mountain lions, *Felis concolor*, Smallwood, 1993; raptors, *Micrastur mirandollei*, Smith, 1969). Secondly, predator vocalisations on their own are said to elicit abnormal behavioural patterns because there is no fixed visual point of origin (Arnold *et al.*, 2008). Thirdly, learning, and experience by association, appears to be more important for auditory recognition of predators than for visual recognition (Berger *et al.*, 2001; Gil-da-Costa *et al.*, 2003). However, the results of Experiments 1 and 2 (Chapters 3 and 4, respectively) have clearly shown that this colony of predator-naive marmosets not only reacted to vocalisations from a variety of predators, but did so in specific ways – not as ‘abnormal’, but rather as typical expressions of fear.

Responses to aversive stimuli can be measured as expressing different levels of fear. Freezing, tonic immobility, hiding, trembling, avoidance, piloerection and fleeing have all been used as measurements of fear responses (Boissy, 1995; Ferrari and Lopes Ferrari, 1990; Masuda *et al.*, 1999; Searcy and Caine, 2003; Stankowich and Blumstein, 2005). There seems to be general agreement that some responses, such as avoidance, generally indicate low-level fear, or indicate anxiety or an initial startle response, while others, such as tonic immobility and trembling, suggest strong levels of fear (Boissy, 1995). All these behavioural responses were observed during the presentation of predator vocalisations in Experiment 1 (Ch. 3). Such varied responses suggest that the vocalisations of predators are of more than just marginal interest.

The experiment presented in this chapter is the result of following up on anecdotal observations made during the identification of effective auditory stimuli (Ch. 3). In Experiment 1, the marmosets not only responded to the vocalisations (leopard growl, bird of prey calls, and snake hiss and rattle), but also did so in distinct and different ways. A separate experiment was therefore devised to test whether any of these observed differences in responses to the sounds of specific predators (leopard, snake and bird of prey) were maintained consistently under controlled conditions.

Notably, felid, snake and raptor all have different hunting methods and vocalise at different frequencies. As discussed in Chapter 4, birds of prey typically produce high-frequency vocalisations while felines give low-frequency calls. The rattle of a rattlesnake, as tested in Experiment 1, has a dominant frequency of around 10 kHz (Fenton and Licht, 1990; Young and Brown, 1993, 1995), while hissing ranges quite variably between 3 and 13 kHz but is similar to white noise (Young, 1991). Although these sounds are within the marmoset’s hearing range, hissing may be more difficult to detect as it may appear to marmosets as background noise, and, as marmosets’ hearing is more skewed to high-frequency sounds, even feline vocalisations could present an auditory challenge. Furthermore, a prey animal with predator experience may be able to associate a particular vocalisation with a specific predator, and therefore its hunting method, and react accordingly. It is equally possible that different frequencies and other cues within the vocalisations themselves may provide even predator-naive animals with general information and lead them to take specific actions. While these cues may not elicit specific threat-appropriate responses (i.e. moving up in response to terrestrial threats and taking cover during aerial threats) in predator-naive animals, they may still induce fear and result in behaviour patterns similar to those observed in anti-predator responses in the wild. Because captive-born, predator-naive cotton-top tamarins (*Saguinus oedipus*) do not discriminate between predator and non-predator vocalisations, Friant *et al*. (2008) suggested that they may have responded to vocal qualities, such as low-frequency sounds, which may indicate large body size (Morton, 1977). Alternatively, general properties may be shared between vocalisations of similar predators (such as large felids), allowing for an extrapolation between the known and unknown, while the vocal properties in different predator classes, such a felid and a raptor, may provide information to trigger aerial or terrestrial vigilance. The observations made during my first experiment, such as looking down and moving up in response to the leopard growl, seemed to provide some evidence to support the latter hypothesis. However, it is important to note that in a natural context these sounds come from a specific direction and this may be the cue that elicits looking up or looking down. In my experiments, the sound source (speaker) was fixed at just above the height of and near the platform used for presenting the visual and olfactory stimuli (90 cm from the ground).

Audition is an ideal modality for measuring responses to predators because frequency, length, tone and bouts can be measured, controlled and quantified, and thus easily compared. Physical (visual) differences between predators can be harder to quantify. It was predicted that the marmosets would show some differentiation in fear responses between the three stimuli, even though these responses might not be as distinct and species-specific as those reported in wild, predator-experienced primates (e.g. Orin, 2009).

7.2 Materials and methods

Twelve marmosets (6 female/6 male; aged 24 to 161 months) were tested for their response to the vocalisations of three different predator types (feline, bird of prey and snake). One male, Delta, who had been tested for his response to the leopard growl in Experiment 2 (Ch. 4), was quite old (aged 150 months as of February 2008) and increasingly had difficulties to move from his home-cage. As this experiment was quite self-contained it was possible to replace Delta with his son, Flint, to maintain a sample size of 12. This had not been possible for Experiment 4 as it required many presentations of stimuli (individual and combinations). Flint's responses were scored for leopard growls, as well as the hawk and snake vocalisations. The results of the responses to the leopard growl in this chapter, therefore, differ slightly from those presented in Chapter 4.

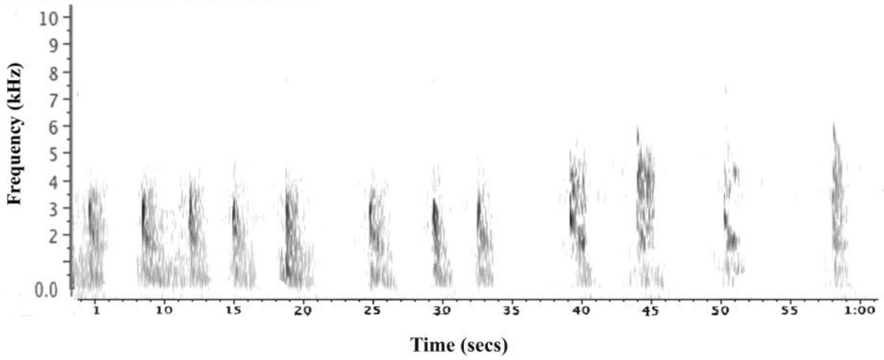
7.2.1 Stimuli

The stimuli consisted of 60-second recordings of typical vocalisations of each type of predator (leopard growl, red-shouldered hawk whistle and snake hiss) (Fig. 7.1). Source details of materials were provided in Chapter 3 (Table 3.1). The vocalisations used in Experiment 1 were lengthened for this experiment by repeating elements/phrases and/or syllables in a naturalistic manner until 60 seconds had been recorded. This was done to test not only immediate but also considered responses, while also not exceeding the marmosets' attention span. The number of elements contained in each recording varied between the stimuli because of the nature of the species-specific vocalisations, i.e. snake hisses tend to be continuous while the sounds of birds of prey tended to be short bursts of single calls with breaks between each call. All sounds were played at 60 dB_{SPL}, measured at a distance of 1 metre from the speaker.

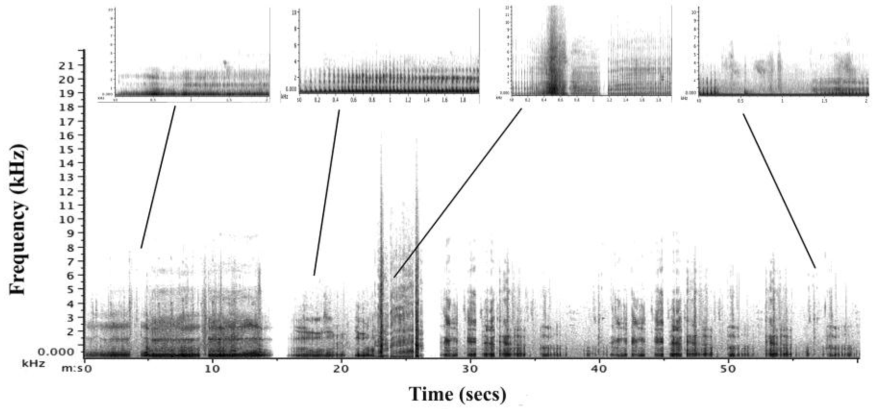
7.2.2 Experimental procedure

The three stimuli were presented in random order to an individual marmoset, twice each (trial 1 and trial 2), with a minimum of one day between each trial following the method adopted throughout all experiments (Ch. 2, Section 2.3 and Ch. 4, Section 4.2.2.3).

A. Red-shouldered hawk call



B. Leopard growl



C. Snake hiss

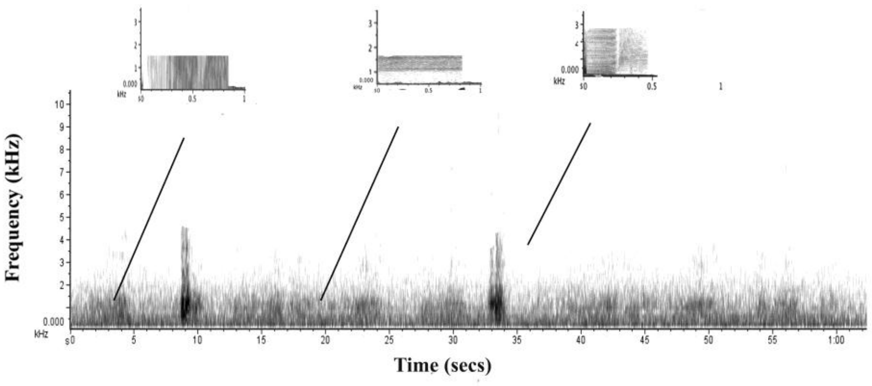


Figure 7.1. Spectrograms of the predator vocalisations: A - red-shouldered hawk call, B - leopard growl, C - snake hiss. The hawk call ranged from 2-4.5 kHz. Excerpt of leopard growl Sections shown

7.2.3 Behaviour scored

The types of behaviour scored included those tested in Experiment 2 and described in Chapter 2: mean number of (virtual) room section movements (activity), mean latency to move, mean number of contact and mobbing/alarm vocalisations, mean latency to vocalise, and looking up and down.

Additionally, hiding and freezing were also scored. Hiding included moving into the runway, sitting inside the nest box provided (it was fully enclosed with an opening at one end) and using a branch for hiding. Freezing differed from a simple stationary position by visible tension in the body of the marmoset. A marmoset was considered to be in a ‘freeze’ position when its body stiffened and its head did not move at all. Stationary marmosets still move their heads. All behaviour was recorded from video footage. Facial expressions were noted and are discussed in detail in Chapter 8. A five-second interval sampling method was used for activity, hiding, freezing, and looking up and down. All contact calls (phee, twitter) and mobbing/alarm calls (tsik, crackle, ock, alarm 2) were scored and latency to move and vocalise were scored in seconds to two decimal places.

7.2.4 Statistical analysis

The statistical analyses used are described in detail in Chapter 2, Section 2.5. The two trials were first compared using two-tailed t-tests for normal data and Wilcoxon signed-rank tests for non-parametric data if transformations were unsuccessful. If the two trials were statistically the same, the mean was taken for each behaviour. Within (pre-test, test and post-test) and between stimuli scores were compared using a repeated measures ANOVA for normal data, with Bonferroni *post hoc* tests, and Friedman’s test, with Wilcoxon signed-rank *post hoc* tests, for non-parametric data.

7.3 Results

No significant differences were found between trials 1 and 2 for any of the behavioural responses scored (two-tailed t-test t values ranged from 0.25 to -1.65 with corresponding p values ranging from 0.81 to 0.13, and Wilcoxon signed-rank Z values ranged from -0.11 to -1.60 with corresponding p values ranging from 0.68 to 0.92). Hence, the means for each behaviour for each stimulus were calculated and used for further analysis. This data is presented in Appendix XI.

7.3.1 Snake hiss pre-test, test and post-test comparisons

The statistical results of the pre-test, test and post-test comparisons for the snake hiss are reported in Table 7.1.

Table 7.1. Statistical comparisons of the responses to the snake hiss, pre-test, test and post-test. Tests of heterogeneity were first performed using a repeated measures ANOVA with ‘Sphericity Assumed’ correction for normal data and a Friedman’s test for non-parametric data. *Post hoc* test results are shown where applicable; Bonferroni pairwise comparisons were used for normal data and Wilcoxon signed-rank tests were used to analyse non-parametric data. Significant differences are in bold. The ‘–’ indicates where statistical tests were not applicable. The same styling applies to Tables 7.2 to 7.5.

	Main or major effect	Pre-test versus test	Test versus post-test	Pre-Test versus post-test
Activity per min	$F_{(2,22)} = 1.27$ $p = 0.30$	–	–	–
Number of contact calls per min	$\mathbf{F_{(2,22)} = 19.40}$ $\mathbf{p \leq 0.001}$	$\mathbf{p \leq 0.001}$	$\mathbf{p = 0.02}$	$\mathbf{p = 0.05}$
Number of mobbing/alarm calls per min	$X^2 = 1.37$ $p = 0.50$	–	–	–
Number of looks upward per min	$X^2 = 1.61$ $p = 0.45$	–	–	–
Number of looks downward per min	$F_{(2,22)} = 1.49$ $p = 0.25$	–	–	–
Number of times spent in hiding per min	$\mathbf{X^2 = 6.87}$ $\mathbf{p = 0.03}$	$\mathbf{Z = -2.02}$ $\mathbf{p = 0.04}$	$Z = -1.26$ $p = 0.21$	$\mathbf{Z = -2.02}$ $\mathbf{p = 0.04}$
Number of times in ‘freeze’ position per min	$\mathbf{X^2 = 15.44}$ $\mathbf{p \leq 0.001}$	$\mathbf{Z = -2.64}$ $\mathbf{p = 0.01}$	$\mathbf{Z = -2.64}$ $\mathbf{p = 0.01}$	$Z = -1.00$ $p = 0.32$

The marmosets gave significantly fewer contact calls in the test period than they did in the pre- ($p \leq 0.001$) or post-test ($p = 0.02$) period (Fig. 7.2 A). The number of contact calls in the post-test was also significantly reduced in comparison to the pre-test ($p = 0.05$).

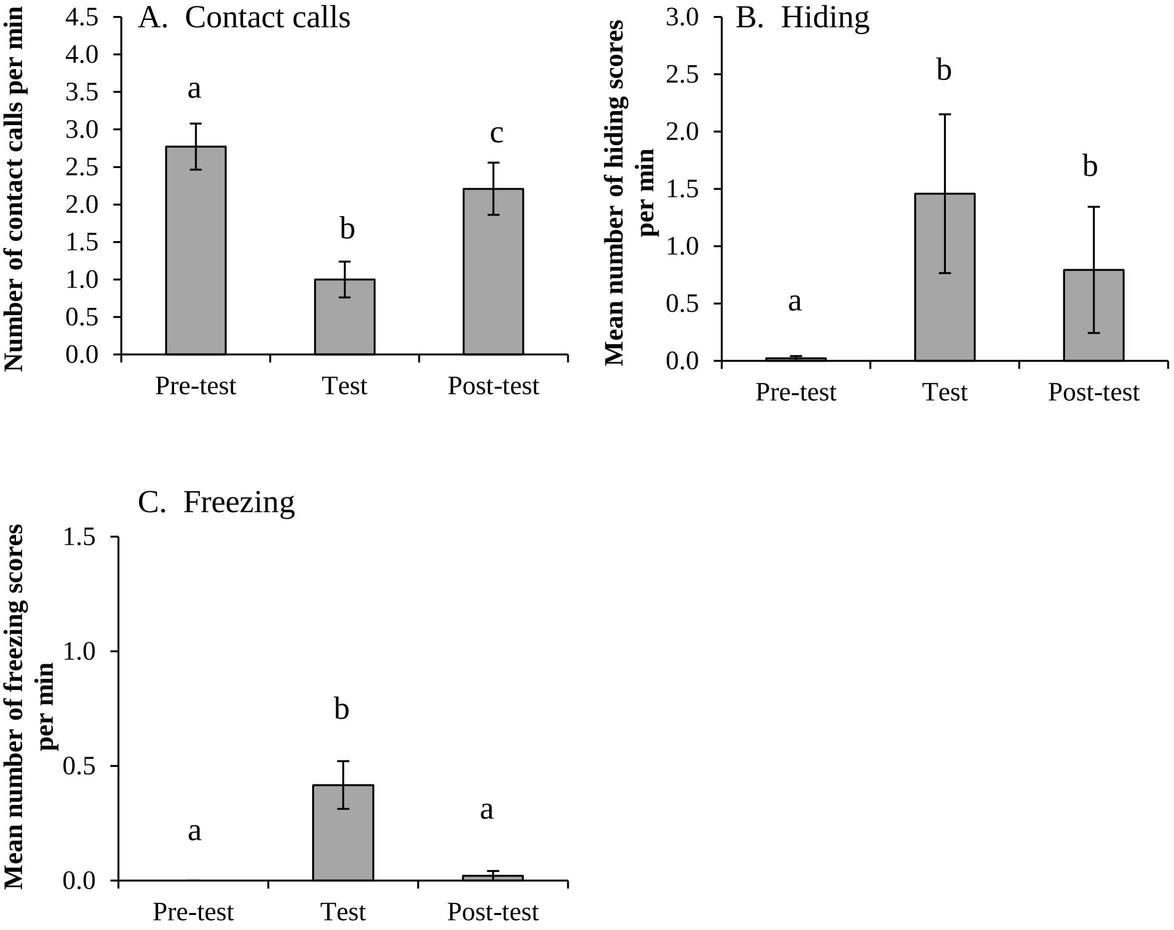


Figure 7.2. Comparison of responses in the pre-test, test and post-test: snake hiss (1 min). A – contact calls, B – hiding scores, C – freezing scores (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’, and ‘c’ is significantly different from both ‘a’ and ‘b’. The marmosets gave fewer contact calls in the test period than before or after, and hid and froze more often in the test period than in the pre-test. Hiding remained elevated in the post-test.

The marmosets hid more often during the test and post-test periods than in the pre-test ($p = 0.04$ and $p = 0.04$, respectively) (Fig. 7.2 B) and ‘froze’ at a higher rate in the test period than in either the pre- ($p = 0.01$) or post-test ($p = 0.01$) period. These differences are shown in Figure 7.2 C.

7.3.2 Red-shouldered hawk call pre-test, test and post-test comparisons

The statistical results of the pre-test, test and post-test comparisons for the red-shouldered hawk call are reported in Table 7.2.

Table 7.2. Statistical comparisons of the responses to the red-shouldered hawk call, pre-test, test and post-test.

	Main or major effect	Pre-test versus test	Test versus post-test	Pre-Test versus post-test
Activity per min	$F_{(2,22)} = 1.33$ $p = 0.28$	–	–	–
Number of contact calls per min	**$F_{(2,22)} = 18.08$** **$p \leq 0.001$**	**$p = 0.004$**	**$p \leq 0.001$**	$p = 1.00$
Number of mobbing/alarm calls per min	**$X^2 = 6.53$** **$p = 0.04$**	$Z = -0.54$ $p = 0.59$	$Z = -1.83$ $p = 0.07$	$Z = -1.83$ $p = 0.07$
Number of looks upward per min	**$X^2 = 13.27$** **$p = 0.001$**	**$Z = -2.83$** **$p = 0.01$**	$Z = -0.97$ $p = 0.33$	**$Z = -2.41$** **$p = 0.02$**
Number of looks downward per min	$F_{(2,22)} = 1.13$ $p = 0.34$	–	–	–
Number of times spent in hiding per min	$X^2 = 4.92$ $p = 0.09$	–	–	–
Number of times in ‘freeze’ position per min	**$X^2 = 20.00$** **$p \leq 0.001$**	**$Z = -2.84$** **$p = 0.01$**	**$Z = -2.84$** **$p = 0.01$**	–

The results presented in Table 7.2 and Figure 7.3 show that the marmosets significantly reduced the number of contact calls during the test period in comparison to the pre-test period ($p = 0.004$); the number then increased in the post-test period ($p \leq 0.001$) (Fig. 7.3 A). Although there was a significant major effect for mobbing/alarm calls across the three time periods ($p = 0.04$) (Table 7.2), *post hoc* tests did not reveal significant differences between the periods (however, trends were found for a decrease in the number of these vocalisations produced in comparison to the pre- and post-test periods).

The marmosets also looked up significantly more often per minute during the test period than they did in the pre-test ($p = 0.01$) (Fig. 7.3 B). The marmosets continued to look up more often in the post-test, with a significant difference from the pre-test found ($p = 0.02$).

The marmosets showed freezing behaviour only during the presentation of the hawk call (Fig. 7.3 C), but not before or after.

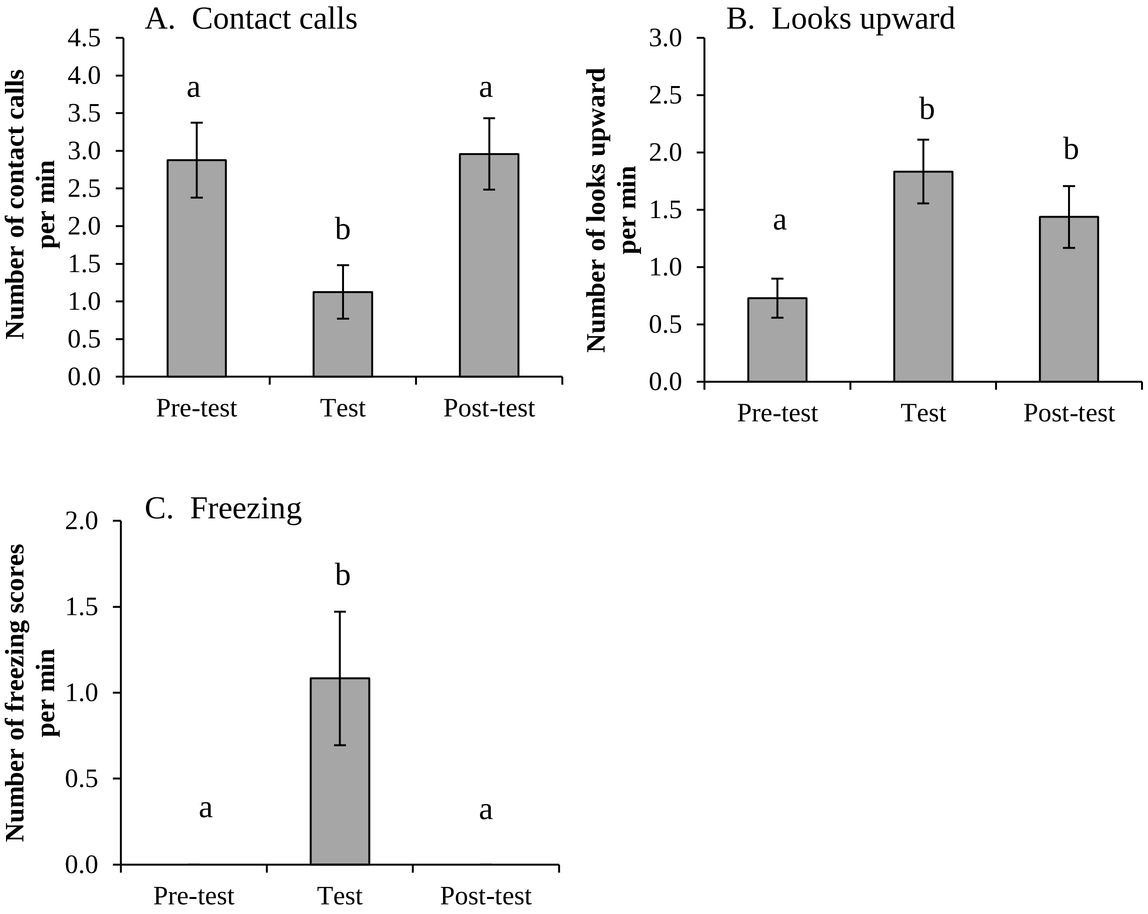


Figure 7.3. Comparison of responses in the pre-test, test and post-test: red-shouldered hawk call (1 min). A – contact calls, B – looks upward, C – freezing (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’. The number of contact calls produced decreased in the test period, while the number of freezing scores increased in comparison to the pre- and post-test periods. The marmosets also looked up more often during and after the vocalisation presentation than they did in the pre-test period.

7.3.3 Leopard growl pre-test, test and post-test comparisons

The statistical results of the pre-test, test and post-test comparisons for the leopard growl stimulus are reported in Table 7.3.

Table 7.3. Statistical comparisons of the responses to the leopard growl, pre-test, test and post-test.

	Main or major effect	Pre-test versus test	Test versus post-test	Pre-test versus post-test
Activity per min	$F_{(2,22)} = 3.16$ $p = 0.06$	–	–	–
Number of contact calls per min	$\mathbf{X^2 = 15.26}$ $\mathbf{p \leq 0.001}$	$\mathbf{Z = -2.94}$ $\mathbf{p = 0.003}$	$\mathbf{Z = -2.96}$ $\mathbf{p = 0.003}$	$Z = -1.87$ $p = 0.06$
Number of mobbing/alarm calls per min	$X^2 = 1.58$ $p = 0.45$	–	–	–
Number of looks upward per min	$F_{(2,22)} = 1.32$ $p = 0.29$	–	–	–
Number of looks downward per min	$F_{(2,22)} = 0.81$ $p = 0.46$	–	–	–
Number of times spent in hiding per min	$X^2 = 3.93$ $p = 0.14$	–	–	–
Number of times in 'freeze' position per min	$\mathbf{X^2 = 7.05}$ $\mathbf{p = 0.03}$	$\mathbf{Z = -2.03}$ $\mathbf{p = 0.04}$	$Z = -1.58$ $p = 0.11$	$Z = -1.34$ $p = 0.18$

As Table 7.3 shows, the marmosets gave fewer contact calls per minute during the test period than they did during the pre- (p = 0.003) or post-test (p = 0.003) period (Fig. 7.4 A). They 'froze' more during the test period than they did during the pre-test (p = 0.04) (Fig. 7.4 B). Freezing scores remained elevated in the post-test period.

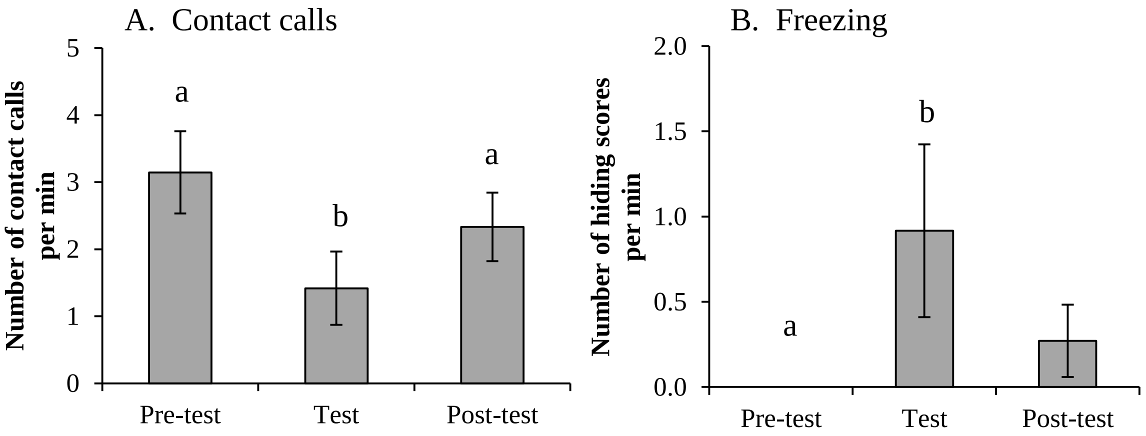


Figure 7.4. Comparison of responses in the pre-test, test and post-test: leopard growl (1 min). A – contact calls, B – freezing (means ± sem). Bars marked 'a' are significantly different from those marked 'b'. The marmosets produced fewer contact calls in the test period than they did in either the pre- or post-test period. The number of freezing scores increased from the pre-test during the presentation of the leopard growl; the scores for the post-test were not significantly different from those of either the pre-test or test period.

7.3.4 Comparisons between stimuli

There was no significant main effect among stimuli for the pre- or post-test (repeated measures ANOVA $F_{(2,22)}$ values ranged from 0.13 to 3.30 with corresponding p values ranging from 0.88 to 0.06; Friedman's test X^2 values ranged from 0.30 to 3.24 with corresponding p values ranging from 0.86 to 0.20). The results of the test-period comparisons are reported in Table 7.2.

Table 7.4. Statistical comparisons of behavioural responses scored in response to the presentation of the three predator vocalisations (test period).

	Main or major effect	Snake hiss versus hawk call	Hawk call versus leopard growl	Leopard growl versus snake hiss
Activity per min	$F_{(2,22)} = 0.57$ $p = 0.58$	–	–	–
Latency to move (secs)	$F_{(2,22)} = 0.04$ $p = 0.97$	–	–	–
Number of contact calls per min	$F_{(2,22)} = 0.26$ $p = 0.77$	–	–	–
Number of mobbing/alarm calls per min	$X^2 = 1.00$ $p = 0.61$	–	–	–
Latency to vocalise (secs)	$F_{(2,22)} = 0.50$ $p = 0.62$	–	–	–
Number of looks upward per min	**$X^2 = 6.29$** **$p = 0.04$**	**$Z = -2.07$** **$p = 0.04$**	**$Z = -2.14$** **$p = 0.03$**	$Z = -0.42$ $p = 0.68$
Number of looks downward per min	$F_{(2,22)} = 2.27$ $p = 0.13$	–	–	–
Number of times spent in hiding per min	$X^2 = 1.74$ $p = 0.42$	–	–	–
Number of times in 'freeze' position per min	$X^2 = 3.30$ $p = 0.19$	–	–	–

As shown in Table 7.4, the marmosets looked up significantly more often in response to the red-shouldered hawk call than they did when presented with either the snake hiss ($p = 0.04$) or leopard growl ($p = 0.03$) (Fig. 7.5). There was no significant difference for this behaviour between the snake hiss and the leopard growl ($p = 0.68$).

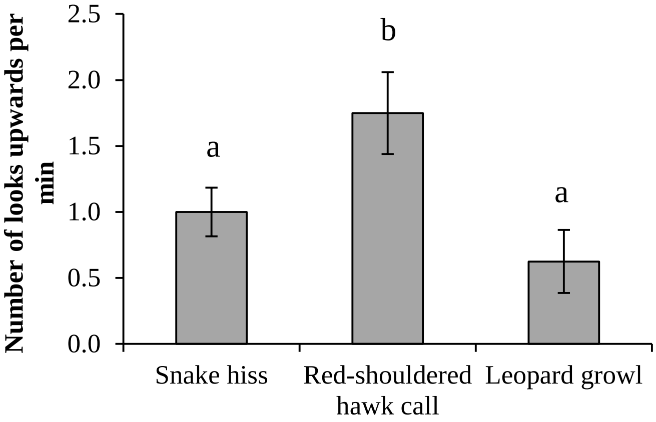


Figure 7.5. Comparison of responses during the test period: snake hiss, hawk call and leopard growl (1 min) – looks upward (means ± sem). Bars marked ‘a’ are significantly different from the bar marked ‘b’. Note that the marmosets looked up more often in response to the red-shouldered hawk call than to the snake hiss or leopard growl.

The responses to the three predator vocalisations were also compared to the results of the pleasant auditory (marmoset food-related calls) stimulus presentation in Experiment 2 (Ch. 4). The pre-test scores were not significantly different from each other (repeated measures ANOVA, $F_{(3,33)} = 1.58$, p = 0.21; Friedman’s test X^2 values ranged from 2.00 to 4.55 with corresponding p values ranging from 0.57 to 0.21), except between the number of looks upward per minute in response to the leopard growl and in response to the marmoset food-related calls (as was reported in the results of Experiment 2, Ch. 4).

Post-test scores were also compared. There were no significant differences between the response to the pleasant auditory stimulus and the three predator vocalisations for activity, latency to move, contact and mobbing/alarm calls, latency to vocalise, looking up, looking down, and freezing (repeated measures ANOVAs $F = 1.29$, $p = 0.29$; Friedman’s test X^2 values ranged from 1.45 to 6.03 with corresponding p values ranging from 0.11 to 0.69). However, there was a significant difference between these stimuli in the number of hiding scores in the post-test period (Friedman’s test, $X^2 = 10.93$, $p = 0.01$). The marmosets hid significantly more often after the presentation of the snake hiss ($Z = -2.21$, $p = 0.03$), red-shouldered hawk call ($Z = -2.23$, $p =$

0.03) and leopard growl (Z = -2.37, p = 0.02) than after the presentation of the marmoset food-related calls.

The results of the test-period comparisons are shown in Table 7.5. It is important to note that hiding and freezing were not observed once in response to the marmoset food-related calls.

Table 7.5. Statistical comparisons of behavioural responses scored during the presentation of the pleasant auditory stimulus (marmoset food-related calls) with responses to each of the three predator vocalisations (test period).

	Main or major effect	Food-related calls versus snake hiss	Food-related calls versus hawk call	Food-related calls versus leopard growl
Activity per min	**$F_{(3,33)}$ = 2.82** **p = 0.05**	**p = 0.03**	p = 0.37	p = 0.47
Latency to move (secs)	$F_{(3,33)}$ = 0.38 p = 0.77	–	–	–
Number of contact calls per min	X^2 = 7.16 p = 0.07	–	–	–
Number of mobbing/alarm calls per min	X^2 = 3.33 p = 0.34	–	–	–
Latency to vocalise (secs)	$F_{(3,33)}$ = 1.17 p = 0.34	–	–	–
Number of looks upward per min	**$F_{(3,33)}$ = 8.22** **$p \leq 0.001$**	p = 0.40	**p = 0.01**	p = 1.00
Number of looks downward per min	X^2 = 2.81 p = 0.42	–	–	–
Number of times spent in hiding per min	X^2 = 9.09 p = 0.03	**Z = -2.02** **p = 0.04**	**Z = -2.38** **p = 0.02**	Z = -1.83 p = 0.07
Number of times in ‘freeze’ position per min	X^2 = 14.77 p = 0.002	**Z = -2.64** **p = 0.01**	**Z = -2.84** **p = 0.01**	**Z = -2.03** **p = 0.04**

As shown in Table 7.5 and Figure 7.6 A, activity rate was significantly lower in response to the snake hiss than it was in response to the marmoset food-related calls (p = 0.03). There had been a significant difference reported in Chapter 4 between the response to the leopard growl and the response to the marmoset food-related calls in activity (p = 0.05), but the use of a replacement male had obviously changed the scores in response to the leopard growl enough to alter this result. The marmosets also looked up significantly more often in response to the hawk call than they did in response to the marmoset food-related calls (p = 0.01) (Fig. 7.6 B). There was a significant difference in hiding scores between the responses to the marmoset food-related calls and the snake hiss (*p* = 0.04) and red-shouldered hawk call (*p* = 0.02), as the marmosets were not observed to hid in response to the pleasant auditory stimulus (Fig. 7.6 C). Interestingly, scores of the number of hiding events did not differ significantly between responses to the food-related calls and to the leopard growl, although there was a trend for a greater number of scores in response to the predator vocalisation (Table 7.5). As no scores of freezing in response to the marmoset food-related calls were made, there were significantly more bouts of freezing in response to the predator vocalisations (snake hiss: *p* = 0.01, hawk call: *p* = 0.01, leopard growl: *p* = 0.04; Fig. 7.6 D).

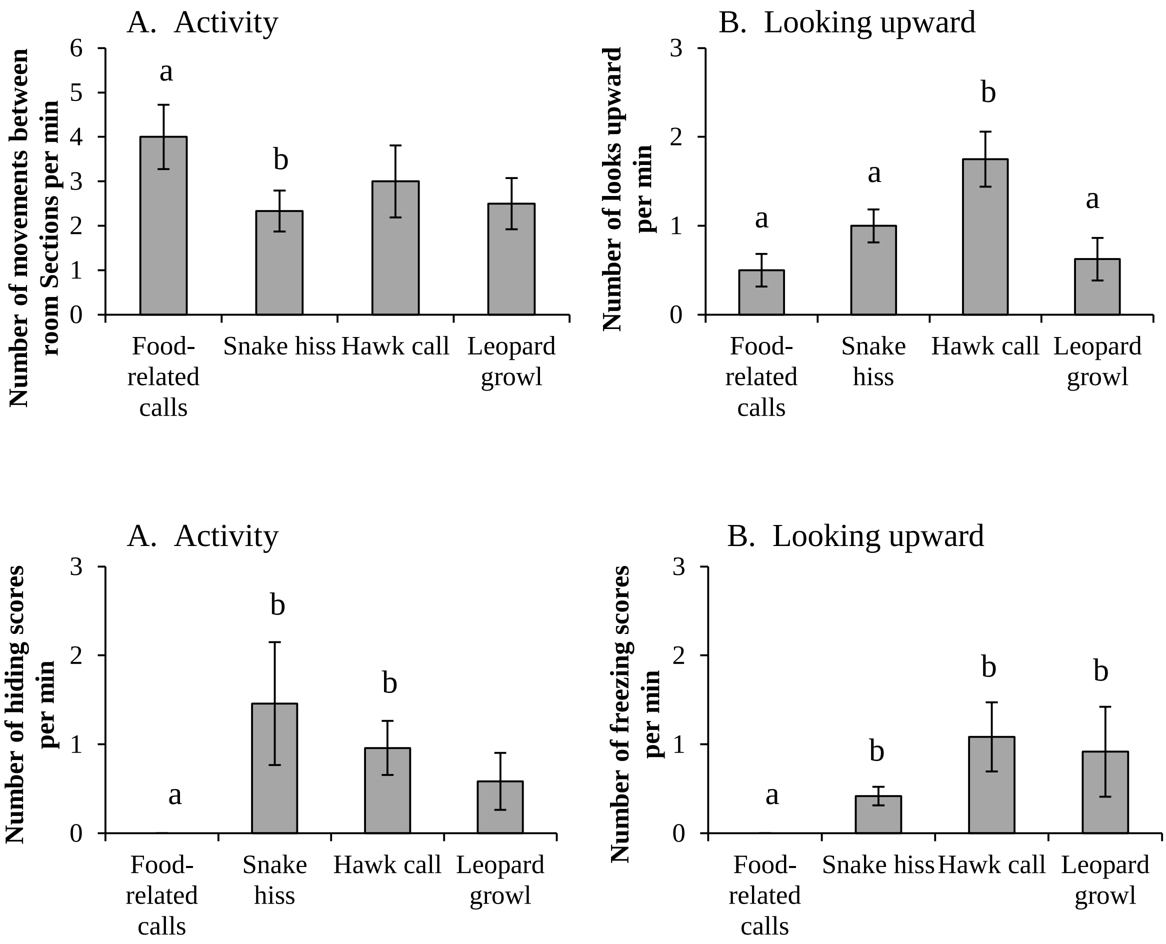


Figure 7.6. Comparison of responses during the test period: marmoset food-related calls versus the three predator vocalisations (1 min). A – movements between room sections (activity), B – looks upward, C – hiding, D – freezing (means ± sem). Bars marked ‘a’ are significantly different from those marked ‘b’. The marmosets did not hide or freeze in response to the pleasant auditory stimulus and did not look up as often in response to the food-related calls as they did to the hawk call.

7.4 Discussion

The prediction that the marmosets would differentiate between the three stimuli, based on anecdotal evidence from Experiment 1, at first glance seemed not entirely confirmed in controlled conditions because the marmosets tended to respond to the three predator vocalisations in similar ways. Indeed, all three stimuli elicited an initial fear reaction (freezing) and the marmosets reduced their predominant vocalisations (contact calls) when presented with these sounds. However, there was one difference that is noteworthy and would support the theory that high versus low frequency sound production results in some important differentiation: a significant difference was found between the stimuli in the number of upward looks. The marmosets looked up significantly more often during the presentation of vocalisations of a red-shouldered hawk than during those of a snake and leopard. This result suggests that the higher frequency of the hawk call may provide information regarding the biological source of the vocalisation as deriving from an aerial, not a terrestrial, source. All three stimuli were played from a speaker in the same location (90 cm above the floor) so that differences in response could only be attributed to the differences in sound properties. Indeed, no other sound tested here or in Experiment 2 (Ch. 4) elicited an increase in looking upward.

Five vastly different sounds (leopard growl, marmoset food-related calls, background noise, snake hiss and red-shouldered hawk call) were played to the marmosets. Of these auditory cues, only the predator vocalisations elicited freezing and/or hiding responses, sometimes even having an after-effect (e.g. hiding still occurred in the post-test after the presentation of the snake hiss), and only the hawk call elicited more looks upward. The marmosets were predator naive and before this research had never been exposed to any of the three predator vocalisations. Yet they continued to look up more often in the post-test after the presentation of the hawk call than they had in the pre-test, suggesting they remained vigilant as if for an aerial attack. Vigilance is considered an important anti-predator behaviour (Lima and Dill, 1989; Caro, 2005). Marmosets are thought to be more vulnerable to aerial attack (Caine and Weldon, 1989) and previous studies have found that they scan aerially more than terrestrially (Barros *et al*., 2004). During the course of all my experiments, results showed that the marmosets looked up only infrequently – perhaps, as suggested in Chapter 4, recognising the ceiling as a physical barrier to aerial threats. This makes the finding of the increased number of looks upward during the hawk call presentation more compelling.

It is possible that these specific marmosets were not altogether unfamiliar with high-frequency raptor sounds and that this finding may therefore be biased by some, albeit very limited, experience. On some occasion, the marmosets may have heard raptor vocalisations while in their outdoor cages. Researchers have never heard birds of prey vocalising nearby the housing facility, but little eagles (*Hieraaetus morphnoides*), wedge-tailed eagles (*Aquila audax*) and brown goshawks (*Accipter fasciatus*) are known to reside in the New England region (Debus, 1984, 1992, 1998; Koboroff, 2009). Sky visibility from the outdoor cages was minimal and it is somewhat unlikely that the marmosets would have been able to view any birds flying overhead. At the very least it can be certain that the marmosets would not have witnessed a predation event by a raptor, given that the area directly next to the outdoor cage area was typically frequented by people and had a small car park.

The number of contact calls made decreased in response to all three predator vocalisations, but this was also observed in response to non-predatory auditory stimuli. That the marmosets vocalised frequently in the pre-test period is not surprising, since they were tested individually: marmosets often give contact calls to maintain group cohesion and determine the location of conspecifics (Bezerra and Souto, 2008; Chen *et al*., 2009). The marmosets then fell almost silent immediately on hearing the predator vocalisations. Mobbing/alarm vocalisations were sparse before the presentation of the sounds and therefore it is not surprising that a reduction in number was not observed. However, it is worth noting that the number of mobbing/alarm calls increased in response to other presentations, particularly visual stimuli and more so to the quoll than the marshmallow. Interestingly, in the post-test period of the snake hiss the marmosets continued to remain silent. As mentioned earlier, snake hisses are thought to be similar to white noise, making their location harder to detect (Young, 1991). It is possible that the marmosets remained silent to improve their chance of detecting a sound that is hard to distinguish and locate. In contrast, there was a trend for an increase of mobbing/alarm vocalisations in the post-test period after the presentation of the hawk call. This may have been due to heightened arousal, but it is possible that the marmosets were alerting conspecifics who would not have been aware of the potential threat. Experiment 2 showed that the marmosets reduced the number of vocalisations they produced in response to even potentially pleasant stimuli, such as the marmoset food-related calls, and even to the background noise (neutral stimulus). Therefore, it would seem that this behaviour occurs in response to any unexpected and prolonged sound. The marmosets may limit vocalising in order to better hear the sound, and to try to determine location and whether a response, such as searching (increased activity, as seen in response to the marmoset food-related calls) or hiding (response to the snake hiss), is required.

In Experiment 2 (Ch. 4), the marmosets had been found to reduce activity rates in response to the leopard growl and maintain that reduction in the post-test; it was therefore predicted that this behaviour would be evident also in response to other predator vocalisations. However, activity was not affected by the snake hiss and hawk call. Furthermore, no significant change in activity was seen in response to the leopard growl (the inclusion of the younger male had changed the results to a trend only). However, this result cannot be taken at face value. As the marmosets ‘froze’ more often in response to the predatory stimuli, thereby spending more time in stationary positions than in the pre-test, an associated decrease in activity was expected. That there was no reduction in overall activity, however, is an indication that after freezing, or in between bouts of freezing, the marmosets actually increased their activity rates. They were observed to move to places within the room that seemed to provide more cover, such as the runway, and then move back to their original spot. Although they hid more often during the presentation of the snake hiss, and had a trend to do so also in response to the hawk vocalisations, than in the pre-test periods, there was no significant difference between stimuli and the marmosets did not tend to stay in one hiding spot for long. Movement can attract the attention of a predator, so many animals respond to predatory threats by remaining as still as possible (Caro, 2005). However, when a predator can be heard but not seen, it is possible that remaining motionless may be a strategy that is detrimental to survival. When marmosets find a predator they often mob (Clara *et al*., 2008; Ferrari and Lopes Ferrari, 1990; Passamani, 1995), as also seen in Experiment 2 in response to the taxidermic specimen of a quoll. Mobbing reduces physiological stress (Clara *et al*., 2008; Cross and Rogers, 2006) and is a behaviour that actively addresses any predation threat.

It is possible that the properties of the vocalisations themselves provided particular information (e.g. to look up). Furthermore, the auditory presentation of predator sounds elicited strong fear responses. As predator-experienced common marmosets (wild) have not been tested for their response to predator vocalisations it is not possible to compare the responses seen in this experiment. However, the general behaviour of the marmosets (freezing, hiding, etc.) was similar to that seen in other primate species, both captive and wild (e.g. Searcy and Caine, 2003; Yorzinski and Ziegler, 2007).

CHAPTER EIGHT

EXPERIMENT 6: RESPONSES TO FACIAL DISPLAYS

8.1 Introduction

An exciting finding during the presentation of the stimuli in the previous experiments was the extensive use of facial expressions. The marmosets responded to the sight, smell and sound of predators and food with an array of facial displays, but particularly to predator-based olfactory and auditory stimuli; indeed, facial displays were often the most obvious response. This finding was unexpected.

The literature on facial displays in marmosets (Epple, 1967; Stevenson and Poole, 1976; van Hooff, 1967) has reported expressions only in response to visual stimuli, and in particular to conspecifics and humans; some of these same facial displays were observed during my experiments. However, there were also some displays that did not appear to fit prior description. This is perhaps not surprising as there have been few occasions when experimenters were able to observe responses to olfactory and auditory stimuli, especially when the stimuli had negative and unpleasant connotations. The facial displays described in this chapter were a response in and of themselves to the stimuli (presented in Ch. 3 to 7), but, given their great variation, it is also possible that they have the potential to be used as a signal among conspecifics.

Facial displays in non-human primates should not be confused with facial ‘expressions’ in humans. In general, studies of facial expressions in non-human primates do not associate facial displays with particular emotions, such as ‘anger’, as is typical of human studies; instead, the features of the display are described (e.g. an open-mouth threat). In non-human primates, the term ‘expression’ may imply an internal state that is difficult to ascertain in animals (Preuschoft, 2000; Sackett, 1966). ‘Compound displays’, as van Hooff (1962, 1967) described facial expressions in non-human primates, may look the same between different species but may in fact have different meanings (van Hooff, 1967), contrary to what Darwin believed (1872). Conversely, two species may make quite different expressions but the purpose of the expressions may be the same. ‘Sadness’ in chimpanzees is expressed with the teeth partially bared and the mouth corners retracted sideways, the jaws separated slightly and the lips protruded and puckered (van Lawick-Goodall, 1968, van Hooff, 1973). In humans, sadness is shown with the mouth corners depressed and the inner corners of the eyebrows raised (Ekman and Friesen, 1969). Therefore, facial expressions in humans, and their meanings, cannot necessarily be transposed to the displays seen in non-human primates (Preuschoft, 2000).

It is also worth noting the external facial physiology of animals that are known to display complex facial expressions. Humans (Darwin, 1872; Ekman and Friesen, 1969), other great apes (Mackinnon, 1974; Maple, 1980; Parr and Waller, 2006; van Lawick-Goodall, 1968), macaques (Hinde and Rowell, 1962; Partan, 2002), marmosets (Epple, 1967; Stevenson and Poole, 1976; van Hooff, 1967), canines (Bekoff, 1974; Fox, 1970), cats (Overall *et al*., 2005), fur seals (Miller, 1975) and mice (Langford *et al*., 2010), for example, are all described as producing facial expressions. All of these species, excepting some breeds of dogs and cats, have limited or short hair/fur on their face. The importance of facial expressions as part of the communication system of a species may be positively correlated with a reduction in facial hair (Campbell, 2009). All marmosets have reduced facial hair, with a ‘face’ clearly defined, although common marmosets appear to have even less facial hair than any of the other marmoset species.

There are six facial expressions of emotion that are widely accepted to be universal to all humans: happiness, surprise, sadness, fear, anger and disgust (Ekman, 1972; Ekman and Friesen, 1969). These expressions apparently occur regardless of ethnic group, culture and isolation from other human societies, and are also observed in people with visual impairments (Matsumoto and Willingham, 2009; Peleg *et al.*, 2006). Five facial muscles are known to be used in the creation of these expressions and are thought to occur in all humans: the zygomaticus major, depressor anguli oris, orbicularis oculi, orbicularis oris, and frontalis (Ekman *et al.*, 2002; Waller *et al.*, 2008). A recent paper has revealed that common marmosets also have these five standard facial muscles (Burrows, 2008). This means that the marmosets should be capable of making the same or similar six expressions seen in humans (Ekman, 1972; Ekman and Friesen, 1969).

The six facial expressions mentioned above can also be displayed, and more genuinely so, as microexpressions (Ekman, 1992, 1999; Ekman and Friesen, 1969). Microexpressions are produced for brief periods of time (1/25 to 1/15 of a second) (Ekman and Friesen, 1969). The expressions observed in the marmosets in my experiments were displayed briefly, but sometimes for up to several seconds.

Notably, research on facial expressions in primates has focused on social situations and their implications and meanings to conspecifics (e.g. Parr and Waller, 2006). This is not surprising given that the most complex and well-known facial expressions appear to occur in highly social species (Burrows, 2008; Burrows *et al.*, 2011) and may be used in communication with conspecifics (Darwin, 1872; Parr and Heintz, 2009; Parr and Waller, 2006; van Lawick-Goodall, 1968). Recently, much attention has been directed at facial displays in a handful of non-human primate species (the term ‘expression’ has been used ubiquitously) and researchers have concluded that the facial expressions tested indeed reflect internal states and that these are understood by conspecifics, judging by their responses (e.g. Hopkins *et al.*, 2011; Parr and de Waal, 1999; Parr and Heintz, 2009; Parr and Waller, 2006; Parr *et al.*, 1998, 2000). Indeed, Darwin (1872) suggested that there was a commonality of purpose between human and animal facial expressions. Based on these findings – that facial displays may reflect internal states that are interpreted by conspecifics – and the discovery of marmoset facial expressions in this project, the question of whether conspecifics could derive specific meaning from these expressions had to be asked.

Epple (1967), Hook-Costigan and Rogers (1998), Stevenson and Poole (1976) and van Hooff (1967) briefly described facial expressions in common marmosets, but to my knowledge these four papers comprise the only literature on this specific aspect of marmoset behaviour (details were provided in Table 2.2, Ch. 2). The 22 facial expressions briefly described by Stevenson and Poole (1976), which included those of Epple (1967) and van Hooff (1967), were combinations of movements of eyes, mouth and ear tufts. They also made one reference to use of the tongue. The one expression described by Hook-Costigan and Rogers (1998), the 'fear' expression, only mentions the movement of the mouth – laterally drawn lips and bared lower teeth. This may be the same as the 'bared teeth' expression described by both Stevenson and Poole (1976) and by van Hooff (1967); however, they do not mention whether the upper, lower or both sets of teeth are exposed and the diagram by Stevenson and Poole (1976) is unclear. All were responses to known and unknown visual stimuli (conspecifics and/or humans, strange objects and/or food). Only the expression described by Hook-Costigan and Rogers (1998) and ten of the expressions described by Stevenson and Poole (1976) had accompanying photographs or diagrams (not all of which were particularly clear), and the descriptions of the other expressions were brief. Often there were only small differences between the expressions. Therefore, it was somewhat difficult to determine whether the expressions observed during my experiments were those previously described in the literature.

Table 8.1 lists the facial expressions observed and described by Epple (1967), Hook-Costigan and Rogers (1998), Stevenson and Poole (1976) and van Hooff (1967) and in which, if any, of my experiments they were observed.

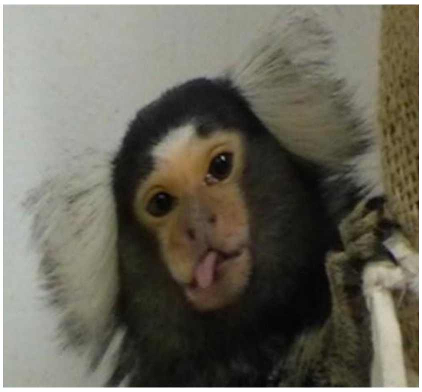
Table 8.1. List of the facial expressions described by Epple (1967), Hook-Costigan and Rogers (1998), Stevenson and Poole (1976) and van Hooff (1967), as described in Chapter 2, Table 2.2, and in which circumstances, if any, they were observed during my research.

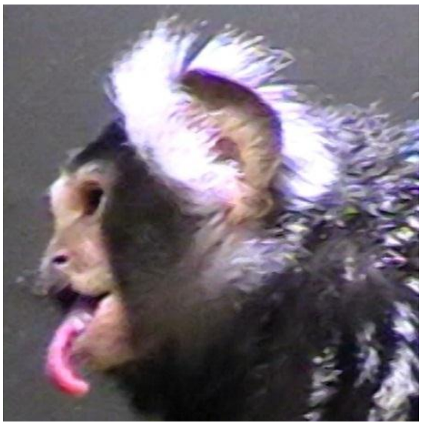
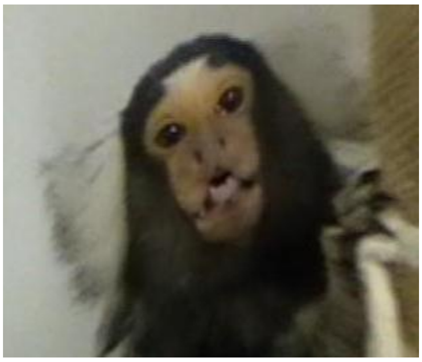
Facial expression	Observed	Situations in which observed
Relaxed face	Yes	All experiments
Lip smacking	No	Observed outside of experiments; sexual situations.
Tongue in/out	No	Observed outside of experiments, usually accompanying lip smacking during sexual behaviour.
Stare (with or without head-cock)	Yes	Response to visual stimuli
Slit stare	Yes	Response to visual stimuli
Frown	No	–
Open mouth	No	–
Partial open mouth	Yes	Response to visual stimuli –
Partial open mouth slit stare	No	–
Pout	No	
Bared teeth gecker face	No	–
Grin	No	–
Bared teeth	No	–
Bared teeth scream	No	–
Tufts flick stare	Yes	Response to visual stimuli
Tufts flick slit stare	Yes	Response to visual and auditory stimuli
Tufts flatten	Yes	Response to aversive stimuli
Tufts erect stare	Yes	Response to aversive visual stimulus
Tufts erect frown	No	–
Fear expression	Yes	Response to looming stimuli (typically people; outside of experiments) and predator vocalisations.
Relaxed face	Yes	All experiments Observed outside of experiments; sexual situations.

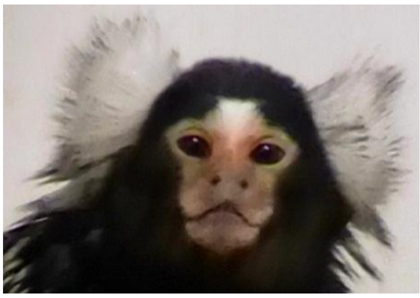
In our colony, the marmosets repeatedly showed facial expressions in response to auditory and olfactory stimuli as well. Moreover, some of the marmosets' complex displays were performed without an audience. Since no other marmosets were present during any of the trials, it cannot be surmised that the displays were made intentionally in order to communicate with conspecifics; one might therefore argue that the expressions may have been the result of involuntary muscle action. Indeed, the most important facial displays in humans, 'microexpressions', are the result of involuntary responses to emotions (Ekman, 1992, 1999; Haggard and Isaacs, 1966).

As mentioned, other facial expressions were observed that did not appear to fit the descriptions provided in the literature. These included movements of the eyes, mouth, ear tufts, brow and tongue, and are shown in Table 8.2. What has been described in the literature as 'tufts flatten' I have termed 'tufts back', as there was no evidence of actual flattening.

Table 8.2. The facial expressions described in this table were observed during my experiments and have not been previously described in the literature.

	Facial expression	Description	Context in which expression was observed
		Relaxed (neutral) expression provided as a reference point	
1.		'Rapid eye blink' with brow down, chin tucked in, tight mouth with lips held together and ears back	Response to predator vocalisations and predator faeces. Also seen outside of experiments when approached abruptly by a human (looming stimulus).
2.		'Lip licking' – the similar expression, 'tongue in/out' was described as occurring only in sexual situations (Stevenson and Poole, 1976). In the sexual context the tongue flicking is a smaller movement of the tongue than we observed in 'lip licking'. We also noted that the rest of the face is relaxed, although ears may be perked	Response to pleasant stimuli, including food
3.		'Long tongue' – extended tongue outside the mouth, typically curled at the tip with position held for longer than seen in the rapid 'lip licking' (approx. 1 second).	Only seen in three individuals, in response to the pleasant odour, but also in response to scent marks made by conspecifics

4.		‘Lip lick’ – small and quick tongue movement in and out; singular. Tufts back, eyes wide.	Response to predator vocalisations and aversive visual stimulus
5.		‘Backward tongue’ – note that the tongue curls in the direction opposite to most tongue actions	Seen only once, in response to combined aversive visual and auditory stimuli
6.		Hook-Costigan and Rogers’s (1998) ‘fear’ expression, mentioned here for additional description: slightly open mouth with bared lower teeth. The jaw is protruded forwards. Tufts are back and the brow is raised.	Response to predator vocalisations and sometimes to the aversive visual stimulus
7.		Unlike the described ‘lip smacking’, this form of ‘smacking of the mouth’ has large movements of the jaws opening and closing. Also seen with tongue movements inside the mouth. Eyes narrowed, face often scrunched.	Response to the faecal odours of carnivores.

8.		Similar to the ‘relaxed face’, but there is a tightness to the face (‘tight face’). The lips are tense and pulled inward slightly. The eyes are also slightly wider than normal, but the inner brow is slightly pinched and the ears are perked forward. Often corresponded with freezing behaviour.	Response to auditory stimuli
9.		‘Freeze face’ – although similar, this expression differed from the ‘partial open mouth’, ‘partial open mouth stare’ and ‘partial open mouth slit stare’ described by Stevenson and Poole (1976) as the mouth is not open as far; the lip corners are retracted but the lower jaw is dropped and the chin pulled in slightly. The eyes are narrowed but not to slits, and the ear tufts are back slightly but not flattened (no mention of tuft flattening or back was described in concurrence with the ‘partial open mouth’ by Stevenson and Poole, 1976). Seen in conjunction with freezing and trembling.	Response to predator vocalisations

Tongue movements contributed to four of the nine expressions in Table 8.2, in response to both aversive and pleasant stimuli, and consisted of a variety of actions: quick, singular, repeated, and small to long emergences from the mouth. Other species, such as felines and canines, are known to lip lick when stressed (e.g. Cannas *et al*., 2010). The marmosets were often observed lip licking in response to the aversive stimuli, and this behaviour may be associated with fear. It is possible that the long extension of the tongue, observed in response to the pleasant odour and to scent marks, may be associated with the marmosets’ vomeronasal organ. It was not possible to confirm this within the confines of this research. It is also worth pointing out that a brief flicker of the tongue outside the mouth with the lips closed was often observed after the phee call was emitted. When phee calling, the marmosets opened their mouth quite widely and the effort of producing such a loud call was visible in the deeply contracting and expanding ribs. It is possible that the lip licking that followed served to stimulate moisture in the mouth and moisten the lips, as is typical of humans. It is also important to note that visible teeth can occur even when the marmoset is displaying a ‘relaxed’ or neutral face, depending on the individual’s teeth structure and any splits in the lip formation, i.e. teeth in the process of falling out or protruding from the mouth and lips that do not fully close.

Common marmosets were initially reported to have sheet-like facial muscles that were generally undifferentiated, mostly between the lateral nasal region and upper lip (Huber, 1931). However, recent work (Burrows, 2008) has shown that common marmosets have numerous individual muscles around the nasolabial region, and a facial musculature with similarities to both strepsirhines and haplorhines. Strepsirhines (galagos, lorises and lemurs) and marmosets have muscles connecting the lips to the external ear (Burrows, 2008). The muscles of the external ear of the marmosets are similar to those of other haplorhines (tarsiers, monkeys and apes), and are attached to wide regions of the external ear cartilage (Burrows, 2008). Furthermore, the well-differentiated individual muscles around the nasolabial region of marmosets are similar to those seen in macaques and chimpanzees (Burrows *et al*., 2006*a*, 2006*b*). However, apes, including humans, still have a more intricate musculature structure than marmosets, with a wider range of independent movement (Burrows, 2008).

There certainly appears to be evidence to suggest that marmoset facial expressions are more varied and complex than previously thought. However, they have not previously been the subject of experimental study. The observations made by Epple (1967), Stevenson and Poole (1976) and van Hooff (1967) suggested that marmosets use expressions as a form of deliberate communication. However, there is also some evidence, both from the aforementioned studies and my own experiments, to suggest that some expressions are involuntary and the result of particular situations and emotions.

From these anecdotal observations, and the studies done on other primates, I hypothesised that different expressions had different intentions or meanings and the information provided in them would be reflected in the response of an observer. As said before, regardless of intention, conspecifics may be able to identify and use any information provided in specific facial expressions. This experiment therefore used video footage of two contrasting facial expressions from a familiar conspecific. One expression selected had been identified as a fear response (negative; expression 9 in Table 8.2) and the other as a response to food (positive; expression 2 in Table 8.2). Both video clips were derived directly from footage recorded during experiments (typically Experiments 2 and 5) and were played on a monitor with a covered food bowl in front of it. It was predicted that the ‘fear’ facial expression would increase the marmosets’ latency to approach the bowl and remove the cover, and decrease time spent on the table, while a favourable facial expression, in this case lip licking, would have the opposite effect and elicit a faster response and longer stay near the monitor.

8.2 Materials and methods

A subsample of eight marmosets (4 males : 4 females, aged 24 to 84 months) was tested. The older marmosets (aged between 150 and 161 months as of February 2008) used in previous experiments were not tested as they had developed limited mobility and were slower in responding to stimuli, raising questions about their eyesight.

8.2.1 Stimuli

Three videos were used as stimuli for this experiment: 1) repellent/negative (expression 9), filmed during presentation of predator-based stimuli, 2) attractant/positive (expression 2), filmed during presentation of favourite food, and 3) neutral (blue square) (Fig. 8.1). Examples of these expressions are presented on the CD provided with this thesis. The negative facial expression showed the marmoset's eyes widening, mouth opening and ears pulling back (expression 9, Table 8.2; also Fig. 8.1A), similar to the partial mouth open display described in Chapter 2, Table 2.2. This expression was displayed during the presentation of predator-based stimuli and may be an expression of fear (different to the 'fear' expression described by Hook-Costigan and Rogers, 1998, as no teeth were bared). In the positive expression presented, a marmoset lip licked rhythmically, as described in Table 8.2, expression 2 (Fig. 8.1 B).

Figure 8.1. Stills of the facial expressions taken from two of the videos used. A – negative expression (listed as number 9 in Table 8.1), B – positive expression (expression 2 in Table 8.1), C – blue square (neutral). Note that the marmosets were played short video sequences on repeat rather than shown these stills.

The videos were displayed on a computer monitor. Video clips were selected over still images for the experiment to ensure that each marmoset tested saw the entire suite of a facial expression in a fluid motion instead of just a snapshot consisting of a single frame of one moment of that expression. It was considered important that the video image appeared continuous and that there were no disruptions to the display so that the marmosets would be exposed to all parts of the expression over time. A refresh rate of 75 Hz is typically used for video clips presented to marmosets (e.g. Bourne *et al*., 2002; Brown, 2008; Kremers and Lee, 1998; Lui *et al*., 2005, 2007) and ensures smooth viewing. The eyes of marmosets are structurally similar to those of humans (Ordy and Samorajski, 1968; Troilo *et al*., 1993). Video images, in colour as well as in black and white, had been used to test the responses of the same marmosets previously in a separate project, and the marmosets had been found to be responsive to videos (Brown, 2008; Brown *et al*., 2010).

Each marmoset was shown videos of only familiar conspecifics (room- or cage-mates), to eliminate the possibility that the signal was confounded by responses to an unknown face. Not all marmosets could be filmed displaying both the selected expressions. Therefore, a marmoset being tested may have been shown a positive expression from one and a negative expression from another room- or cage-mate. However, when possible this was avoided. The blue square (Fig. 8.1 C) had been tested previously as a neutral stimulus in our laboratory and found to elicit no interest (Brown, 2008).

8.2.2 Experimental procedure

The experiment was conducted in the playroom. The marmosets were tested between 09:00 and 12:00 h. Each marmoset was individually encouraged into the playroom as already described in detail (Ch. 2). Prior to the marmoset’s arrival in the playroom a single table was set up with a 400 mm computer monitor (Diamondtron NF Diamond View) facing towards the climbing structures (Fig. 8.2). A white food bowl, the same as was used before (presenting olfactory stimuli and the pleasant visual stimulus), was placed 15 cm in front of the monitor. A single mealworm was placed inside the bowl and a black cardboard cover was placed on top of the bowl. In our colony, mealworms had been used intermittently as treats and food items in previous experiments; the marmosets had been shown to regularly retrieve them (Stewart, 2009). Mealworms were chosen here as they have relatively little to no odour (certainly none detectable by the human nose) and make no discernible noise, and could therefore not be detected before the removal of the cardboard cover. Marmosets had learned in previous experiments to remove covers from bowls. At this point of the research, bowl and cover had the added bonus of being associated with any type of stimulus, be it pleasant, aversive or neutral, and hence the marmosets could not be certain of the content of the bowl until they had approached and removed the cover. This set-up had the further advantage that the experiment could present video images of facial expressions in response to both pleasant and aversive stimuli, because both were now part of the marmosets' experiences. There had been no single example in any of the previous experiments in which the marmosets ignored a food bowl; invariably, they approached and checked the contents.

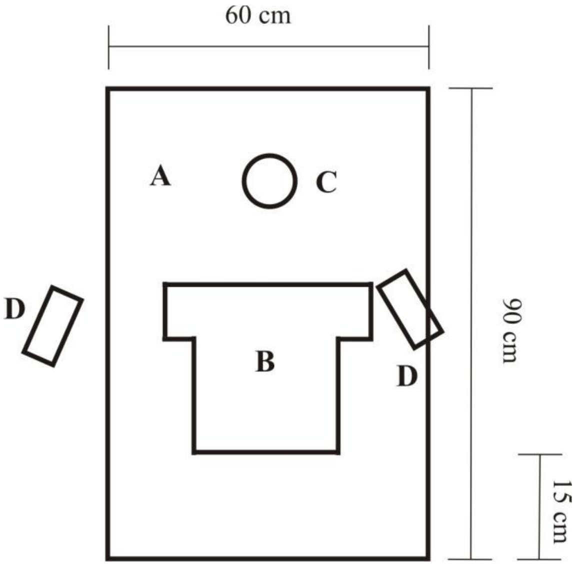


Figure 8.2. View of the table set-up (from above) used for this experiment. A – table, B – computer monitor, C – covered food bowl, D – video cameras.

The three stimuli (negative, positive and neutral) were played in random order twice, i.e. six stimulus presentations were presented in total per trial per marmoset. Each stimulus was shown for 60 seconds and there was a two-minute interval between stimulus presentations. Each marmoset was tested twice, with a minimum of one day between trials. In total, each marmoset saw each stimulus four times.

The experiment began when the marmoset was no closer than 1 m and no further than 1.5 m away from the screen and in a position to view the monitor, i.e. the marmosets were among the climbing structures and facing the monitor. The video clips were positioned slightly below centre of the monitor screen to put them at eye level of the marmosets when they were sitting on their haunches facing the monitor at the bowl. This is the position the marmosets typically take when at the bowl so they could look down into it. The video images were relatively small, only 80 mm in diameter on the screen. This was to avoid pixelation and distortion of the image, particularly at close range, and to simulate the actual size of the face of a marmoset. The small size was also meant to eliminate intimidation as an effect. As mentioned previously, only cage- or room-mates were shown to each marmoset, i.e. if the marmoset being tested was from Room 1, the video clips of the facial expression were derived from a marmoset from that room.

Two digital Panasonic HD40 video cameras with 40 GB internal memory were used to film the trials. One was mounted on a tripod and positioned to the side of the table to capture a diagonal view across the front of the table, particularly focused on the side view of the monitor and the bowl, allowing the camera to record a marmoset’s approach. The second camera was placed next to the monitor, facing directly towards the bowl (Fig. 8.2). This provided a close-up view of the marmoset’s face in order to determine eye gaze. The cameras were focused on the table and the area of the indoor room directly in front of the table; no camera was trained on marmosets outside this area, as the behaviour was scored exclusively when they were at the table. I remained present throughout the experiment, controlling the video clips played on the monitor, replacing the mealworm after every trial and taking notes on the marmosets’ behaviour during trials.

8.2.3 Behaviour scored

All scores were taken from the video footage obtained during the trials. Four behavioural responses were scored: latency to approach (secs), latency to remove the cardboard lid (secs), length of time (secs) the marmoset spent on the table, and number of glances the marmoset directed at the screen.

Latency to approach was measured as the time it took the marmoset from the start of playing the video on the monitor to land on the table. The table was positioned some distance from the closest branch so that the marmoset had to jump onto the table; they never landed on the monitor. Pre-trials had found that the marmosets always approached the bowl directly and jumped onto the table in front of the bowl. Latency to approach was timed to two decimal places.

Latency to remove the cardboard lid was scored as the time taken from the marmoset landing on the table to removing the lid, or at least pushing it aside enough to be able to reach in and remove the mealworm. Latency to remove the cardboard lid was timed to two decimal places.

Scores of looking at the screen were counted after the marmoset had landed on the table. It was impossible to determine whether the marmosets had looked at the screen when they were further away as the cameras had a limited view. Eye gaze of the marmoset had to be directed at the middle of the monitor to be scored.

Timing began when the marmoset landed on the table and stopped when it either left the table or went around the monitor or jumped on top of it. Length of time spent on the table was a measure of how long the marmoset remained in front of the monitor. Presence on the table, if walking around the monitor or at the back of it, was excluded from the total count, i.e. the marmoset was outside the viewing area of the video clip displayed on the monitor. However, this occurred only rarely. Additionally, one marmoset (Aziz, M, 84 months) sat on top of the monitor twice after removing the mealworm and remained there for the duration of the tests. This was not included in his total score. If the marmoset then returned to the table, or moved back to being in front of the monitor, the time that it was on the table again was added to the original score. If the marmoset remained on the table in front of the monitor until the end of the test (i.e. to the end of the 60-second period) the timing was still stopped at that point. Length of time spent on the table was also scored to two decimal places.

8.2.4 Statistical analysis

Due to the small sample size ($n = 8$), non-parametric tests were used. Trials were tested for significant differences using Friedman's test. If there were no significant differences, the mean of the four trials for each behaviour was calculated. Comparisons between stimuli were also made using Friedman's test. Wilcoxon signed-rank tests were conducted *post hoc* when a significant difference in heterogeneity was found.

8.3 Results

In only five of the 96 trials did a marmoset not approach the table and/or computer monitor. These trials were not included in the analysis. There were no statistically significant differences between the four trials of each of the stimuli and for any of the behavioural responses scored (Friedman X^2 values ranged from 0.47 to 4.67 with corresponding p values ranging from 0.97 to 0.20). All trials were therefore combined and a mean taken for each behaviour for each stimulus for further analysis. Table 8.3 shows the mean values of each behavioural response scored ± the standard error for all stimuli presented.

Table 8.3. Mean values for each behavioural response scored (± sem) to the negative expression, positive expression and neutral stimulus (blue square).

	Negative expression	Positive expression	Blue square
Mean latency to approach (seconds)	5.11 (± 0.94)	6.13 (± 1.02)	5.69 (± 0.83)
Mean latency to remove the cardboard cover (seconds)	1.91 (± 0.39)	1.52 (± 0.44)	1.55 (± 0.33)
Mean time spent on the	14.88	22.51	19.78

table (seconds)	(± 1.95)	(± 2.99)	(± 4.07)
Mean number of looks at the screen per minute	1.93 (± 0.12)	2.43 (± 0.26)	1.72 (± 0.25)

There was a significant difference in the time (secs) spent on the table between the three stimuli (Friedman’s test, $X^2 = 7.00$, $p = 0.03$) (Fig. 8.3 A). Wilcoxon signed-rank *post hoc* tests found a significant difference for this behaviour between the negative and the positive expression ($Z = -2.52$, $p = 0.01$), i.e. the marmosets spent the least time on the table during the presentation of the negative expression. There was no significant difference between the negative expression and the blue square ($Z = -1.68$, $p = 0.09$) or between the positive expression and the blue square ($Z = -0.56$, $p = 0.58$). Marmosets spent more time on the table during the presentation of the positive expression than they did the negative, although in some marmosets this was only a minor increase (Fig. 8.3 B).

As latency to remove the cardboard cover and time spent on the table were both measured from the moment the marmoset landed on the table, there was some overlap; however, there was no significant difference found for latency to remove the cover (Friedman’s test, $X^2 = 0.25$, $p = 0.88$).

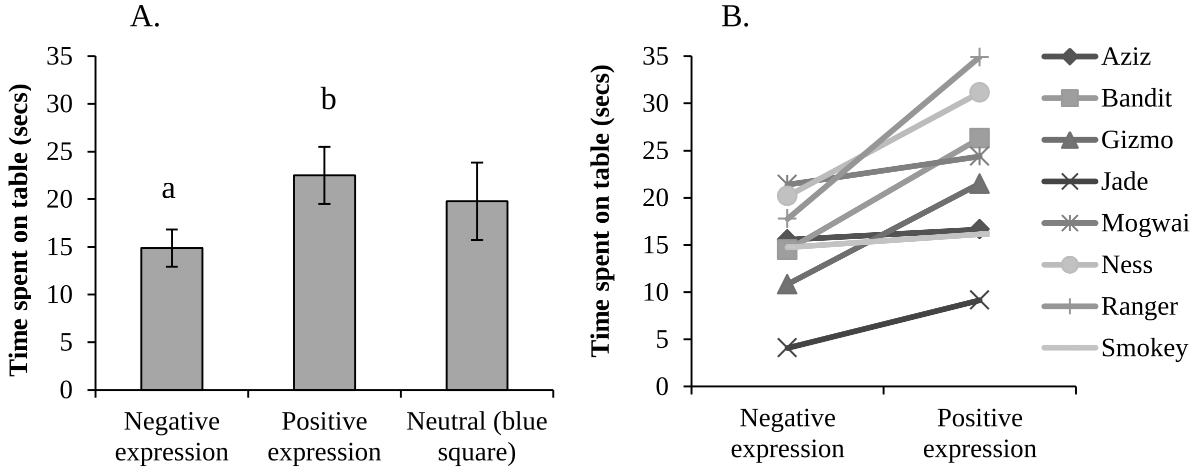


Figure 8.3. Time spent on the table (secs). A – mean values (± sem) of the responses to the two facial expressions and the neutral stimulus. B – responses of the individual marmosets to the two facial expressions. The bar marked ‘a’ is significantly different from the bar marked ‘b’ ($p \leq 0.05$). Note that all marmosets spent the least amount of time on the table during the presentation of the negative facial expression (made in response to predator vocalisations), and most marmosets increased time spent on the table during the presentation of the positive facial expression (except for three with just a marginal increase).

Therefore, the significant difference found for time spent on the table must have been due to the period of time after the cover had been removed. The time scores for only this period were compared among the three stimuli and significant mean difference was found (Friedman's test, $X^2 = 9.25$, $p = 0.01$). The marmosets spent a mean of 12.97 seconds (± 1.95) on the table during the presentation of the negative expression after the cover was removed. This was significantly less time than they spent there in response to the positive expression (21.00 secs ± 2.82) (Wilcoxon signed-rank test, $Z = -2.52$, $p = 0.01$) or the blue screen (18.23 secs ± 3.90) (Wilcoxon signed-rank test, $Z = -1.96$, $p = 0.05$). There was no significant difference in time spent on the table after the removal of the cover between the positive expression and the blue screen (Wilcoxon signed-rank test, $Z = -0.70$, $p = 0.48$).

There were no significant mean differences found for latency to approach (Friedman's test, $X^2 = 0.25$, $p = 0.88$) or the number of looks at the screen per minute (Friedman's test, $X^2 = 3.86$, $p = 0.16$).

8.4 Discussion

The main finding of this experiment confirmed that marmosets were affected by the facial expressions of conspecifics seen on the screen. The marmosets spent considerably less time in the vicinity of the monitor (time spent on the table) when it showed the negative facial expression than when it was playing the video clip of the positive facial expression.

The fact that latency to approach and to remove the cardboard cover remained the same, regardless of the video clip being displayed, suggests that the marmosets' motivation was to first investigate the food bowl rather than the stimulus on the computer monitor. It had been predicted that the negative, or fearful, expression would delay approach and removal of the cover. This did not occur, and may be due partly to the marmosets' tendency not to look at the screen directly or for any length of time, before or when approaching the table. Some marmosets looked at the monitor after landing on the table, prior to removing the cover from the bowl, but most glances were directed at the bowl and only switched to the monitor after the mealworm had been retrieved. The mealworm was retrieved quickly once it had been revealed. As shown by the results, the period of time after removal of the cardboard cover was the period when the marmosets were most affected by the displayed video clip, suggesting that their focus had changed, and the fearful expression elicited a more rapid departure from the table. Furthermore, the results of the analysis of this behavioural response support the interpretation that approach was in response to the food bowl and possible food source (curiosity to investigate the bowl), but once the mealworm had been found and then eaten, promptly after the lid was removed, the stimulus on the screen affected the secondary (non-food-related) response.

A recent study by Morimoto and Fujita (2011) found that capuchin monkeys (*Cebus apella*), also a New World primate, were sensitive to a conspecifics' emotional expression, including facial displays. They found that an observer capuchin was more likely to show interest in a hidden object if the demonstrator monkey, who was able to observe the contents of the container, reacted with a positive expression than with a negative or neutral expression (Morimoto and Fujita, 2011). The marmosets in my study did not appear to make the same connection between the expression of a conspecific and the covered food bowl. However, Morimoto and Fujita (2011) used a live demonstrator and this may have had the desired effect because the observer could follow the eye gaze of the demonstrator monkey. The marmosets on the screen in my experiment were not looking in the direction of the bowl. It is possible that without specific context the marmosets instead focused on first checking the bowl before attending to the facial expression on the monitor.

The findings of this experiment suggest that the marmosets a) perceived a signal and b) gained some information from the two facial expressions presented. Facial expressions in response to odours (and tastes) have been described in humans (e.g. Steiner, 1979; Weiland *et al*., 2010); interestingly, these facial expressions are intensified when they are being observed (Jäncke and Kaufmann, 1994). In a search of the literature I was unable to find any studies specifically describing facial expressions in response to auditory stimuli in non-human primates. While some of the facial expressions displayed by the marmosets were observed only during the presentation of predator vocalisations (such as the mouth partially open, eyes wide, ears back expression), it cannot be determined whether these expressions are directly related to specific emotions. Further study is required to determine the extent of facial expressions in marmosets and the role they may play in communication.

CHAPTER NINE

GENERAL DISCUSSION

9.1 Introduction

This research was designed to test the importance of different sensory cues presented simultaneously and to test whether it was possible to use Partan and Marler's model (1999) of multimodal signalling also in the context of food- and predator-based stimuli. It was shown that the stimuli in different sensory modalities typically interacted to elicit a response (modulation), and the marmosets responded to both sensory stimuli although, in some cases, dominance of one modality over another occurred, suggesting a hierarchy. The number of strategies and variation in response showed clearly a large repertoire of possible decision making, giving olfaction and audition a much more important role to play in predator recognition and anti-predator strategies, but also in food recognition. Another important discovery was the extensive use of facial expressions in all experiments, but most unexpectedly in response to aversive olfactory and auditory cues. Furthermore, several facial expressions not described in the literature were noted.

It is important to establish that the marmosets did not habituate appreciably to any of the six main stimuli used in these experiments (taxidermic specimen of a quoll, marshmallow, cat faeces odour, marshmallow odour, leopard growl and marmoset food-related calls) in order to analyse the results. Habituation could have been masked in the altered responses to the combinations from the original presentation (Experiment 2); to ensure that understanding of the results is based on the effect of multiple stimuli presented together and not habituation it was necessary to determine whether habituation did occur. This is particularly important for the predatory stimuli as repeated exposure to static objects without real threat may have led to them being regarded as no longer aversive, let alone threatening or frightening. Indeed, Dacier *et al*. (2006) found that captive animals can habituate quickly to a mounted oncilla cat (*Leopardus tigrinus*) when no training of aversive association occurs. This did not happen during my experiments. Any difference in the marmosets' response to a particular stimulus when presented in a combination was due to the presence of another modality or stimulus. In contrast, habituation clearly occurred in response to the neutral stimuli (PVC tube, tea infuser and marmoset housing background noise) with only two presentations, as shown in Appendices I, II and III, after an initial weak show of transitory curiosity in the first trial.

The decision to test each marmoset on its own had been made for several reasons. Firstly, it was important to test the response of the individual to the stimuli. This was to avoid other marmosets affecting the behaviour of the marmoset being observed. It had been noted that not every marmoset responded in the same manner to the stimuli; indeed, some marmosets were quite bold in their response to the predatory stimuli, while others were cautious (Kemp and Kaplan, 2011). It was possible that the presence of a conspecific might have altered the immediate reaction of the marmoset. Testing animals in groups, i.e. 'safety in numbers', may make animals bolder when responding to predatory threats (Colquhoun, 2007). Also, as food-based stimuli were also used in these experiments it was important that competition for resources did not confound the results. It is important to note, however, that most of the behavioural responses scored were consistent throughout the group and it was typically only in high-risk situations that strong individual differences occurred (i.e. retrieving or not retrieving the marshmallow when the quoll was present). Secondly, it was possible to conduct the experiments in this way as the marmosets were accustomed to being separated from cage mates for testing and could maintain vocal contact with conspecifics while in the indoor room. Furthermore, immediately after each trial had finished the slide blocking access from the indoor room was removed so that the marmoset could access the runway leading back to their home cage. Thirdly, the experiments were kept short so as to avoid causing unnecessary stress due to separation.

However, it is important to keep in mind that wild marmosets live in groups. Perception and responses may be modified by social interactions, the presence of conspecifics and the number of conspecifics. Individuals who respond strongly to predatory stimuli on their own may show less reaction when a conspecific who does not respond is present, and vice versa. Furthermore, there may be a relationship between the number of individuals present and the boldness of the group, expressed as mobbing, when faced with a predator (Gursky, 2005; Poiani, 1991; Wiklund and Andersson, 1994). We know that animals learn from the behaviour of conspecifics and inexperienced individuals can show appropriate anti-predator behaviour after being exposed to the responses of experienced individuals (e.g. Mineka and Cook, 1988). There is validation to testing groups of animals, and in some cases there may be no other choice (e.g. field studies); certainly for social animals such as marmosets it would be more ecologically relevant. However, it is still important, when possible, to examine the response of individuals in order to establish any differences between individuals and the perceptual basis of response first, before introducing an affecting factor such as conspecifics. Additionally, marmosets are thought to be scramble foragers, i.e. they often forage separately, maintaining only auditory contact (Voelkl and Huber, 2007). As field observations of marmosets (Gisela Kaplan, personal communication) and the closely related saddleback tamarin (*Saguinus fuscicollis*), with a similar feeding ecology to common marmosets (Goldizen, 1987), show, close group member presence is not always observed during foraging. It is therefore possible that the perception of stimuli and predation events may occur while only one individual is in the vicinity. It would be of interest to conduct field studies on the responses of common marmosets when visually distanced from each other and when one or more conspecifics are present.

9.2 Perception of stimuli

9.2.1 Predator recognition

The results of my research show that the marmosets responded to aversive stimuli by displaying anti-predator behaviour, despite their lack of experience with predators, and did so in different ways. That is, they mobbed the quoll, avoided the cat faeces odour, and hid, ‘froze’ and became silent in response to the leopard growl. These differences in response may be due to specific information provided within each stimulus, perhaps indicating different levels of risk.

Importantly, the responses of the marmosets to the aversive olfactory and auditory stimuli reflected those seen in the three other studies on captive primates (e.g. avoidance as also seen in captive red-bellied tamarins, *Saguinus labiatus*, Caine and Weldon, 1989; cotton-top tamarins, *S. oedipus*, Buchanan-Smith *et al*., 1993; and gray mouse lemurs, *Microcebus murinus*, Sündermann *et al*., 2008). Non-primate species tested in the wild also showed avoidance to the odour of predator faeces (e.g. brushtail possums, *Trichosurus vulpecula*, Morgan and Woolhouse, 1995). Other species, such as western grey kangaroos (*Macropus fuliginosus*) have been shown to not only discriminate between predatory and non-predatory odours but also between sympatric and novel predatory odours (Parsons and Blumstein, 2010; Parsons *et al*., 2007). Furthermore, the marmosets distinguished between the faecal odours of predators and that of a herbivore (rabbit, Ch.3). Two marmosets even produced a known mobbing/alarm call towards two of the predatory odours (Ch. 3) and there was some evidence that the odour of cat faeces elicited terrestrial vigilance (Ch. 4 and 5). Evidence of such responses suggests, a point also made by Nolte and colleagues (1994), that there is some important information in the faeces of predators that is more arousing for prey animals than the faeces of true herbivores. The findings of my study imply that the marmosets considered the predator-based odours not just ‘aversive’ but possibly as a threat.

The marmosets showed strong fear responses to all the predator vocalisations presented (Ch. 3 and 7), and some of these sounds elicited species-specific responses. This finding was unexpected since audition has been theorised to require the most learning and experience for predator recognition (Berger *et al.*, 2001; Gil-da-Costa *et al.*, 2003). Two particularly interesting behavioural responses were noted. One marmoset (Ash, F, 161 months) responded to the snake hiss by clinging to the underside of a branch (Experiment 1). This behaviour was not repeated in Experiment 5 and it was only displayed by this one individual. However, as an immediate reaction to a sound that was played amongst a variety of other sounds this is certainly a strong and distinctive reaction. Other individuals hid during the presentation of this predator sound (Ch. 7) and continued to do so even after the sound had ended. Ferrari (2009) suggested that predation on New World primates by snakes may constitute a more important and even disproportionate level of threat than the number of actual predation events witnessed would suggest. There is also some evidence that juveniles are more at risk of predation by snakes than other age groups (Corrêa and Coutinho, 1997; Ferrari and Beltrão-Mendes, 2011; Ferrari and Lopes Ferrari, 1990). Potentially, old marmosets with limited mobility may also be at risk. Ash, who had shown the strong response of clinging to a branch, was the oldest marmoset in our colony and was certainly not as agile as other members. Furthermore, what made her reaction to the snake particularly remarkable is that she rarely showed strong anti-predator responses to any of the other stimuli I presented.

Equally noteworthy was the vigilance behaviour in response to the calls of the red-shouldered hawk; the marmosets looked up frequently, something they had not done in any other experiment. Other studies have shown that captive marmosets tested in open (i.e. no roof) outdoor enclosures scan the sky frequently (Barros *et al.*, 2004), suggesting an expectation of risk of predation from aerial attacks (Caine and Weldon, 1989). Had the marmosets recognised the speaker as the sound source they would not have looked up. All sounds were played from the same location - a speaker placed on a ledge just behind the table, a position closer to the ground than to the ceiling. The marmosets did not follow the sound source but looked up at an imaginary sky as if the sound was expected to come from above. This finding is especially important because it suggests that the specific characteristics of the sound might have triggered this behaviour. Auditory awareness is discussed further in Section 9.2.2.3.

9.2.2 Hierarchy in sensory perception

In the General Introduction of this thesis it was suggested that it was unlikely that stimuli in different sensory modalities would be processed in a hierarchal manner as this would not allow animals to respond differently to the same stimuli in different contexts. However, Partan and Marler (2005) have also suggested that each sensory component may not have equal weight in processing importance, and this is certainly backed up with the behavioural evidence from some of their signalling classifications. Welch and Warren (1980) suggested that a hierarchy may be dependent on the appropriateness of a particular modality to a specific task; that is, visual stimuli are dominant in spatial tasks while auditory cues are more important in temporal tasks. Still, this is not a strict hierarchy and the importance of one modality over another may be dependent on the quality of the stimuli and the responses they evoke (Alais and Burr, 2004). Uncertainty regarding a stimulus in one modality may require other modalities in order to locate and recognise the original stimulus (Alais and Burr, 2004). This may have been the case when presenting the odour of cat faeces, as is discussed later (Section 9.3.1).

9.2.2.1 Vision

As mentioned throughout this thesis, primates are considered to be visually orientated (Buchanan-Smith, 2005; Laska *et al.*, 2000) and indeed the marmosets responded strongly to the quoll and marshmallow. The marmosets approached both the quoll and the marshmallow, albeit keeping a greater distance from the quoll (Ch. 4). Mobbing/alarm calls, interestingly, were made during the presentation of both stimuli, although there were significantly more such calls in response to the quoll, and sooner, than to the marshmallow, and they looked at the quoll more than at the marshmallow. It seems from these findings that marmosets may have a relatively set suite of responses to visual stimuli in general (approach, vocalising, looking), typical perhaps of inspection behaviour. Indications of the type of stimulus can be gleaned from finer distinctions and intensity of responses.

When the marmosets were faced with two conflicting, but potentially equally dominant, visual stimuli, they were forced to make choices between the two. Based on the literature, it was predicted that the quoll, as a predatory stimulus, would have been dominant over the marshmallow as it represents a risk; since the marmosets were not starved, not retrieving the marshmallow would not have been a major loss. The results showed that, contrary to this prediction, the visual presence of the marshmallow was equal to that of the quoll, if not possibly dominant since its presence encouraged the marmosets to approach the quoll more closely than they would have done if the quoll had been presented on its own. It is possible that the marmosets would not have risked approaching for a less desirable food item, or one they received often. It was not possible to test these ideas within the confines of this study, but it may be that the influence of visual stimuli is dependent not only on type but the strength of desirability or repellence.

When the quoll and odour of cat faeces were presented simultaneously (Ch. 5, related combinations only), responses showed clearly that the visual component was dominant over the olfactory one, in the sense that there was no change in behaviour between responses to the quoll alone and in combination with the aversive odour. This was not unexpected. Being wary of a predator that may be in the vicinity, a response elicited by discovering its faeces, is pointless when already visually faced with a predator, thereby requiring an immediate response that is not necessary to the odour alone. However, the pleasant combination of the edible marshmallow (visual stimulus) and marshmallow odour elicited responses that were modulated rather than identical with the responses to the visual cue alone. The presence of the marshmallow odour encouraged and increased attempts to gain access to the food inside the bowl rather than lead to fast departure, as seen after the retrieval of the accessible marshmallow presented without the odour. This suggests that there was an interaction between the visual and olfactory cues which enhanced the response seen to the individually-presented stimulus. The interaction of these cues may have increased the attractiveness of the marshmallow. It is also possible that the presence of the odour suggested an additional food source that the marmosets could access.

The visual stimuli, when presented simultaneously with auditory stimuli (both related and conflicting), were clearly affected by the presence of a sound, regardless of type. This was more evident in the bimodal aversive combination than it was in the pleasant (Ch. 5). The marmosets' mean distance from the quoll was greater when the leopard growl was also presented, they had a longer latency to approach, did not produce as many mobbing/alarm calls and looked down more often than they did when the quoll was presented alone. The greater distance and longer latency to approach indicate that the combination of quoll and leopard growl created greater uncertainty, even fear, and might have been seen as an increased threat. The threat-sensitivity predator-avoidance (TSPA) hypothesis (Helfman, 1989) is relevant in this context as it has suggested that animals will improve their recognition and threat assessment of predators when multiple cues are provided (Helfman, 1989; Smith and Belk, 2001). This bimodal aversive combination (visual and auditory) elicited stronger withdrawal responses than any of the cues presented on its own and would therefore seem to support Helfman's hypothesis. Indeed, graded risk assessment of aversive stimuli was evident throughout all combinations presented, both related and conflicting.

However, the results also showed that the allure of the marshmallow could entice the marmosets to approach a potential threat, even when responses suggested that the risk level was perceived as high (i.e. quoll presented together with the leopard growl, as opposed to just the quoll or leopard growl). This shows clearly that the marshmallow was such a strong attractant that caution was ‘thrown to the wind’, and if the quoll had been a moving (i.e. live) predator, the attraction to the marshmallow may have been fatal in some cases. This is especially important to consider in captive breeding-release programs – it is not just knowledge of risk and danger of which animals must be aware, but also they must to resist the temptation of responding to enticing stimuli at times of high risk.

9.2.3.2 Olfaction

It was an important aspect of this study to determine how marmosets respond to odours and the influence other sensory modalities might have on their behavioural response to these odours. Despite evidence suggesting that olfaction is an important modality in the social communication systems of many primate species, and certainly of marmosets (Lazaro-Perea *et al*., 1999), this is not reflected in the number of studies found in the literature on this field. This is especially the case for predator and food recognition. The response of the marmosets to the faecal odours of carnivores showed not just perceptual awareness, but assessment awareness, as defined by Sommerville and Broom (1998). That is, the marmosets showed long-term responses to these odours and not just instantaneous reactive behaviour.

Firstly, it was established that the marmosets detected and responded to odours that had been diluted; as the marmosets’ own bodily odours tend to be quite pungent there was always the possibility that this would not occur. Squirrel monkeys (*Saimiri sciureus*), also New World primates, have been found to be able to still detect some food-based odours at a dilution ratio of

1:10000 (Laska *et al*., 2000). It is known that some primates use odours to discriminate between edible and inedible fruits; that is, they use the information in the olfactory cue to determine ripeness, which changes over time (e.g. black-handed spider monkeys, *Ateles geoggroyi*, Hiramatsu *et al*., 2009). However, in terms of perceiving information about potential predators from olfactory cues, very little is known in primates. As odours dissipate over time, it would not only be interesting to test if primates can detect the scent of a predator that is several hours old or heavily diluted, but also to determine if their response indicates they differentiate between fresh and old, strong and weak, scents. Wild dogs can certainly read and perceive levels of information (social, locational, temporal and sexual) from scat and urine markings (Rogers and Kaplan, 2000) and, as was stated before (Ch. 1), some primates have been found to compare well with dogs in their olfactory perception of some odours (Danilova and Hellekant, 2000, 2002; Hellekant *et al*., 1997; Hübener and Laska, 2001; Laska and Seibt, 2002; Laska *et al*., 2000, 2007; Siemers *et al*., 2007). Olfactory sensitivities appear to be very strong in the marmoset. Indeed, the strongest response to indicate aversion, as to the odour of cat faeces, was the use of facial expressions and led to the discovery of new facial expressions in this research project. One of these expressions observed in response to the faecal odour had physical commonalities with those seen in humans expressing ‘disgust’ (Ekman and Friesen, 1969). Although the marmosets did not mob, hide or ‘freeze’ in response to the odour of cat faeces, this facial expression appeared to suggest a strong dislike or aversion to the odour.

9.2.4.3 Audition

There are different levels of auditory awareness, most notably ‘sensation’ and ‘perception’ (Heffner, 1998). Sensation refers to the ability to respond to sounds, while perception is the ability to respond to the biological characteristics of the sound source (Bullot and Égré, 2010; Heffner, 1998). The behaviour of the marmosets showed clearly that they could do both, triggering some instantaneous responses (e.g. freezing), and others that may have been based on certain frequencies (e.g. looking up in response to the high-frequency call of the red-shouldered hawk). That is to say, just as some basic visual elements (e.g. frontally placed eyes) appear to be known triggers of fear, growls and high whistles may also be processed as fear-inducing.

The behaviour most affected by the presence of an auditory stimulus was the marmosets' own vocalisations, the number of which typically decreased during the presentation of a sound. This result was also found during the presentation of conflicting combinations involving an auditory stimulus (Ch. 6) and the predator vocalisations (Ch. 7). By reducing their rate of vocalising, the marmosets may have been able to focus more on the unexpected sound and/or the other stimulus present. Normally, marmosets respond vocally at least to a conspecific's phee or twitter call (Chen *et al*., 2009; also personal observation); however, no increase in contact calling, or any other vocalisation, was scored after the presentation of their own food-related calls.

Falling silent is a common response of prey animals to predator vocalisations (e.g. Gleason and Norconk, 2002). However, Diana monkeys (*Cercopithecus diana*) only fall silent when played the vocalisations of pursuit hunters (such as chimpanzees), not surprise hunters (such as leopards) (Seyfarth and Cheney, 1997; Zuberbühler *et al*., 1997, 1999). Interestingly, surprise hunters are thought to leave the area if their prey alarm calls, indicating that the element of surprising is gone (Seyfarth and Cheney, 1997). However, the marmosets did not respond in this way. It is not known if wild marmosets distinguish between pursuit and surprise hunters and if they respond differently to the vocalisations of both, but should this be the case in the wild it may highlight the essential role of learning and experience. The marmosets in this colony would not know the difference. Indeed, as mentioned before, predator recognition in the auditory modality is thought to be reliant on experience in order to distinguish between similar sounds and understand the biological source behind the vocalisation (Berger *et al*., 2001; Gil-da-Costa *et* *al*., 2003). Nevertheless, research on captive-born California ground squirrels reared in social isolation for three years indicates that, after hearing chatter and whistle vocalisations, they act as if a snake were nearby (Tromborg, 1999).

Furthermore, the results also showed that the marmosets responded to sounds presented at different frequencies, both high and low. It has been suggested that marmoset hearing is orientated towards high rather than low-frequency sounds, although their range is believed to be between 125 Hz to 36 kHz (Coleman and Ross, 2004; Osmanski and Wang, 2011; Seiden, 1958). Marmoset vocalisations are typically at high-frequencies (Bezerra and Souto, 2008). Whether or not the marmosets would even perceive the low-frequency leopard and snake sounds was questionable as the peak sensitivity of hearing by marmosets is 7 kHz (Osmanski and Wang, 2011; Seiden, 1958); perception of the snake hiss was further debateable due to its ‘white noise’ properties (Young, 1991). However, the behaviour of the marmosets demonstrated that the sounds were perceived and elicited fear responses. Still, while one behaviour scored (looking up) differed significantly between the two low-frequency sounds and the high-frequency sound of the red-shouldered hawk, there was no significant difference between the other responses to the three predator vocalisations, i.e. activity, latency to move and vocalise, vocalisations, looks downward, hiding and freezing. This suggests that there may be a general pattern of response by predator-inexperienced animals to predator vocalisations of any frequency. Indeed, this has been found to be true of predator-inexperienced rabbits in response to visual stimuli (Vitale, 1989).

Thus, odours and sounds by themselves not only elicited strong responses but had specific meanings or provided specific information. This supports the argument that these modalities are important and marmosets may not just use cues in these modalities for social communication. Indeed, these modalities may be important for primates in identifying or tracking the long-term movements of predators and in visually-occluded environments where only short-range visual tracking is possible (Ache, 1991; Apfelbach *et al*., 2005; Blumstein *et al*., 2008; Coss *et al*., 2005; Dominy *et al*., 2001). These modalities are also likely to be important for detecting food in environments where vision is limited (Dominy *et al*., 2001). Although there is some evidence to suggest a trade-off in sensory ability between vision and olfaction in primates (Dominy *et al*., 2001), and to some degree between vision and audition (Heffner, 2004), that is not to say that that these modalities are always of secondary importance or ignored for information about the environment (Ghazanfar and Santos, 2003).

9.3 Multimodal signalling

As argued before (Ch. 1), a single event may have multiple stimuli that integrate to provide not only a richer experience (De Gelder and Bertelson, 2003) but also may improve the likelihood of recognition of the stimulus or event (Calvert *et al*., 2004). Indeed, the marmosets' responses to the combinations of stimuli showed that their behaviour was affected, and made more complex, by the amalgamation of these stimuli. The multimodal signalling model proposed by Partan and Marler (1999) suggests that a signal or cue is expressed through multiple modalities and the perceiver responds to the incorporation of all these cues or stimuli (Partan, 2004). If the signal is broken down into its various components and each cue is tested individually, the receiver may respond to the cues in similar (redundant signalling) or different (non-redundant signalling) ways. However, the cues that I presented to the marmosets were not from the same stimulus, as is typically studied in multimodal communication. Indeed, the field of multimodal studies has been characterised by studies on sexual and other social displays by a conspecific, not generally on predator- and food-based stimuli. Moreover, cues, even in different modalities, are typically congruent, i.e. visual and auditory cues come from the same individual and for a unified purpose. Still, even without a common origin to all components of a signal, they may be perceived as one as long as the cues are presented simultaneously. Indeed, Partan and Marler (2005) classified the response of chickens (*Gallus domesticus*) to artificially combined (i.e. not a naturally occurring signal) visual and chemical stimuli, to determine aversive to unpalatable prey items (Rowe and Guilford, 1996), as an experiment testing multimodal signalling. Combinations I presented in the research for this thesis are shown using Partan and Marler's model (1999) of redundant and non-redundant signalling in Table 9.1 (this follows the same format as used in Table 1.1, Ch. 1). Examples of enhanced redundant signalling, independence, dominance and modulation non-redundant signalling were found. I have also presented one combination in this table that shows how scoring two behavioural responses can suggest different signalling classifications. True independence was hard to classify and to some degree modulation tended to occur, even when the marmosets tried to respond to both stimuli presented. In general, responses to combinations indicated a mixture of signal classifications, as shown in the last example presented in Table 9.1 below.

One of the issues in research on multimodal signalling that Partan and Marler (2005) addressed was that the classification of the signal can change depending on the number of behavioural responses measured. Indeed, in response to the quoll and marshmallow presented together, had only food-related calls been measured, the combination would have been classified as non-redundant dominance signalling, supposedly showing that the quoll had a greater influence on the marmosets' response. However, if only mean distance had been scored the classification would be non-redundant independence signalling. Perhaps the level of complexity needed to classify conflicting situations is not provided in Partan and Marler's model (1999). This issue is discussed further in Section 9.3.2.

Table 9.1. Examples of Partan and Marler's signalling model (1999) using the combinations presented in my research.

Sensory Cue	Response	Multimodal signal	Response	Multimodal signal type
Cat faeces odour	No significant difference between any of the responses scored	Aversive olfactory/aversive auditory	Increased distance from the odour Increased number of looks down	**Enhancement: redundant signalling**
Leopard growl				
Cat faeces odour	Avoidance	Aversive visual/pleasant auditory	Avoidance Few vocalisations	**Independence: non-redundant signalling**
Marmoset food-related calls	Few vocalisations			
Marshmallow odour	Mobbing/alarm and food-related calling	Pleasant olfactory/pleasant auditory	Differences were only between the responses to the combination and the marshmallow odour alone –reduction in mobbing/alarm and food calling; also greater mean distance, longer latency to vocalise and more looks down during the presentation of the combination	**Dominance (of auditory stimulus): non-redundant signalling**
Marmoset food-related calls	No mobbing/alarm calls or food calls			
Quoll	Mobbing/alarm calling	Aversive visual/aversive auditory	Mobbing/alarm calls were produced; fewer than given to the quoll alone but more than to the leopard growl alone	**Modulation: non-redundant signalling**
Leopard growl	No mobbing/alarm calls			
Quoll	Approached slightly; no food calling	Aversive visual/pleasant visual	Mean distance was in between the approach distances to both stimuli presented alone. Food calling was not significantly different from the quoll alone	**Independence (distance) AND dominance (food calling): non-redundant signalling**
Marshmallow	Approached closely; food calling			

9.3.1 Redundant signalling

Other studies have found that when a signal consists of multiple components but in different modalities, these cues may still elicit the same response (e.g. reference), i.e. redundant signalling (Partan and Marler, 1999). The presentation of the cat faeces odour and leopard growl in Experiment 3 provided one opportunity to test whether the response of the marmosets to the combination of two aversive stimuli would result in equivalent or enhanced redundant signalling.

It was shown that the degree of response was enhanced by the simultaneous presentation of these stimuli in terms of distance from the combination (from the odour component) and number of looks down (Table 9.1). Indeed, the marmosets looked down more often in response to the cat faeces odour and leopard combination than they did to any other aversive combination presented, suggesting that both cues were necessary in order for the marmosets to perceive information regarding the terrestrial origins of the stimulus (enhancement of a redundant signal). This may have been due to some ambiguity in the information perceived from the cat faeces odour. As suggested previously, it is not possible to determine from the responses of the marmosets whether they perceived information regarding a predator in the faecal odour or if they found it simply unpleasant. This uncertainty in the type of stimulus may have required another stimulus in a different modality in order to refine (or enhance) the response.

9.3.2 Non-redundant signalling

Partan and Marler (1999) had described four possible outcomes to a non-redundant multimodal signal: independence, dominance, modulation and emergence. Diurnal primates are considered to be visually orientated, as said before, and it seemed plausible that if any stimulus would elicit a response that demonstrated its dominance over another modality or modalities, it would be the visual component. Indeed, the marmosets did attend to the visual stimuli in more ways than they did to other sensory stimuli presented. However, independence, dominance and modulation of the responses to the individually-presented stimuli were all observed in response to both related and conflicting combinations, even with a visual stimulus present, and sometimes all three in response to one combination (as shown in Tables 5.13 and 6.9). For example, mean distance from the marshmallow was not affected by the presence of the marmoset food-related calls; this behaviour indicated dominance of the visual stimulus. However, the number of mobbing/alarm calls suggested that the response to both stimuli had been modulated; the marmosets made significantly fewer mobbing/alarm calls in response to the combination than they did to the marshmallow alone but significantly more than to the auditory stimulus alone. It was therefore not always possible to classify a combination using Partan and Marler's model (1999) when considering all the responses scored, and it was perhaps not designed for this much complexity.

Another problem associated with this model derives from determining whether the responses to the individually-presented cues are the same (i.e. redundant) or different (i.e. non-redundant) responses. I would like to readdress the experiment first described in the General Introduction by Rybak *et al*. (2002) used by Partan and Marler (2005) as a type of enhanced redundant signalling. Both cues in the signal made by the male fruit fly (*Drosophila melanogaster*) elicited the same behaviour, but at significantly different rates (Rybak *et al*., 2002), ultimately suggesting that they are different responses, which is indicative of non-redundant signalling. As mentioned before in this chapter, the marmosets showed the same types of responses to both the quoll and the marshmallow, but to significantly different degrees. However, redundant signalling would not fully cover the complexity of response that I scored when both visual stimuli were presented together. In other words, the model might work for one or two combinations if the measured outcome concerns only one or two alternative responses, i.e. mating will or will not take place. However, in anti-predator behaviour there are many subtleties and strategies that, together, may lead to changed outcomes. I would therefore conclude that Partan and Marler's model was important to investigate and seminal for the development of my research questions but, beyond simple combinations and connections, this construct may have lost its explanatory power.

9.4 Biological basis

The results of Experiments 3 and 4 showed that often when presenting stimuli from different modalities the response of the marmosets altered, indicating that the two stimuli had interacted in some way. It has been suggested that stimuli from cross-modalities activate neural mechanisms that could not be predicted through a unimodal approach (Stein *et al*., 2004). That is, multiple stimuli from different modalities presented together (both spatially and temporally) are required to activate some processes which do not respond when only a single stimulus is presented (Meredith and Stein, 1983, 1986; Meredith *et al*., 1987; Stein and Meredith, 1993). Indeed, there is a heightened dependence on multisensory integration as uncertainty increases regarding the stimulus in individual sensory domains (Alais & Burr, 2004). For example, a blurry visual stimulus may require a corresponding auditory stimulus in order for it to be identified and/or located (Alais and Burr, 2004). Furthermore, the principle of inverse effectiveness suggests that multisensory integration is more likely to occur when the stimuli elicit relatively weak responses when presented individually (Meredith and Stein, 1983). The ability to integrate and process these sensory cues from multiple modalities is possible due to multisensory neurons capable of responding to stimuli from different senses (Stein and Stanford, 2008).

Multisensory neurons are present at all levels of the mammalian brain, even those previously thought to be modal specific, occur in clusters at the borders of cerebral lobes, and often integrate with unisensory neurons (Wallace *et al*., 2004). The superior colliculus (SC), a midbrain structure, has many multisensory, mostly bimodal, neurons, capable of processing visual, auditory and somatosensory stimuli (Stein and Meredith, 1993). A smaller number of multisensory neurons in the SC are able to integrate data from stimuli in three sensory modalities (Wallace and Stein, 2001). This capacity of the SC enhances the salience of the initiating event, allowing it to stand out from neighbouring stimuli and affecting orientation behaviour to otherwise minimally effective environmental cues (Meredith and Stein, 1983; Stein *et al*., 1988). This is essential because animals have a limited capacity to focus their perceptual and cognitive resources on available sensory data (Dukas, 2002).

Multisensory neurons have also been found in the amygdala (Calvert *et al*., 2004), the portion of the midbrain responsible for processing fear (LeDoux, 2000; Ohman, 2005). These neurons have been shown to respond to corresponding visual and auditory stimuli, such as the fear facial expression and matching vocalisation of rhesus macaques (*Macaca mulatta*, Kuraoka and Nakamura, 2007). It appears that this structure is less flexible in learning the associations between stimuli in different sensory modalities than is the orbitofrontal cortex, for example (Calvert *et al*., 2004), and it may be more responsible for instantaneous survival mechanisms (Kaplan, 2008).

Most literature has focused on cross-modal perception and processing of visual and auditory stimuli together (e.g. Bullot and Égré, 2010; Calvert *et al*., 2004; Kubovy and Schutz, 2010; Mattiessen, 2010; Nudds, 2010; Spence and Driver, 2004). Examples are not only evident from events in which the visual and auditory stimuli come from the same location (e.g. a macaque displaying a facial expression while vocalising; Partan, 2002), but there is also evidence that incongruent stimuli in these modalities can influence the way in which they are processed and how an individual may respond to them. These may be strongly incongruent: a human example of this is the problem motorists have concentrating on driving or reading street signs when listening to the radio or talking on their phone (Shomstein and Yantis, 2004). This problem occurs due to limited capacity for attending to stimuli (Dukas, 1998) and the interplay of incongruent and distracting auditory and visual modalities. Multisensory neurons and/or the perception of stimuli together can also occur via the ‘ventriloquist effect’ (Spence and Driver, 2004), whereby the auditory component is displaced and associated directly with the visual cue. This type of binding is especially important for the presentation of the quoll and the leopard growl. Unlike a ventriloquist act, there was no specific visual cue from the quoll that the marmosets could directly associate with the leopard growl (i.e. a moving mouth), but it appears that this was not necessary. It may be that the presence of both the visual and auditory stimuli was enough to synchronise firing of separate, but interconnected regions of the brain (Treisman, 1996), allowing these stimuli to be associated and processed together.

Behavioural and neurological evidence is beginning to emerge suggesting that there are pathways, at least in the human brain, for associating visual and olfactory stimuli with each other (e.g. Gottfried and Dolan, 2003; also spider monkeys, Hiramatsu *et al*., 2009; Österbauer *et al*., 2005; Thesen *et al*., 2004). For example, an odour on a piece of coloured card is more readily identifiable by humans when the two components correspond (Zellner *et al*., 1991). That is, when a cherry odour is presented on a piece of red card humans correctly guess the odour more often than when the same coloured card is presented with a lemon odour (Zellner *et al*., 1991). A recent experiment using 4 month old human infants has found that olfaction can shape and alter visual behaviour (Durand *et al*., 2011). As the brain has generally learnt from an early age to associate these stimuli (visual information, such as colour or a feature and a corresponding odour) together, it may be that learning is required in order for binding to occur. This was evident in my research in that the response of the marmosets suggested that they associated the marshmallow with its odour, but not the quoll with the odour of cat faeces. The marmosets had prior experience with marshmallow, but no learning experience to connect the odour of cat faeces with the quoll. It would be interesting to determine whether this type of binding occurred after one or several encounters with both stimuli together. That is, would the marmosets respond to the faecal odour with mobbing behaviour as they do to the quoll because the two stimuli are now associated? As this research project was concerned with immediate responses to stimuli this was not tested.

Furthermore, there has been little if any exploration of olfactory and auditory stimuli, although there is behavioural evidence (e.g. Anton *et al*., 2011; Skals *et al*., 2005), including the findings of this research, to suggest that such integrative processing pathways exist, in insects at least.

9.5 Facial expressions and cognition

There are many studies associating diversity of facial expressions used by any given primate species in social contexts with neurological structures, group size, phylogeny and motor control (e.g. Burrows, 2008; Burrows *et al*., 2009; Diogo *et al*., 2009). Humans are considered to have the most varied and complex expressions, and are said to have a greater ability to process and associate them with internal emotional states, than other primates (Burrows, 2008; Ekman, 1999). The other great apes, particularly the more sociable ones (i.e. not including orang-utans because they are considered to be only semi-social), have the next degree of complexity, followed by the Old World monkeys and then the New World monkeys. In particular, it is believed that New World monkeys do not have the complexity of facial musculature required to produce a wide diversity of expressions, nor do they have the complex social structure seen in the ‘higher’ primates which would require a variety of expressions (Burrows, 2008). Furthermore, it is believed that the platyrrhines may be more reliant on olfactory rather than visual signals from conspecifics to communicate (Barton, 2006; Dobson and Sherwood, 2011). However, although they may lack the fine motor control required for particular definitions and movements of facial structures, that is not to say that marmosets are unable to produce a variety of facial expressions and potentially have them understood by conspecifics.

There appears to be a difference in the ability of platyrrhines and catarrhines in processing and producing facial expressions in that the expansion of the primary visual cortices (V1), and ultimately facial expression and processing, is correlated with social group size and facial motor control (Dobson and Sherwood, 2011), but only in catarrhines. Indeed, Ku and colleagues (2011) found that when rhesus macaques viewed the facial expressions of unknown conspecifics the superior temporal sulcus, prefrontal cortex, amygdala, ventral temporal lobe, hippocampus, entorhinal cortex and medial temporal lobe were all active – the same areas as found to be used by humans (Ku *et al*., 2011). This has not been studied in New World primates, but is suspected not to occur. However, these numerous arguments as to the reduced reliance and complexity on facial expressions in platyrrhines do not explain why the marmosets used facial expressions extensively in my study or why conspecifics seemed to differentiate between a negatively- and positively-based expression when presented on a screen.

The recent study by Morimoto and Fujita (2011) showed that New World capuchin monkeys (*Cebus paella*) are sensitive to the facial expressions of conspecifics; this ability was previously only attributed to humans and other great apes (Morimoto and Fujita, 2011). Still, the debate can be made that capuchins can live in large social groups and are considered to be one of the most cognitively complex New World primates (Lee, 2007). However, the results of my experiment testing two facial expressions produced by the marmosets in response to stimuli indicate that the ability to distinguish between expressions and deduce certain qualities from them is also present in this species. That is, the marmosets felt more comfortable remaining on the table in the presence of a screen showing a conspecific displaying a positive reaction – lip licking – after the food had been eaten (initial motivation), than they did when the conspecific displayed a negative expression – fear. This implies that the marmosets may be aware of or sensitive to facial expressions that may suggest internal states. As most of the expressions observed were instantaneous after the perception of stimuli they were likely to be involuntary and therefore most likely a result of an internal state (as is the case with ‘microexpressions’ in humans: Ekman, 1992, 1999; Ekman and Friesen, 1969).

9.6 Conclusion

Testing visual, olfactory and auditory stimuli in various combinations with each other showed that in general the marmosets’ behaviour was modified by the presence of all stimuli. That is, they attended to both, or all three, cues and adjusted their behaviour according to the information perceived. Partan and Marler’s model (1999) was important to test and relevant up to a point. It could not adequately cover the complexity of changes in behaviour that were shown by scoring multiple responses. Anecdotal observations led to the discovery of discrimination by the marmosets between the vocalisations of different predator types and between two facial expressions displayed in response to opposing stimuli. Importantly, this research demonstrated that olfactory and auditory stimuli influenced the behaviour of the marmosets and often altered the response of the marmosets to the visual stimuli, which suggests that these modalities may be more relevant than the current literature coverage would suggest.

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Appendix I. Recipes of the cake and meatloaf fed to the marmosets.

Monkey cake recipe

Ingredients:

Uncooked brown rice 25g
Polenta 105g
Desiccated coconut 25g
Sunflower seeds 15
Crushed peanuts 30g
Olive oil 25g
Egg 1
Brown sugar 25g
Mashed banana 1
Skim milk powder 25g
Sultanas 25g
Rice cakes 1
Dical-phos 10g

Methods:

Step 1. Rice must be boiled for around 25 mins (in the microwave, on high) in 2x volume of water until cooked

Step 2. Polenta must be boiled in 3x volume of hot water until it is cooked and the water has been absorbed into the polenta flour (3 containers of polenta will cook in a microwave on high in around 20 mins).

Step 3. Weigh out and mix all of the dry ingredients, excluding polenta and rice. Crush the rice cake and mix well.

Step 4. Mix the mashed banana, egg, oil, cooked rice and cooked polenta (add polenta while it is still hot).

Step 5. Pour ingredients into microwave dish and cook in a microwave on high for 20 mins.

Once cooked, cakes are tipped out from microwave dishes and allowed to cool before being chopped into 25 equal-sized pieces. Freeze for storage.

Tips: The rice can be cooked ahead of time, frozen and thawed when required.
When weighing out the dry ingredients it is easier and quicker to weigh out enough ingredients for several cakes (even tens of cakes) at a time, then do each cake individually.

Monkey Meatloaf

Ingredients:
Quality mince 600g
Brown wholemeal bread 6 slices
Dical-phos 20g
Eggs 2
Bran cereal 45g
Vitamin C 7g
"luv" soft pellet 45g
Water 1 cup

Methods:
Chop the slices of bread and the "luv" soft pellets into small pieces and combine with all the other ingredients. Mix very well.

Place mixture into a microwave dish and microwave on high for 20 mins.

Once cooked, tip out the cake onto a paper towel and allow to cool. Cut the cake into rectangular pieces that are around 1cm by 1cm x the height of the cake. Place 21 pieces into a freezer bag and freeze.

Appendix II. Statistical comparisons and results for the neutral visual stimulus (PVC tube) tested in Experiment 2 (Ch. 4). Table A shows the results of the statistical comparisons of trials 1 and 2 and the pre-test, test and post-test periods. For the cases in which the trials were significantly different (bolded), the two trials were kept separate for analyses of the pre-test, test and post-test periods. The mean of the trials was taken when no significant difference was found. Table B shows the data used for these comparisons – the responses to both trials are shown when they were found to be significantly different, otherwise the mean is given (as indicated). The pre- and post-test periods were divided by two to be comparable with the test period (as shown by '/2'). Table C shows the results of the statistical comparisons between the pre-test, test and post-test periods of the three visual stimuli (taxidermic specimen of a quoll, marshmallow and tube). When the trials of the tube presentation were significantly different (as shown in A) only trial 1 was used for comparisons with the other visual stimuli. Repeated measures ANOVAs and two-tailed t-tests were used for normal data, with *post hoc* Bonferroni pairwise comparisons used when significant heterogeneity ($p \leq 0.05$) was found. Friedman's test and Wilcoxon signed-rank tests were used for non-parametric data when transformation was unsuccessful. These statistical analyses were used throughout these appendices.

A	Trial 1 versus trial 2		Heterogeneity	Pre-test versus test	Test versus post-test	Pre-test versus post-test
Mean distance from stimulus (cm)	**$Z = -3.05$** **$p = 0.002$**	Trial 1	**$F_{(2,22)} = 25.43$** **$p \leq 0.001$**	**$p = 0.002$**	**$p \leq 0.001$**	$p = 0.87$
		Trial 2	$X^2 = 4.38$ $p = 0.11$			
Closest distance to stimulus (cm)	**$Z = -2.83$** **$p = 0.01$**					
Latency to approach (secs)	**$Z = -2.04$** **$p = 0.04$**					
Activity per min	$t = -0.54$ $p = 0.59$	Mean	**$F_{(2,22)} = 3.75$** **$p = 0.04$**	$p = 0.32$	**$p = 0.04$**	$p = 1.00$
Contact calls per min	**$t = -2.38$** **$p = 0.02$**	Trial 1	$F_{(2,22)} = 1.92$ $p = 0.17$			
		Trial 2	$F_{(2,22)} = 0.40$ $p = 0.68$			
Mobbing/alarm calls per min	$Z = -0.26$ $p = 0.80$	Mean	**$X^2 = 9.92$** **$p = 0.01$**	**$Z = -2.32$** **$p = 0.02$**	$Z = -2.38$ $p = 0.02$	$Z = -1.07$ $p = 0.29$
Latency to vocalise (secs)	$Z = -1.88$ $p = 0.06$					
Looks upwards per min	$Z = -1.90$ $p = 0.06$	Mean	$X^2 = 2.23$ $p = 0.33$			
Looks downwards per min	$Z = -1.73$ $p = 0.08$	Mean	**$X^2 = 6.58$** **$p = 0.04$**	**$Z = -2.01$** **$p = 0.05$**	$Z = -1.92$ $p = 0.06$	$Z = -0.31$ $p = 0.76$
Looks at stimulus per min	**$Z = -2.73$** **$p = 0.01$**					

B	Mean distance from stimulus (cm)					
Marmoset	**Pre-test**		**Test**		**Post-test**	
	Trial 1	**Trial 2**	**Trial 1**	**Trial 2**	**Trial 1**	**Trial 2**
Ness	195.70	214.24	59.54	213.77	234.52	207.76
Bandit	181.20	180.00	96.73	158.36	174.20	199.52
Mogwai	165.00	270.00	126.77	207.00	185.48	174.64
Jade	181.23	184.32	109.40	169.15	206.00	169.67
Mackybe	230.84	186.52	133.54	128.38	205.32	183.08
Ash	152.64	149.64	54.00	123.38	135.12	172.64
Smokey	118.96	174.68	129.38	167.00	194.24	130.20
Ranger	173.40	162.40	129.00	189.31	180.32	173.44
Gizmo	179.24	220.00	101.38	220.00	201.84	194.12
Inca	209.44	175.28	5.77	201.92	189.96	205.00
Aziz	100.00	169.20	97.23	158.69	96.88	161.43
Delta	157.44	184.48	30.69	75.33	152.44	179.64
Mean	**170.42**	**189.23**	**89.45**	**167.69**	**179.69**	**179.26**
sem	10.39	9.26	12.23	12.39	10.59	6.18

Marmoset	**Closest distance from stimulus (cm)** **Test period only**			**Activity per min (means)**		
	Trial 1	**Trial 2**		**Pre-test/2**	**Test**	**Post-test/2**
Ness	0	207		2.5	1	1.75
Bandit	5	15		4.75	5.5	3.75
Mogwai	5	207		0	3	1.25
Jade	0	148		3	5.5	2.5
Mackybe	10	85		2.75	3.5	3.25
Ash	5	15		1.25	3.5	1
Smokey	15	137		3.25	5.5	4.25
Ranger	15	148		2.25	4	1.5
Gizmo	5	220		0.25	2	2.5
Inca	0	170		4.75	1	1
Aziz	97	94		1.75	2	2.25
Delta	12.5	5		3.75	5.5	2.25
Mean	**14.13**	**120.92**		**2.52**	**3.50**	**2.27**
sem	7.70	22.47		0.44	0.50	0.31

Marmoset	**Latency to approach (secs) Test period only**		**Mobbing/alarm calls per min (means)**		
	Trial 1	**Trial 2**	**Pre-test/2**	**Test**	**Post-test/2**
Ness	0	60	0.5	0	0
Bandit	0	0	0	1	0
Mogwai	0	60	0	0	0
Jade	0	60	0	4	0
Mackybe	0	34.96	0	1.5	0
Ash	0	9.13	0	4	0
Smokey	5.16	60	0	0.5	0.25
Ranger	0	60	1.5	4	0
Gizmo	19.29	60	0	0	0
Inca	0	60	0	0	0
Aziz	60	0	0	0	0
Delta	14.97	0	0	8.5	0
Mean	**8.29**	**38.67**	**0.17**	**1.96**	**0.02**
sem	5.07	8.05	0.13	0.77	0.02

Marmoset	**Contact calls per min Pre-test/2**		**Test**		**Post-test/2**	
	Trial 1	**Trial 2**	**Trial 1**	**Trial 2**	**Trial 1**	**Trial 2**
Ness	4	6.5	2	6	2.5	6
Bandit	3	5	2	5	3	5
Mogwai	0	0	3	1	2.5	1.5
Jade	4	0	2	0	2	0
Mackybe	5.5	3.5	4	1	4	4
Ash	0	2.5	0	0	0	5.5
Smokey	1	2.5	0	3	1	2
Ranger	1.5	3	0	2	1	1
Gizmo	2.5	0	0	1	1	0
Inca	0	4	0	3	3.5	2.5
Aziz	0	3	0	5	0	3
Delta	0	2	0	0	0.5	0
Mean	**1.79**	**2.67**	**1.08**	**2.25**	**1.75**	**2.54**
sem	0.57	0.58	0.42	0.62	0.39	0.63

Marmoset	Latency to vocalise (secs) Test period only Mean	Looks upwards per min (means) Pre-test/2	Test	Post-test/2
Ness	18.63	0.5	0	0.25
Bandit	3.79	2.5	2	3.25
Mogwai	17.26	0	0	0.5
Jade	13.53	0.5	1	0.75
Mackybe	21.01	1.25	0.5	0.75
Ash	9.82	1	1	0.5
Smokey	40.48	0.5	1	1.25
Ranger	12.16	1.5	2	1.25
Gizmo	29.12	1.25	1	0.75
Inca	35.27	0.25	0	0.25
Aziz	40.31	2.25	1.5	1.5
Delta	12.33	1.5	0.5	1
Mean	**21.14**	**1.08**	**0.88**	**1.00**
sem	3.56	0.22	0.21	0.23

Marmoset	Looks downwards per min (means) Pre-test/2	Test	Post-test/2	Looks at stimulus per min Test period only Trial 1	Trial 2
Ness	2.75	1.5	1.5	6	0
Bandit	2.5	1	1.5	3	0
Mogwai	7.5	3.5	3.75	2	2
Jade	4	1.5	3.25	1	0
Mackybe	2	2	3.75	0	1
Ash	4	1.5	2.75	4	1
Smokey	4.25	5	4.25	1	0
Ranger	1.75	1.5	3.25	3	0
Gizmo	3	4.5	2.75	2	0
Inca	2.75	1.5	3.5	9	0
Aziz	4.25	4	4.5	2	1
Delta	2.75	1.5	3.75	7	3
Mean	**3.46**	**2.42**	**3.21**	**3.33**	**0.67**
sem	0.44	0.41	0.27	0.78	0.28

C	Pre-test	Test			Post-test
	Heterogeneity	Heterogeneity	Tube versus quoll	Tube versus marshmallow	Heterogeneity
Mean distance from stimulus (cm)	$F_{(2,22)} = 0.25$ $p = 0.78$	**$F_{(2,22)} = 11.59$** **$p \leq 0.001$**	**$p = 0.01$**	$p = 1.00$	$F_{(2,22)} = 0.79$ $p = 0.47$
Closest distance to stimulus (cm)	n/a	**$X^2 = 16.84$** **$p \leq 0.001$**	**$Z = -2.98$** **$p = 0.003$**	$Z = -0.06$ $p = 0.95$	n/a
Latency to approach (secs)	n/a	**$X^2 = 8.98$** **$p = 0.01$**	**$Z = -2.04$** **$p = 0.04$**	$Z = -1.16$ $p = 0.25$	n/a
Activity per min	$F_{(2,22)} = 0.90$ $p = 0.42$	$F_{(2,22)} = 0.61$ $p = 0.55$			$F_{(2,22)} = 2.25$ $p = 0.13$
Contact calls per min	$F_{(2,22)} = 2.48$ $p = 0.11$	X2 = 2.60 $p = 0.27$			$F_{(2,22)} = 1.65$ $p = 0.22$
Mobbing/alarm calls per min	$X^2 = 1.75$ $p = 0.42$	**$X^2 = 15.17$** **$p = 0.001$**	**$Z = -2.90$** **$p = 0.004$**	**$Z = -2.67$** **$p = 0.01$**	$X^2 = 2.47$ $p = 0.29$
Food-related calls per min	n/a	**$X^2 = 18.00$** **$p \leq 0.001$**	**$Z = 0.00$** **$p = 1.00$**	**$Z = -2.67$** **$p = 0.01$**	n/a
Latency to vocalise (secs)	n/a	$F_{(2,22)} = 2.96$ $p = 0.07$			n/a
Looks upwards per min	$X^2 = 1.44$ $p = 0.49$	$X^2 = 0.87$ $p = 0.65$			$X^2 = 0.05$ $p = 0.98$
Looks downwards per min	$X^2 = 1.67$ $p = 0.43$	**$X^2 = 14.00$** **$p = 0.001$**	**$Z = -2.85$** **$p = 0.004$**	$Z = -1.61$ $p = 0.11$	$X^2 = 0.04$ $p = 0.98$
Looks at stimulus per min		**$X^2 = 8.17$** **$p = 0.02$**	**$Z = -2.59$** **$p = 0.01$**	$Z = -1.89$ $p = 0.06$	

Appendix III. Statistical comparisons and results for the neutral olfactory stimulus (odour of the tea infuser) tested in Experiment 2 (Ch. 4). Tables A, B and C are as detailed in Appendix I. Table C shows the results of the statistical comparisons between the pre-test, test and post-test periods of the three olfactory stimuli (odour of odour of cat faeces, marshmallow odour and odour of the tea infuser).

A		**Pre-test versus test versus post-test**				
	Trial 1 versus trial 2		**Heterogeneity**	**Pre-test versus test**	**Test versus post-test**	**Pre-test versus post-test**
Mean distance from stimulus (cm)	**$t = -3.75$** **$p = 0.001$**	Trial 1				**$t = -2.84$** **$p = 0.02$**
		Trial 2				$t = -1.68$ $p = 0.12$
Activity per min	$t = -0.04$ $p = 0.97$	Mean	$F_{(2,22)} = 0.59$ $p = 0.57$			
Contact calls per min	$t = -1.72$ $p = 0.09$	Mean	**$F_{(2,22)} = 6.82$** **$p = 0.01$**	**$p = 0.02$**	$p = 0.07$	$p = 1.00$
Mobbing/alarm calls per min	**$Z = -2.08$** **$p = 0.04$**	Trial 1	$X^2 = 3.71$ $p = 0.16$			
		Trial 2	$X^2 = 4.63$ $p = 0.10$			
Latency to vocalise (secs)	$t = -0.73$ $p = 0.48$					
Looks upwards per min	$Z = -1.48$ $p = 0.14$	Mean	$X^2 = 0.55$ $p = 0.76$			
Looks downwards per min	$t = -0.35$ $p = 0.73$	Mean	**$F_{(2,22)} = 4.74$** **$p = 0.02$**	$p = 0.12$	$p = 1.00$	$p = 0.03$

B	Mean distance from stimulus (cm)					
Marmoset	Pre-test		Test		Post-test	
	Trial 1	Trial 2	Trial 1	Trial 2	Trial 1	Trial 2
Ness	95.17	200.08	0.00	157.54	114.21	201.00
Bandit	180.64	195.04	26.27	178.50	156.75	185.56
Mogwai	209.44	144.44	133.89	118.15	208.35	175.00
Jade	188.24	178.80	173.00	197.62	223.30	216.00
Mackybe	163.48	183.56	83.17	187.31	164.00	193.60
Ash	141.36	158.12	6.92	91.45	189.48	170.32
Smokey	104.38	147.63	99.70	92.11	161.26	193.32
Ranger	168.00	192.04	89.44	177.62	175.64	188.44
Gizmo	191.32	220.00	173.62	143.54	217.84	204.40
Inca	166.36	157.28	10.71	136.42	178.00	167.45
Aziz	156.56	177.24	141.27	144.00	166.04	160.68
Delta	92.52	173.76	17.88	108.85	124.88	189.92
Mean	**154.79**	**177.33**	**79.66**	**144.42**	**173.31**	**187.14**
sem	11.23	6.55	19.04	10.54	9.69	4.71

	Activity per min (means)			Contact calls per min (means)		
Marmoset	Pre-test/2	Test	Post-test/2	Pre-test/2	Test	Post-test/2
Ness	2	3.5	2.75	3.75	1.5	5.25
Bandit	6.25	4	5.25	1.5	3	1
Mogwai	2	2.5	4	3	2.5	3.75
Jade	1.75	3.5	0.5	2.75	1.5	1.25
Mackybe	5.75	4	4	1.75	0	2.5
Ash	2.25	2	1.5	0.5	0	0.25
Smokey	5	4.5	4.75	1.75	1	2.5
Ranger	2.25	4.5	2.5	2.5	0	2.75
Gizmo	0.5	4	0.5	3.5	1.5	2.5
Inca	4.25	3	2	1.5	0.5	0.5
Aziz	3.75	3	5	3.75	0.5	3.25
Delta	3.75	1	1.25	0	0	1
Mean	**3.29**	**3.29**	**2.83**	**2.19**	**1.00**	**2.21**
sem	0.51	0.30	0.50	0.36	0.30	0.43

Marmoset	Mobbing/alarm calls per min Pre-test/2		Test		Post-test/2	
	Trial 1	Trial 2	Trial 1	Trial 2	Trial 1	Trial 2
Ness	4	0	3	19	0	0
Bandit	0	0	0	0	0	0
Mogwai	1	0	0	4	0	0
Jade	0	11	0	12	0	2
Mackybe	0	0	0	0	0	5
Ash	0	0	0	0	0	0
Smokey	0	0	0	4	0	0
Ranger	0	0	0	0	0	0
Gizmo	0	0	0	0	0	0
Inca	0	0	0	0	0	0
Aziz	0	0	0	0	0	0
Delta	0	0	0	0	0	0
Mean	**0.42**	**0.92**	**0.25**	**3.25**	**0.00**	**0.58**
sem	0.34	0.92	0.25	1.76	0.00	0.43

Marmoset	Latency to vocalise (secs) Test period only (means)	Looks upwards per min (means) Pre-test/2	Test	Post-test/2
Ness	11.70	1.25	0	0.25
Bandit	8.23	0.75	0.5	0
Mogwai	17.66	0.25	0.5	0
Jade	17.60	0	0.5	0.25
Mackybe	60.00	1	1.5	2.75
Ash	60.00	0.25	0	1.25
Smokey	14.34	0.75	0	0.5
Ranger	60.00	0.5	0	0.25
Gizmo	39.87	0.25	0.5	0
Inca	49.45	1.25	0	0
Aziz	30.24	0.25	1.5	0.75
Delta	60.00	1.25	0.5	3
Mean	**35.76**	**0.65**	**0.46**	**0.75**
sem	6.18	0.13	0.16	0.31

Marmoset	**Looks downwards per min (means)**		
	Pre-test/2	**Test**	**Post-test/2**
Ness	3.75	2	3.75
Bandit	1	2	0.75
Mogwai	1.25	2	0.75
Jade	3.75	2.5	2.75
Mackybe	2.25	2	2.25
Ash	3.25	0	0.75
Smokey	5.25	2	2
Ranger	6	4	5.5
Gizmo	3.25	4.5	2.75
Inca	2.5	0	1
Aziz	2	2	1
Delta	2.75	1	2.75
Mean	**3.08**	**2.00**	**2.17**
sem	0.43	0.38	0.42

C	**Pre-test**	**Test**			**Post-test**
	Heterogeneity	**Heterogeneity**	**Odour of the tea infuser versus odour of cat faeces**	**Odour of the tea infuser versus odour of marshmallow**	**Heterogeneity**
Mean distance from stimulus (cm)	$F_{(2,22)} = 0.66$ $p = 0.53$	**$F_{(2,22)} = 10.54$** **$p = 0.001$**	$p = 0.09$	$p = 0.46$	$X^2 = 0.17$ $p = 0.92$
Activity per min	$F_{(2,22)} = 0.44$ $p = 0.65$	**$F_{(2,22)} = 4.38$** **$p = 0.03$**	$p = 1.00$	$p = 0.06$	$F_{(2,22)} = 0.73$ $p = 0.50$
Contact calls per min	$F_{(2,22)} = 0.03$ $p = 0.97$	$F_{(2,22)} = 2.18$ $p = 0.14$			$F_{(2,22)} = 1.03$ $p = 0.37$
Mobbing/alarm calls per min	$X^2 = 0.43$ $p = 0.81$	$X^2 = 5.63$ $p = 0.06$			$X^2 = 3.50$ $p = 0.17$
Latency to vocalise (secs)	n/a	$F_{(2,22)} = 1.14$ $p = 0.34$			n/a
Looks upwards per min	$X^2 = 0.59$ $p = 0.74$	$F_{(2,22)} = 0.09$ $p = 0.91$			$X^2 = 0.06$ $p = 0.97$
Looks downwards per min	$F_{(2,22)} = 0.65$ $p = 0.53$	$F_{(2,22)} = 2.95$ $p = 0.07$			$X^2 = 4.41$ $p = 0.11$

Appendix IV. Statistical comparisons and results for the neutral auditory stimulus (marmoset housing background noise) tested in Experiment 2 (Ch. 4). Tables A, B and C are as detailed in Appendix I. Table C shows the results of the statistical comparisons between the pre-test, test and post-test periods of the three auditory stimuli (leopard growl, marmoset food-related calls, background noise).

A			**Pre-test versus test versus post-test**			
	Trial 1 vs trial 2		**Heterogeneity**	**Pre-test versus test**	**Test versus post-test**	**Pre-test versus post-test**
Activity per min	$t = 0.33$ $p = 0.74$	Mean	$F_{(2,22)} = 0.31$ $p = 0.74$			
Latency to move (secs)	$z = -0.39$ $p = 0.70$					
Contact calls per min	$t = -0.79$ $p = 0.44$	Mean	**$X^2 = 10.53$** **$p = 0.01$**	**$z = -2.50$** **$p = 0.01$**	**$z = -1.95$** **$p = 0.05$**	$z = -1.30$ $p = 0.19$
Mobbing/alarm calls per min	$Z = -1.16$ $p = 0.25$	Mean	$X^2 = 1.93$ $p = 0.38$			
Latency to vocalise (secs)	$t = 0.84$ $p = 0.42$					
Looks upwards per min	$Z = -0.39$ $p = 0.70$	Mean	$X^2 = 1.22$ $p = 0.54$			
Looks downwards per min	$t = -2.03$ $p = 0.07$	Mean	$F_{(2,22)} = 1.00$ $p = 0.39$			

B	**Activity per min**			**Contact calls per min**		
Marmoset	**Pre-test/2 Mean**	**Test Mean**	**Post-test/2 Mean**	**Pre-test/2 Mean**	**Test Mean**	**Post-test/2 Mean**
Ness	1.5	3.5	0.25	2.75	2	2
Bandit	5	4	3.5	2.75	4	2.5
Mogwai	3.25	2	1	2.75	1	2
Jade	2.5	4	4.25	1.5	0.5	1.75
Mackybe	2.5	3	3	1.75	1.5	2.25
Ash	1	2	1.5	3.75	2	2.75
Smokey	5	2.5	4	3.5	1	1.75
Ranger	3	2	1.75	1.5	0	0.75
Gizmo	3.5	1.5	2.75	2.25	0.5	4.75
Inca	5.75	5.5	5.25	2.75	2.5	2.5
Aziz	5.25	6.5	6	2	0	1.5
Delta	2.25	3	3.75	1	1	1.25
Mean	3.38	3.29	3.08	2.35	1.33	2.15
SE	0.45	0.44	0.50	0.24	0.33	0.29

	Mobbing/alarm calls per min			**Latency to move**
Marmoset	**Pre-test/2 Mean**	**Test Mean**	**Post-test/2 Mean**	**Test period only Mean**
Ness	0.5	0	0	14.03
Bandit	0.5	1.5	0.25	6.14
Mogwai	0.25	0	0.75	29.92
Jade	1.25	0	2	5.52
Mackybe	1.5	0	1.75	21.24
Ash	0	0	1	24.58
Smokey	0	0	0	12.83
Ranger	0	0	0	41.11
Gizmo	0	0	0	18.44
Inca	0	0.5	0	7.85
Aziz	0	0	0	9.58

Delta	5.25	0	2		22.30	
Mean	0.77	0.17	0.65		17.79	
SE	0.43	0.13	0.24		3.09	
	Latency to vocalise (secs)			**Looks upwards per min**		
Marmoset	**Test period only**			**Pre-test/2**	**Test**	**Post-test/2**
	Mean			**Mean**	**Mean**	**Mean**
Ness	32.55			0.75	1	0
Bandit	9.13			2	3.5	1.25
Mogwai	4.94			0	1	1
Jade	35.51			0.75	0.5	1.75
Mackybe	45.14			2.75	1.5	2
Ash	35.72			1.75	0.5	2
Smokey	35.88			0	3.5	1.25
Ranger	60.00			0.5	2.5	0.75
Gizmo	43.79			0.5	1	3.5
Inca	15.66			0.5	1	0.25
Aziz	60.00			1	2.5	0.75
Delta	31.53			0.75	0.5	0.5
Mean	34.15			0.94	1.58	1.25
SE	5.07			0.24	0.32	0.28
	Looks downwards per min					
Marmoset	**Pre-test/2**	**Test**	**Post-test/2**			
	Mean	**Mean**	**Mean**			
Ness	2	4	2.75			
Bandit	2.25	3	3			
Mogwai	1.25	0.5	3.25			
Jade	4.25	3	2.75			
Mackybe	2.5	2	3.5			
Ash	1.25	1	2			
Smokey	3.75	3.5	3.5			
Ranger	2.75	3.5	2			
Gizmo	4	0.5	2			

Inca	3	1.5	4
Aziz	3.5	4	1.75
Delta	2.5	1	4
Mean	2.75	2.29	2.88
SE	0.29	0.39	0.23

C	**Pre-test**	**Test**			**Post-test**
	Heterogeneity	**Heterogeneity**	**Background noise vs leopard growl**	**Background noise vs food-related calls**	**Heterogeneity**
Activity per minute	$F_{(2,22)} = 0.32$ $p = 0.73$	$\mathbf{F_{(2,22)} = 4.01}$ $\mathbf{p = 0.03}$	$p = 0.20$	$p = 0.58$	$\mathrm{F}_{(2,22)} = 0.83$ $\mathrm{p} = 0.45$
Latency to move (secs)	-	$F_{(2,22)} = 0.76$ $p = 0.48$			-
Contact calls per min	$X^2 = 0.81$ $p = 0.67$	$X^2 = 2.98$ $p = 0.22$			$X^2 = 1.70$ $p = 0.43$
Mobbing/alarm calls per min	$X^2 = 1.31$ $p = 0.52$	$X^2 = 5.00$ $p = 0.08$			$X^2 = 0.21$ $p = 0.90$
Latency to vocalise (secs)	-	$F_{(2,22)} = 3.22$ $p = 0.06$			-
Looks upwards per min	$X^2 = 1.59$ $p = 0.45$	$\mathbf{X^2 = 14.76}$ $\mathbf{p = 0.001}$	$\mathbf{z = -2.68}$ $\mathbf{p = 0.01}$	$\mathbf{z = -2.83}$ $\mathbf{p = 0.01}$	$X^2 = 4.58$ $p = 0.10$
Looks downwards per min	$F_{(2,22)} = 0.81$ $p = 0.46$	$X^2 = 1.27$ $p = 0.53$			$F_{(2,22)} = 0.56$ $p = 0.58$

Appendix V. Individual and mean (± sem) scores for each behavioural response scored in the pre-test, test and post-test periods in tests of the related combinations (of same type, such as aversive visual/aversive auditory: Ch. 5).

Distance

	Quoll/cat faeces			**Quoll/leopard growl**			**Cat faeces/leopard growl**			**Quoll/cat faeces/leopard growl**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	196.40	143.04	200.04	207.52	163.32	207.68	188.16	248.00	290.00	185.56	219.84	214.00
Bandit	188.00	173.44	197.20	201.56	135.84	200.84	198.80	179.92	191.8	170.68	176.52	179.52
Mogwai	215.76	155.60	193.72	175.36	176.80	176.48	145.44	188.60	208.00	189.72	176.12	188.56
Jade	168.53	153.62	170.65	149.80	185.40	184.24	184.88	168.92	192.72	209.20	197.68	200.52
Mackybe	203.12	194.16	198.24	208.00	158.64	170.08	270.00	188.64	273.24	215.00	215.00	215.00
Ash	165.00	185.60	134.68	188.28	199.48	186.40	163.20	154.52	157.00	197.76	166.28	188.32
Smokey	182.00	189.60	190.88	170.00	121.20	198.72	202.28	172.68	213.72	182.84	166.92	174.08
Ranger	150.56	128.52	202.20	177.64	185.40	184.24	116.24	168.92	175.12	179.60	197.68	200.52
Gizmo	208.48	112.48	211.36	220.00	220.00	220.00	205.44	197.76	211.48	230.28	185.48	204.80
Inca	175.24	179.72	164.76	179.20	154.72	203.00	107.20	110.64	159.96	206.64	203.12	201.52
Aziz	193.48	130.36	196.36	175.60	113.04	194.24	177.12	206.72	197.12	168.72	188.36	176.28
Delta	55.76	193.76	109.88	160.84	230.96	238.00	220.00	134.56	175.20	117.16	210.00	183.68
Mean	**175.19**	**161.66**	**180.83**	**184.48**	**170.40**	**196.99**	**181.56**	**176.66**	**203.78**	**187.76**	**191.92**	**193.90**
SE	12.17	8.19	8.86	6.07	10.59	5.48	12.94	10.11	11.84	8.35	5.26	4.07

	Marshmallow/marshmallow odour			**Marshmallow/marmoset food-related calls**			**Marshmallow odour/marmoset food-related calls**			**Marshmallow/marshmallow odour/marmoset food-related calls**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	214.80	74.04	111.20	215.04	41.32	126.12	212.72	207.88	217.00	211.88	129.12	212.44
Bandit	170.68	155.60	187.44	196.88	170.68	208.00	155.80	186.84	203.52	174.80	110.08	204.32
Mogwai	178.56	49.12	159.48	176.44	127.28	198.48	158.60	142.16	228.56	192.72	116.44	200.20
Jade	191.12	56.24	180.40	166.04	88.24	187.80	196.64	165.88	189.04	186.94	145.98	200.12
Mackybe	201.88	95.92	217.96	208.00	51.92	181.84	260.00	150.48	165.00	204.24	208.00	208.00
Ash	144.00	94.64	167.96	194.64	34.32	198.88	174.32	133.48	173.96	163.64	112.08	151.36
Smokey	191.08	38.20	177.52	183.72	83.52	144.84	157.40	150.48	162.28	184.50	117.12	170.74
Ranger	176.04	56.24	185.00	181.56	88.24	183.20	160.00	165.88	220.00	163.80	129.68	152.24
Gizmo	203.44	62.00	155.00	221.12	101.40	207.28	230.00	197.20	230.00	221.32	148.04	218.96
Inca	214.44	59.84	187.4	193.44	37.96	200.88	212.76	111.04	160.36	211.28	210.92	158.80
Aziz	187.92	94.32	201.00	153.16	49.32	211.12	165.80	126.96	193.80	169.88	74.08	185.40
Delta	154.68	69.92	191.36	112.60	100.40	183.88	72.84	2.00	75.80	144.00	78.68	162.72

Mean	**185.72**	**75.51**	**176.81**	**183.55**	**81.22**	**186.03**	**179.74**	**145.02**	**184.94**	**185.75**	**131.69**	**185.44**
SE	6.39	9.06	7.76	8.58	11.85	7.50	13.76	15.43	12.36	6.79	12.31	7.21

Activity

	Quoll/cat faeces			**Quoll/leopard growl**			**Cat faeces/leopard growl**			**Quoll/cat faeces/leopard growl**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	6	19	5	4	12	1	4	3	0	1	7	2
Bandit	11	11	7	7	4	7	7	10	18	18	18	13
Mogwai	2	7	4	8	9	10	1	3	0	10	10	8
Jade	8	9	5	0	6	3	11	10	8	8	1	7
Mackybe	3	1	3	0	3	3	0	2	2	0	0	0
Ash	0	2	4	4	3	2	1	4	2	5	4	4
Smokey	4	7	3	10	8	10	6	6	7	11	12	10
Ranger	3	8	1	1	1	3	6	8	3	4	9	6
Gizmo	8	10	4	1	0	0	3	7	3	5	9	7
Inca	7	2	2	7	9	11	2	4	1	5	9	11
Aziz	15	15	10	8	12	10	13	10	4	13	16	7
Delta	4	4	2	8	1	0	0	7	1	6	0	9
Mean	**5.92**	**7.92**	**4.17**	**4.83**	**5.67**	**5.00**	**4.50**	**6.17**	**4.08**	**7.17**	**7.92**	**7.00**
SE	1.21	1.56	0.71	1.04	1.23	1.24	1.23	0.85	1.46	1.48	1.70	1.07
	Marshmallow/marshmallow odour			**Marshmallow/marmoset food-related calls**			**Marshmallow odour/marmoset food-related calls**			**Marshmallow/marshmallow odour/marmoset food-related calls**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	2	4	1	4	4	4	3	7	1	3	3	2
Bandit	16	14	14	9	9	14	15	6	2	9	13	5
Mogwai	7	2	0	6	8	5	8	5	4	4	7	2
Jade	7	7	4	4	6	7	8	7	5	9	9	5
Mackybe	6	4	4	0	3	3	0	4	0	3	0	0
Ash	0	5	5	3	7	5	2	2	1	5	8	1
Smokey	9	5	2	6	5	8	11	12	7	1	5	4
Ranger	1	7	3	7	9	8	0	3	0	3	7	2
Gizmo	6	3	0	2	12	4	0	6	0	8	7	6

Inca	5	6	11	10	4	5	6	1	2	7	6	13
Aziz	7	6	10	2	5	4	1	10	12	10	9	12
Delta	2	3	4	5	2	1	5	0	4	0	7	3
Mean	**5.67**	**5.50**	**4.83**	**4.83**	**6.17**	**5.67**	**4.92**	**5.25**	**3.17**	**5.17**	**6.75**	**4.58**
SE	1.25	0.90	1.30	0.85	0.84	0.96	1.40	1.02	1.03	0.97	0.93	1.18

Contact calls

	Quoll/cat faeces			**Quoll/leopard growl**			**Cat faeces/leopard growl**			**Quoll/cat faeces/leopard growl**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	11	5	11	8	1	4	4	0	0	7	5	9
Bandit	7	3	5	10	7	7	3	9	7	13	16	13
Mogwai	3	1	2	3	2	3	7	4	5	11	8	7
Jade	4	5	6	2	5	3	1	1	3	8	3	4
Mackybe	5	0	4	5	1	5	0	1	8	0	0	0
Ash	3	4	2	2	1	2	5	8	5	2	4	2
Smokey	10	0	6	9	1	8	7	0	5	8	0	7
Ranger	4	0	5	2	0	5	5	0	2	3	0	4
Gizmo	7	2	10	1	1	3	5	4	2	7	5	6
Inca	3	2	3	1	0	0	4	0	0	8	1	31
Aziz	5	0	7	7	0	4	5	5	0	6	5	13
Delta	1	3	1	4	0	1	5	0	0	2	0	3
Mean	**5.25**	**2.08**	**5.17**	**4.50**	**1.58**	**3.75**	**4.25**	**2.67**	**3.08**	**6.25**	**3.92**	**8.25**
SE	0.86	0.56	0.89	0.93	0.63	0.66	0.60	0.95	0.83	1.12	1.34	2.37
	Marshmallow/marshmallow odour			**Marshmallow/marmoset food calls**			**Marshmallow odour/marmoset food calls**			**Marshmallow/marshmallow odour/marmoset food calls**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	9	1	0	4	1	8	6	1	5	5	1	7
Bandit	6	7	6	11	9	7	10	7	10	6	3	6
Mogwai	7	0	4	2	2	6	4	6	4	6	0	6
Jade	8	0	6	3	1	4	6	4	3	5	2	6
Mackybe	12	5	7	5	2	7	0	1	1	3	0	4
Ash	0	0	0	5	0	2	3	1	6	2	0	2
Smokey	2	0	3	6	0	1	7	1	8	4	2	5
Ranger	6	0	5	5	0	2	1	0	2	1	0	5

Gizmo	10	1	6	10	0	6	2	3	6	9	5	9
Inca	19	2	18	2	0	8	4	0	1	8	6	5
Aziz	8	1	4	6	0	3	6	1	0	3	1	9
Delta	1	0	1	0	0	0	0	0	0	1	1	3
Mean	**7.33**	**1.42**	**5.00**	**4.92**	**1.25**	**4.50**	**4.08**	**2.08**	**3.83**	**4.42**	**1.75**	**5.58**
SE	1.49	0.66	1.37	0.92	0.74	0.82	0.88	0.69	0.94	0.74	0.58	0.61

Mobbing/alarm calls

	Quoll/cat faeces			**Quoll/leopard growl**			**Cat faeces/leopard growl**			**Quoll/cat faeces/leopard growl**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	0	85	0	0	59	0	0	0	0	0	27	0
Bandit	6	8	9	1	6	1	0	0	0	0	0	0
Mogwai	0	126	0	2	75	0	4	0	0	29	65	3
Jade	19	36	1	0	15	0	3	1	0	5	0	8
Mackybe	0	30	13	0	46	0	0	0	8	0	0	0
Ash	0	0	0	2	0	0	0	0	0	0	12	0
Smokey	0	77	0	1	72	0	0	2	0	0	58	0
Ranger	0	98	0	19	4	0	0	0	0	0	62	1
Gizmo	0	57	0	0	0	0	0	0	0	0	12	0
Inca	0	9	0	0	61	0	0	0	0	0	0	0
Aziz	39	46	0	0	90	0	0	3	0	0	30	0
Delta	0	4	0	0	5	0	0	0	0	0	0	0
Mean	**5.33**	**48.00**	**1.92**	**2.08**	**36.08**	**0.08**	**0.58**	**0.50**	**0.67**	**2.83**	**22.17**	**1.00**
SE	3.46	11.90	1.25	1.55	9.89	0.08	0.40	0.29	0.67	2.41	7.51	0.69

	Marshmallow/marshmallow odour			**Marshmallow/marmoset food calls**			**Marshmallow odour/marmoset food calls**			**Marshmallow/marshmallow odour/marmoset food calls**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	4	18	0	0	21	0	0	0	0	1	0	0
Bandit	0	0	0	5	3	1	2	0	0	0	0	0
Mogwai	0	18	0	12	1	2	2	0	0	0	22	0
Jade	3	7	4	0	23	0	0	1	0	0	2	0
Mackybe	3	6	0	0	0	0	0	0	0	0	0	0
Ash	3	0	0	0	0	0	0	0	0	0	3	0

Smokey	4	2	0	0	18	34	0	0	2	0	4	0
Ranger	0	3	0	0	4	0	0	0	18	0	0	0
Gizmo	0	5	0	0	33	0	0	0	0	0	1	0
Inca	0	32	3	0	10	0	0	0	0	0	0	0
Aziz	0	0	0	0	1	0	0	0	0	0	0	0
Delta	0	0	0	0	21	0	0	0	0	0	2	0
Mean	**1.42**	**7.58**	**0.58**	**1.42**	**11.25**	**3.08**	**0.33**	**0.08**	**1.67**	**0.08**	**2.83**	**0.00**
SE	0.51	2.89	0.40	1.05	3.29	2.82	0.22	0.08	1.49	0.08	1.79	0.00

Food-related calls

	Quoll/cat faeces			**Quoll/leopard growl**			**Cat faeces/leopard growl**			**Quoll/cat faeces/leopard growl**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	0	0	0	0	0	0	0	0	0	0	0	0
Bandit	2	6	0	1	0	2	0	0	0	0	0	0
Mogwai	0	0	0	0	0	0	2	0	0	0	0	0
Jade	0	0	0	0	0	0	0	0	0	0	0	0
Mackybe	0	0	0	0	0	0	0	0	8	0	0	0
Ash	0	0	0	0	0	0	0	0	0	0	0	0
Smokey	0	0	0	0	0	0	0	0	0	0	0	0
Ranger	0	0	0	0	0	0	0	0	0	0	0	0
Gizmo	0	0	0	0	0	0	0	0	7	0	0	0
Inca	0	0	0	0	0	0	0	0	0	0	0	0
Aziz	0	0	0	0	0	0	0	0	0	0	0	0
Delta	6	0	0	0	0	0	0	0	0	0	0	0
Mean	**0.67**	**0.50**	**0.00**	**0.08**	**0.00**	**0.17**	**0.17**	**0.00**	**1.25**	**0.00**	**0.00**	**0.00**
SE	0.51	0.50	0.00	0.08	0.00	0.17	0.17	0.00	0.84	0.00	0.00	0.00
	Marshmallow/marshmallow odour			**Marshmallow/marmoset food-related calls**			**Marshmallow odour/marmoset food-related calls**			**Marshmallow/marshmallow odour/marmoset food-related calls**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	0	0	0	0	4	0	0	0	0	0	0	0
Bandit	0	0	0	1	1	1	0	0	0	0	3	0
Mogwai	0	0	0	0	0	0	0	0	0	0	0	0

Jade	0	16	0	0	23	0	0	0	0	0	2	0
Mackybe	0	0	0	0	0	0	0	0	0	0	0	0
Ash	0	0	0	0	0	0	0	0	0	0	0	0
Smokey	0	14	0	0	2	2	0	0	0	0	1	0
Ranger	0	6	0	0	4	0	0	0	0	0	0	0
Gizmo	0	7	0	0	0	0	0	0	0	0	7	0
Inca	0	0	0	0	0	0	0	1	0	0	0	0
Aziz	0	0	0	0	8	0	0	0	0	0	0	0
Delta	0	15	0	0	0	0	0	0	0	0	5	0
Mean	**0.00**	**4.83**	**0.00**	**0.08**	**3.50**	**0.25**	**0.00**	**0.08**	**0.00**	**0.00**	**1.50**	**0.00**
SE	0.00	1.91	0.00	0.08	1.91	0.18	0.00	0.08	0.00	0.00	0.68	0.00

Looks upwards

	Quoll/cat faeces			**Quoll/leopard growl**			**Cat faeces/leopard growl**			**Quoll/cat faeces/leopard growl**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	2	0	1	0	1	1	3	0	0	0	2	2
Bandit	0	1	5	4	2	9	6	4	2	0	1	7
Mogwai	1	1	1	1	3	2	1	0	0	2	2	4
Jade	2	0	3	2	3	1	2	3	5	3	2	5
Mackybe	2	1	3	0	2	5	0	1	12	3	0	5
Ash	1	2	2	1	2	1	1	2	0	0	0	4
Smokey	0	1	1	1	4	1	0	1	0	0	1	3
Ranger	2	0	3	2	6	0	3	1	3	3	0	0
Gizmo	2	1	0	1	0	1	0	1	0	0	0	0
Inca	0	0	2	3	0	2	3	2	2	1	1	0
Aziz	1	0	1	4	0	1	3	3	1	5	1	2
Delta	1	1	3	1	0	4	1	3	2	2	1	2
Mean	**1.17**	**0.67**	**2.08**	**1.67**	**1.92**	**2.33**	**1.92**	**1.75**	**2.25**	**1.58**	**0.92**	**2.83**
SE	0.24	0.19	0.40	0.40	0.54	0.73	0.51	0.37	0.99	0.48	0.23	0.65
	Marshmallow/marshmallow odour			**Marshmallow/marmoset food-related calls**			**Marshmallow odour/marmoset food-related calls**			**Marshmallow/marshmallow odour/marmoset food-related calls**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-**

												test
Ness	0	4	6	1	4	5	0	3	2	2	3	2
Bandit	0	1	4	2	3	0	1	5	4	5	3	4
Mogwai	0	2	2	0	0	1	0	0	1	1	2	1
Jade	0	0	4	2	1	0	1	3	4	2	2	3
Mackybe	0	4	5	1	6	6	2	0	0	0	2	2
Ash	1	2	1	0	4	1	1	6	1	0	1	6
Smokey	0	1	5	2	0	3	2	2	3	0	1	3
Ranger	5	0	1	0	0	1	1	1	0	0	2	1
Gizmo	1	1	5	2	0	1	0	2	1	1	0	1
Inca	0	1	0	1	1	1	2	8	2	0	0	2
Aziz	2	4	1	5	0	1	4	1	6	2	1	6
Delta	4	1	1	0	0	1	2	3	2	1	2	4
Mean	**1.08**	**1.75**	**2.92**	**1.33**	**1.58**	**1.75**	**1.33**	**2.83**	**2.17**	**1.17**	**1.58**	**2.92**
SE	0.50	0.43	0.61	0.41	0.61	0.55	0.33	0.71	0.52	0.42	0.29	0.51

Looks downwards

	Quoll/cat faeces			**Quoll/leopard growl**			**Cat faeces/leopard growl**			**Quoll/cat faeces/leopard growl**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	8	2	3	5	3	3	9	11	12	4	9	12
Bandit	3	1	2	0	6	2	5	5	5	1	1	0
Mogwai	12	3	8	11	4	5	12	14	13	4	5	10
Jade	9	0	6	10	5	5	8	10	7	6	8	3
Mackybe	7	8	5	6	5	6	9	11	4	5	4	8
Ash	5	5	5	10	11	8	8	12	11	6	4	7
Smokey	5	4	6	9	2	8	9	6	9	13	2	5
Ranger	11	3	4	16	3	9	7	11	6	9	5	9
Gizmo	2	3	9	8	1	9	5	7	16	9	8	9
Inca	9	4	8	8	2	5	11	17	9	3	7	9
Aziz	4	3	5	7	2	2	3	4	4	8	1	5
Delta	9	5	8	7	8	9	7	9	8	7	7	8
Mean	**7.00**	**3.42**	**5.75**	**8.08**	**4.33**	**5.92**	**7.75**	**9.75**	**8.67**	**6.25**	**5.08**	**7.08**
SE	0.92	0.60	0.63	1.10	0.84	0.77	0.74	1.09	1.09	0.93	0.80	0.96

	Marshmallow/marshmallow odour			**Marshmallow/marmoset food-related calls**			**Marshmallow odour/marmoset food-related calls**			**Marshmallow/marshmallow odour/marmoset food-related calls**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	5	3	9	2	4	2	4	9	10	8	7	9
Bandit	1	1	1	3	1	1	6	6	6	4	4	8
Mogwai	5	1	11	2	3	3	7	6	6	3	2	10
Jade	9	4	6	4	9	6	8	9	7	9	3	9
Mackybe	3	2	6	11	5	4	9	6	11	9	8	12
Ash	10	5	5	7	2	9	9	6	6	7	3	9
Smokey	8	4	5	7	8	18	9	6	5	7	6	8
Ranger	8	3	9	13	10	13	17	8	5	15	8	14
Gizmo	4	4	4	3	8	6	4	11	4	15	3	8
Inca	6	1	4	8	3	6	6	5	5	6	2	1
Aziz	7	2	4	7	8	4	10	8	1	2	2	5

Delta	9	4	6	11	8	13	5	0	2	9	4	7
Mean	**6.25**	**2.83**	**5.83**	**6.50**	**5.75**	**7.08**	**7.83**	**6.67**	**5.67**	**7.83**	**4.33**	**8.33**
SE	0.79	0.41	0.79	1.09	0.89	1.49	1.02	0.79	0.82	1.18	0.67	0.94

	Marmoset	**Quoll/cat faeces odour**	**Quoll/ leopard growl**	**Cat faeces odour/ leopard growl**	**Quoll/cat faeces odour/ leopard growl**	**Marshmallow/ marshmallow odour**	**Marshmallow / food-related calls**	**Marshmallow odour/ food-related calls**	**Marshmallow / marshmallow odour/ food calls**
Closest distance (cm)	Ness	68	75	-	122	0	0	-	0
	Bandit	65	68	-	30	0	0	-	0
	Mogwai	113	113	-	140	0	0	-	0
	Jade	100	157	-	154	0	0	-	0
	Mackybe	189	115	-	215	0	0	-	208
	Ash	150	152	-	150	0	0	-	0
	Smokey	87	30	-	92	0	0	-	0
	Ranger	75	187	-	94	0	0	-	0
	Gizmo	20	220	-	94	0	0	-	0
	Inca	144	82	-	150	0	0	-	170
	Aziz	30	70	-	94	0	0	-	0
	Delta	82	150	-	210	0	50	-	0
	Mean	**93.58**	**118.25**	-	**128.75**	**0.00**	**4.17**	-	**31.50**
	SE	14.22	16.19	-	15.20	0.00	4.17	-	21.37
Latency to	Ness	0	32.94	-	120	2.82	0	-	0
	Bandit	0	0	-	11.1	0	0	-	20.88

approach	Mogwai	120	10.38	-	120	0	4.41	-	35.31
(seconds)	Jade	59.64	120	-	120	0	3.72	-	0
	Mackybe	120	59.88	-	120	0	0	-	120
	Ash	120	120	-	120	6.51	0	-	0
	Smokey	69.54	21	-	34.12	6.87	23.84	-	0
	Ranger	44.59	120	-	30.77	4.88	29.12	-	36.19
	Gizmo	0	120	-	25.21	0	0	-	10.13
	Inca	120	9.97	-	120	0	0	-	120
	Aziz	0	1.46	-	13.94	0	0	-	0
	Delta	120	120	-	120	8.04	120	-	0
	Mean	**64.48**	**61.30**	-	**79.60**	**2.43**	**15.09**	-	**28.54**
	SE	15.69	15.62	-	14.52	0.93	9.97	-	12.94
Latency to vocalise (seconds)	Ness	0	1.56	120	2.45	8	21.4	78.27	81.68
	Bandit	0	8.56	11.44	120	7.25	14.19	10.06	14.5
	Mogwai	0	1	13.58	0	48.89	50.25	31.53	17.71
	Jade	17.7	74.63	9	120	23.31	10.03	1.27	56.13
	Mackybe	57.67	31.37	31.97	120	18.22	39.76	45.55	120
	Ash	120	120	8.34	99.23	120	120	57.99	15.01
	Smokey	0	0	105.22	8.66	36.84	14.68	37.64	44.18
	Ranger	0	31.32	120	10.68	16.99	34.2	120	72.47
	Gizmo	0	120	28.99	6.81	4	6.88	35.23	29.78
	Inca	0	0	23.41	120	4.7	32.32	31.22	12.67
	Aziz	0	3.77	28.99	4.16	4	29.5	120	95.98
	Delta	22.9	22.82	120	120	18.54	78.82	120	41.37

	Mean	**18.19**	**34.59**	**51.75**	**61.00**	**25.90**	**37.67**	**57.40**	**50.12**
	SE	10.51	13.08	14.00	16.84	9.45	9.45	12.30	10.30

		Quoll/ cat faeces odour	**Quoll/ leopard growl**	**Cat faeces odour/ leopard growl**	**Quoll/cat faeces odour/ leopard growl**	**Marshmallow/ marshmallow odour**	**Marshmallow / marmoset food-related calls**	**Marshmallow odour/ marmoset food-related calls**	**Marshmallow / marshmallow odour/ food-related calls**
Looks at stimulus per 2 minutes	Ness	11	14	-	7	8	8	-	8
	Bandit	2	9	-	0	2	2	-	11
	Mogwai	16	12	-	6	13	6	-	10
	Jade	10	3	-	2	11	6	-	5
	Mackybe	11	12	-	11	10	7	-	2
	Ash	0	4	-	3	13	14	-	7
	Smokey	9	16	-	12	10	12	-	10
	Ranger	19	8	-	14	7	10	-	10
	Gizmo	13	11	-	8	9	7	-	10
	Inca	9	12	-	6	8	13	-	3
	Aziz	8	17	-	10	12	11	-	6
	Delta	3	2	-	5	8	16	-	7
	Mean	**9.25**	**10.00**	-	**7.00**	**9.25**	**9.33**	-	**7.42**
	SE	1.61	1.42	-	1.22	0.88	1.16	-	0.86

Appendix VI. Results of the statistical comparisons of the first and second minute of the test period of the related combinations (Ch. 5).

	Visual/olfactory	**Visual/auditory**	**Olfactory/auditory**	**Visual/olfactory/auditory**
Aversive combinations				
Mean distance (cm)	*t* = -1.87 *p* = 0.09	*t* = -1.01 *p* = 0.34	-	*t* = -2.08 *p* = 0.06
Closest distance (cm)	*t* = -1.39 *p* = 0.20	*t* = -1.19 *p* = 0.26	-	***t* = -3.42** ***p* = 0.01**
Activity per min	*t* = 0.13 *p* = 0.90	*t* = 0.80 *p* = 0.44	*Z* = -1.62 *p* = 0.11	*t* = 0.21 *p* = 0.84
Contact calls per min	*Z* = -0.71 *p* = 0.48	*Z* = -0.63 *p* = 0.53	*Z* = -1.38 *p* = 0.17	*Z* = -0.71 *p* = 0.48
Mobbing/alarm calls per min	*t* = 1.20 *p* = 0.26	*t* = 1.59 *p* = 0.14	*Z* = -1.60 *p* = 0.11	*t* = 0.07 *p* = 0.95
Looks upwards per min	*t* = -0.43 *p* = 0.68	*Z* = -0.21 *p* = 0.83	*t* = 0.22 *p* = 0.83	*Z* = -0.33 *p* = 0.74
Looks downwards per min	*t* = 0.50 *p* = 0.62	*t* = -1.34 *p* = 0.21	*t* = -0.50 *p* = 0.63	*t* = -0.22 *p* = 0.83
Looks at stimulus per min	***t* = 3.84** ***p* = 0.004**	*t* = 2.13 *p* = 0.06	-	***t* = 2.17** ***p* = 0.05**

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	Visual/olfactory	**Visual/auditory**	**Olfactory/auditory**	**Visual/olfactory/auditory**
Pleasant combinations				
Mean distance (cm)	$t = -1.88$ $p = 0.09$	$t = -1.66$ $p = 0.13$	**$Z = -2.82$** **$p = 0.01$**	$t = -2.02$ $p = 0.07$
Closest distance (cm)	$Z = -1.83$ $p = 0.07$	$Z = -0.45$ $p = 0.66$	-	$Z = -1.17$ $p = 0.27$
Activity per min	$t = -1.81$ $p = 0.26$	$t = 0.00$ $p = 1.00$	$t = 0.79$ $p = 0.45$	$t = -0.42$ $p = 0.69$
Contact calls per min	$Z = -0.43$ $p = 0.67$	$Z = -1.84$ $p = 0.07$	$Z = -0.25$ $p = 0.80$	$Z = -1.51$ $p = 0.13$
Mobbing/alarm calls per min	$Z = -0.51$ $p = 0.61$	$Z = -0.21$ $p = 0.84$	$Z = -1.00$ $p = 0.32$	$Z = -1.83$ $p = 0.07$
Food-related calls per min	**$Z = -2.02$** **$p = 0.04$**	**$Z = -2.21$** **$p = 0.03$**	$Z = -1.00$ $p = 0.32$	$Z = -1.60$ $p = 0.11$
Looks upwards per min	$Z = -1.40$ $p = 0.16$	$Z = -0.14$ $p = 0.89$	$Z = -0.35$ $p = 0.73$	**$Z = -2.23$** **$p = 0.03$**
Looks downwards per min	$t = 0.62$ $p = 0.55$	$t = 0.70$ $p = 0.50$	$Z = -0.17$ $p = 0.86$	$t = -1.65$ $p = 0.13$
Looks at stimulus per min	$t = 1.20$ $p = 0.25$	$t = 0.40$ $p = 0.70$	-	**$t = -2.94$** **$p = 0.02$**

Appendix VII. Statistical comparisons of the responses scored in the pre- and post-test periods of each related combination (of the same type, such as aversive visual/aversive auditory: Ch. 5) and the individually presented stimuli (Ch. 4). 'Comb' refers to 'combination'.

	Quoll/ odour of cat faeces	**Quoll/ leopard growl**	**Cat faeces/ leopard growl**	**Quoll/odour of cat faeces/ leopard growl**	**Marshmallow/ marshmallow odour**	**Marshmallow/ marmoset food-directed calls**	**Marshmallow odour/ food-directed calls**	**Marshmallow/ marshmallow odour/ food-directed calls**
Pre-test								
Mean distance (cm)	$Z = -0.46$ $p = 0.65$	**$t = 2.37$** **$p = 0.04$**	$t = 1.21$ $p = 0.25$	$t = 2.07$ $p = 0.06$	$t = 1.74$ $p = 0.11$	$t = 1.23$ $p = 0.24$	$Z = -0.86$ $p = 0.39$	$t = 1.89$ $p = 0.09$
Activity per 2 mins	$F_{(2,22)} = 0.23$ $p = 0.80$	$F_{(2,22)} = 2.25$ $p = 0.13$	$F_{(2,22)} = 1.82$ $p = 0.19$	$F_{(3,33)} = 0.67$ $p = 0.58$	$F_{(2,22)} = 0.32$ $p = 0.73$	$F_{(2,22)} = 1.12$ $p = 0.34$	$F_{(2,22)} = 0.50$ $p = 0.62$	$F_{(3,33)} = 0.36$ $p = 0.78$
Contact calls per 2 mins	$F_{(2,22)} = 0.82$ $p = 0.45$	$F_{(2,22)} = 0.67$ $p = 0.52$	$F_{(2,22)} = 1.39$ $p = 0.27$	$F_{(3,33)} = 1.06$ $p = 0.38$	$F_{(2,22)} = 2.73$ $p = 0.09$	$F_{(2,22)} = 1.30$ $p = 0.29$	$F_{(2,22)} = 0.07$ $p = 0.94$	$F_{(3,33)} = 1.17$ $p = 0.31$
Mobbing/alarm calls per 2 mins	$X^2 = 0.26$ $p = 0.88$	$X^2 = 0.20$ $p = 0.91$	$X^2 = 0.44$ $p = 0.80$	$X^2 = 0.62$ $p = 0.89$	$X^2 = 2.79$ $p = 0.25$	$X^2 = 1.00$ $p = 0.61$	$X^2 = 1.04$ $p = 0.59$	$X^2 = 4.33$ $p = 0.23$
Food-related calls per 2 mins	$X^2 = 4.00$ $p = 0.14$	$X^2 = 2.00$ $p = 0.37$	$X^2 = 2.00$ $p = 0.37$	-	-	$X^2 = 2.00$ $p = 0.37$	-	-
Looks upwards per 2 mins	$X^2 = 1.17$ $p = 0.56$	$X^2 = 0.05$ $p = 0.98$	$X^2 = 3.17$ $p = 0.21$	$X^2 = 2.68$ $p = 0.44$	$X^2 = 4.87$ $p = 0.09$	$X^2 = 0.91$ $p = 0.63$	$X^2 = 1.73$ $p = 0.42$	$X^2 = 3.20$ $p = 0.36$
Looks downwards per 2 mins	$F_{(2,22)} = 0.40$ $p = 0.54$	**$F_{(2,22)} = 9.65$** **$p = 0.001$** Comb vs quoll: $p = 0.55$ **Comb vs leopard growl: $p = 0.004$**	**$F_{(2,22)} = 6.15$** **$p = 0.01$** Comb vs faeces odour: $p = 1.00$ **Comb vs leopard growl: $p = 0.03$**	$F_{(3,33)} = 2.71$ $p = 0.06$	$F_{(2,22)} = 2.70$ $p = 0.09$	$X^2 = 4.55$ $p = 0.10$	$X^2 = 2.17$ $p = 0.34$	$F_{(3,33)} = 2.45$ $p = 0.09$

(Continued from previous page)

	Quoll/ odour of cat faeces	**Quoll/ leopard growl**	**Cat faeces/ leopard growl**	**Quoll/odour of cat faeces/ leopard growl**	**Marshmallow/ marshmallow odour**	**Marshmallow/ marmoset food-directed calls**	**Marshmallow odour/ food-directed calls**	**Marshmallow/ marshmallow odour/ food-directed calls**
Post-test								
Mean distance (cm)	$Z = -1.17$ $p = 0.24$	**$t = 3.67$** **$p = 0.004$**	**$Z = -2.28$** **$p = 0.02$**	**$t = 4.06$** **$p = 0.002$**	$t = 0.39$ $p = 0.71$	$Z = -1.02$ $p = 0.31$	$Z = -1.49$ $p = 0.14$	$t = 1.57$ $p = 0.15$
Activity per 2 mins	$F_{(2,22)} = 0.84$ $p = 0.45$	$F_{(2,22)} = 0.99$ $p = 0.39$	$X^2 = 0.32$ $p = 0.85$	$F_{(3,33)} = 2.21$ $p = 0.11$	$F_{(2,22)} = 0.17$ $p = 0.85$	$X^2 = 0.81$ $p = 0.67$	$X^2 = 4.87$ $p = 0.09$	$X^2 = 3.55$ $p = 0.32$
Contact calls per 2 mins	$F_{(2,22)} = 0.16$ $p = 0.85$	$X^2 = 0.89$ $p = 0.64$	$X^2 = 0.91$ $p = 0.63$	$X^2 = 4.03$ $p = 0.30$	$X^2 = 1.83$ $p = 0.40$	$F_{(2,22)} = 0.26$ $p = 0.78$	$F_{(2,22)} = 1.19$ $p = 0.32$	$F_{(3,33)} = 1.18$ $p = 0.34$
Mobbing/alarm calls per 2 mins	$X^2 = 0.30$ $p = 0.86$	$X^2 = 4.33$ $p = 0.12$	$X^2 = 2.27$ $p = 0.32$	$X^2 = 1.89$ $p = 0.60$	$X^2 = 1.78$ $p = 0.41$	$X^2 = 0.47$ $p = 0.79$	$X^2 = 1.41$ $p = 0.49$	$X^2 = 2.46$ $p = 0.48$
Food-related calls per 2 mins	-	$X^2 = 2.00$ $p = 0.37$	$X^2 = 4.00$ $p = 0.14$	-	$X^2 = 2.00$ $p = 0.37$	$X^2 = 4.00$ $p = 0.14$	$X^2 = 2.00$ $p = 0.37$	-
Looks upwards per 2 mins	$X^2 = 2.06$ $p = 0.36$	$X^2 = 0.83$ $p = 0.66$	$X^2 = 0.14$ $p = 0.93$	$X^2 = 2.12$ $p = 0.55$	$F_{(2,22)} = 2.95$ $p = 0.07$	$X^2 = 1.17$ $p = 0.56$	$F_{(2,22)} = 1.99$ $p = 0.16$	**$F_{(3,33)} = 3.11$** **$p = 0.04$** Comb/marshmallow: $p = 1.00$ Comb/marshmallow odour: $p = 0.30$ **Comb/marmoset food-directed calls: $p = 0.01$**
Looks downwards per 2 minutes	$F_{(2,22)} = 0.61.$ $p = 0.55$	$F_{(2,22)} = 0.04$ $p = 0.96$	$F_{(2,22)} = 2.37$ $p = 0.12$	$F_{(3,33)} = 0.16$ $p = 0.71$	$X^2 = 0.61$ $p = 0.55$	$X^2 = 0.38$ $p = 0.83$	$X^2 = 2.13$ $p = 0.35$	$X^2 = 7.13$ $p = 0.07$

Appendix VIII. Individual and mean (± sem) scores for each behavioural response scored in the pre-test, test and post-test periods in tests of the conflicting combinations (of different types, such as aversive visual/pleasant auditory: Ch. 6).

Distance from stimulus (cm)

	Quoll/marmoset food-directed calls			**Marshmallow/leopard growl**			**Cat faeces/marmoset food-directed calls**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	168.24	114	233	207.68	17.28	206.52	215.80	194.52	199.96
Bandit	189.4	171.84	202.44	151.8	108.2	194.04	197.92	176.80	193.52
Mogwai	196.24	177.24	166.96	173.48	24.56	194.56	151.04	112.16	136.80
Jade	205.44	202.36	168.96	204.64	124.6	183.64	183.96	210.24	190.64
Mackybe	208	262.56	202.68	212	223.04	210.48	179.64	133.16	208.00
Ash	176.4	180.44	148.6	171.24	81.28	188.64	194.52	176.16	187.16
Smokey	143.72	146.04	170.32	172.44	26.56	161.4	147.16	127.88	143.60
Ranger	191.16	170.44	144.96	165.24	94.96	195.56	147.40	156.36	165.32
Gizmo	228	177.6	217.8	226.64	135.68	219.28	220.00	187.28	218.24
Inca	186.2	191.88	190.6	176.52	59.28	91	191.48	172.84	184.20
Aziz	186.44	181.28	172.88	155.48	66.76	174.52	132.16	194.88	211.00
Mean	**189.02**	**179.61**	**183.56**	**183.38**	**87.47**	**183.60**	**178.28**	**167.48**	**185.31**
sem	6.65	10.93	8.46	7.54	18.20	10.47	8.94	9.45	8.02

	Marshmallow odour/leopard growls			**Quoll/marshmallow**			**Quoll/marshmallow/leopard growl**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	168.08	141.72	199.52	207.76	136.68	215	213.56	112.36	210.24
Bandit	192.08	165.12	193.56	157.84	66.36	193.6	176.08	125.64	143.84
Mogwai	174.60	94.92	199.56	162.92	141.48	184.36	153.96	130.40	190.80
Jade	175.96	124.08	195.20	208.08	125.08	192.24	198.68	158.88	185.84
Mackybe	208.00	42.80	201.64	239.8	244.36	187.44	253.04	231.24	220.00
Ash	201.52	129.04	165.00	162.52	172.2	156.8	191	190.04	195.68
Smokey	164.40	87.20	155.32	156	89.44	161.24	165.08	126.28	183.48
Ranger	163.28	129.56	160.88	171.12	110.2	195.92	180.68	139.16	218.32
Gizmo	220.00	142.80	228.16	217.64	98.72	205.76	218.4	135.76	217.64

Inca	126.72	92.60	192.84	206.08	122.28	160.12	200.36	149.76	197.40
Aziz	152.56	91.80	171.16	185.88	79.32	191.92	172.44	128.92	169.84
Mean	**177.02**	**112.88**	**187.53**	**188.69**	**126.01**	**185.85**	**193.03**	**148.04**	**193.92**
sem	8.09	10.39	6.60	8.62	14.95	5.72	8.49	10.43	7.00

Activity per 2 minutes

	Quoll/marmoset food-directed calls			**Marshmallow/leopard growl**			**Cat faeces/marmoset food-directed calls**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	7	12	1	3	4	2	4	3	7
Bandit	13	15	12	8	15	11	13	16	12
Mogwai	8	11	6	2	4	5	2	6	0
Jade	9	8	7	9	13	9	6	6	10
Mackybe	0	1	4	0	3	1	3	3	0
Ash	2	1	1	4	9	2	2	2	1
Smokey	11	19	14	15	6	13	12	17	12
Ranger	6	8	3	10	14	6	5	9	7
Gizmo	0	4	1	6	12	1	0	3	2
Inca	7	4	4	5	3	3	6	7	4
Aziz	3	13	9	9	8	6	8	3	5
Mean	**6.00**	**8.73**	**5.64**	**6.45**	**8.27**	**5.36**	**5.55**	**6.82**	**5.45**
sem	1.30	1.77	1.35	1.29	1.39	1.25	1.24	1.58	1.36
	Marshmallow odour/leopard growls			**Quoll/marshmallow**			**Quoll/marshmallow/leopard growl**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	7	9	7	5	13	0	7	9	3
Bandit	8	12	12	12	13	8	7	10	10
Mogwai	7	10	6	5	10	8	3	10	4
Jade	10	9	12	9	14	10	9	13	12

Mackybe	0	1	2	3	2	1	0	4	0
Ash	2	3	0	3	2	1	0	2	1
Smokey	10	9	11	9	8	11	9	12	10
Ranger	7	7	13	7	12	6	7	9	3
Gizmo	0	11	1	3	6	4	0	11	4
Inca	9	8	6	2	8	6	2	6	5
Aziz	7	12	12	13	11	11	6	12	4
Mean	**6.09**	**8.27**	**7.45**	**6.45**	**9.00**	**6.00**	**4.55**	**8.91**	**5.09**
sem	1.12	1.05	1.47	1.15	1.28	1.22	1.09	1.06	1.17

Contact calls per 2 minutes

Marmoset	Quoll/marmoset food-directed calls			Marshmallow/leopard growl			Cat faeces/marmoset food-directed calls		
	Pre-test	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	4	0	6	9	0	7	10	3	8
Bandit	10	6	8	11	5	8	11	8	6
Mogwai	9	2	8	7	0	4	4	2	6
Jade	4	4	3	6	1	4	2	2	4
Mackybe	3	0	2	3	0	5	1	1	3
Ash	0	0	0	2	1	0	0	0	0
Smokey	6	0	4	3	0	2	11	2	7
Ranger	5	0	7	6	3	7	6	1	6
Gizmo	5	0	1	6	3	6	4	2	7
Inca	4	10	10	3	1	0	4	1	4
Aziz	9	3	10	4	0	6	1	0	6
Mean	**5.36**	**2.27**	**5.36**	**5.45**	**1.27**	**4.45**	**4.91**	**2.00**	**5.18**
sem	0.90	0.99	1.07	0.85	0.51	0.84	1.23	0.66	0.69

Marmoset	Marshmallow odour/leopard growls			Quoll/marshmallow			Quoll/marshmallow/leopard growl		
	Pre-test	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	9	8	8	10	2	5	9	0	9
Bandit	6	8	7	5	3	6	11	3	5
Mogwai	5	3	5	6	0	6	2	0	1
Jade	2	1	5	4	1	2	3	1	3
Mackybe	6	0	1	3	1	5	8	4	5
Ash	1	0	1	4	0	0	4	0	1
Smokey	10	5	12	4	0	7	8	1	6
Ranger	7	6	7	5	0	6	1	0	4
Gizmo	4	3	5	9	0	6	8	0	7
Inca	0	3	5	6	1	2	5	2	6

Aziz	2	0	5	2	0	8	6	0	6
Mean	**4.73**	**3.36**	**5.55**	**5.27**	**0.73**	**4.82**	**5.91**	**1.00**	**4.82**
sem	0.98	0.92	0.93	0.73	0.30	0.74	0.96	0.43	0.74

Mobbing/alarm calls per 2 minutes

	Quoll/marmoset food-directed calls			**Marshmallow/leopard growl**			**Cat faeces/marmoset food-directed calls**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	7	75	0	0	41	0	0	0	6
Bandit	0	0	0	0	4	0	3	0	0
Mogwai	0	55	0	0	36	0	0	0	0
Jade	27	0	6	6	26	3	0	1	4
Mackybe	0	0	0	0	0	0	0	0	0
Ash	0	0	0	0	0	0	0	0	0
Smokey	9	48	1	0	12	0	0	0	0
Ranger	6	53	0	0	3	1	0	0	0
Gizmo	0	24	0	0	0	0	0	0	0
Inca	0	11	0	0	6	0	0	0	0
Aziz	0	3	0	0	0	0	0	0	0
Mean	**4.45**	**24.45**	**0.64**	**0.55**	**11.64**	**0.36**	**0.27**	**0.09**	**0.91**
sem	2.48	8.47	0.54	0.55	4.64	0.28	0.27	0.09	0.62
	Marshmallow odour/leopard growls			**Quoll/marshmallow**			**Quoll/marshmallow/leopard growl**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	6	7	0	1	70	0	0	59	0
Bandit	0	0	20	0	15	0	0	4	0
Mogwai	9	2	1	0	119	0	0	69	0
Jade	0	6	0	21	37	0	27	27	11

Mackybe	0	0	0	0	0	0	0	7	0
Ash	0	0	0	0	0	1	0	0	0
Smokey	0	1	0	4	66	0	2	46	0
Ranger	0	24	0	0	64	0	1	48	0
Gizmo	0	2	0	0	43	0	0	55	0
Inca	0	0	0	0	125	0	0	61	0
Aziz	0	0	0	0	57	0	0	27	0
Mean	**1.36**	**3.82**	**1.91**	**2.36**	**54.18**	**0.09**	**2.73**	**36.64**	**1.00**
sem	0.94	2.15	1.81	1.90	12.63	0.09	2.43	7.49	1.00

Food-related calls per 2 minutes

	Quoll/marmoset food-directed calls			**Marshmallow/leopard growl**			**Cat faeces/marmoset food-directed calls**		
Marmoset	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	0	0	0	0	0	0	0	0	0
Bandit	0	0	0	0	0	0	1	0	0
Mogwai	0	0	0	0	0	0	0	0	0
Jade	0	0	0	0	26	3	0	0	0
Mackybe	0	0	0	0	0	0	0	0	0
Ash	0	0	0	0	0	0	0	0	0
Smokey	0	0	0	0	11	0	0	0	0
Ranger	0	0	0	0	0	0	0	0	0
Gizmo	0	0	0	0	5	0	0	0	0
Inca	0	0	0	0	0	0	0	0	0
Aziz	0	0	0	0	1	0	0	0	0
Mean	**0.00**	**0.00**	**0.00**	**0.00**	**3.91**	**0.27**	**0.09**	**0.00**	**0.00**

sem	0.00	0.00	0.00	0.00	2.44	0.27	0.09	0.00	0.00

Marmoset	Marshmallow odour/leopard growls			Quoll/marshmallow			Quoll/marshmallow/leopard growl		
	Pre-test	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	0	0	0	0	0	0	0	0	0
Bandit	0	0	4	0	5	0	0	1	0
Mogwai	0	0	0	0	0	0	0	0	0
Jade	0	13	0	0	0	0	0	0	0
Mackybe	0	0	0	0	0	0	0	0	0
Ash	0	0	0	0	0	0	0	0	0
Smokey	0	0	0	0	0	0	0	0	0
Ranger	0	3	0	0	0	0	0	0	0
Gizmo	0	5	0	0	0	0	0	0	0
Inca	0	0	0	0	0	0	0	0	0
Aziz	0	0	0	0	0	0	0	0	0
Mean	**0.00**	**1.91**	**0.36**	**0.00**	**0.45**	**0.00**	**0.00**	**0.09**	**0.00**
sem	0.00	1.22	0.36	0.00	0.45	0.00	0.00	0.09	0.00

Looks upwards per 2 minutes

Marmoset	Quoll/marmoset food-directed calls			Marshmallow/leopard growl			Cat faeces/marmoset food-directed calls		
	Pre-test	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	6	1	1	4	0	3	7	0	2
Bandit	4	6	2	9	1	4	2	3	3
Mogwai	0	1	2	4	0	1	9	4	5
Jade	0	0	2	1	0	3	2	0	3
Mackybe	0	2	4	2	1	2	1	4	2
Ash	1	5	3	2	1	4	0	1	1

Smokey	0	1	2	1	0	0	1	1	4
Ranger	1	1	6	4	2	1	6	3	1
Gizmo	2	1	1	0	2	2	2	2	1
Inca	1	0	1	0	3	1	0	1	1
Aziz	7	2	7	2	2	9	3	2	1
Mean	**2.00**	**1.82**	**2.82**	**2.64**	**1.09**	**2.73**	**3.00**	**1.91**	**2.18**
sem	0.76	0.58	0.62	0.78	0.31	0.74	0.90	0.44	0.42

Marmoset	**Marshmallow odour/leopard growls**			**Quoll/marshmallow**			**Quoll/marshmallow/leopard growl**		
	Pre-test	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	1	1	1	0	0	4	1	1	1
Bandit	0	2	4	2	0	2	8	1	8
Mogwai	0	3	0	4	0	2	3	0	0
Jade	1	0	0	0	0	1	5	1	1
Mackybe	2	6	2	2	0	1	0	0	1
Ash	3	1	2	0	1	3	0	2	1
Smokey	1	3	4	0	0	0	1	0	1
Ranger	1	2	2	2	0	3	1	1	1
Gizmo	1	1	6	1	1	0	0	2	1
Inca	0	0	0	0	1	0	0	1	0
Aziz	3	1	1	2	0	2	6	3	3
Mean	**1.18**	**1.82**	**2.00**	**1.18**	**0.27**	**1.64**	**2.27**	**1.09**	**1.64**
sem	0.33	0.52	0.59	0.40	0.14	0.41	0.85	0.28	0.68

Looks downwards per 2 minutes

Marmoset	Quoll/marmoset food-directed calls			Marshmallow/leopard growl			Cat faeces/marmoset food-directed calls		
	Pre-test	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	10	2	5	11	2	10	7	6	7
Bandit	2	1	2	3	4	3	1	4	4
Mogwai	8	2	5	8	1	6	8	9	11
Jade	7	7	5	5	4	6	5	7	6
Mackybe	12	4	8	7	8	7	4	9	11
Ash	11	4	13	5	6	4	3	10	5
Smokey	9	3	5	6	4	5	8	5	7
Ranger	15	0	8	3	8	6	10	9	6
Gizmo	7	8	3	7	5	5	5	7	11
Inca	7	8	4	7	8	11	3	7	3
Aziz	1	1	3	5	9	2	9	9	5
Mean	**8.09**	**3.64**	**5.55**	**6.09**	**5.36**	**5.91**	**5.73**	**7.45**	**6.91**
sem	1.23	0.87	0.94	0.69	0.80	0.81	0.86	0.58	0.87

Marmoset	Marshmallow odour/leopard growls			Quoll/marshmallow			Quoll/marshmallow/leopard growl		
	Pre-test	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**	**Pre-test**	**Test**	**Post-test**
Ness	10	9	6	6	0	4	4	0	4
Bandit	2	7	4	0	1	1	1	1	5
Mogwai	9	6	4	2	2	4	7	1	5
Jade	8	6	6	5	1	5	8	1	7
Mackybe	11	6	10	6	4	5	2	3	5
Ash	8	6	10	7	7	16	10	3	6
Smokey	3	1	4	5	3	5	1	1	10
Ranger	7	15	8	7	4	5	12	1	7
Gizmo	4	9	6	2	2	8	5	1	2
Inca	12	8	10	8	1	5	8	0	2

Aziz	6	7	4	4	1	1	6	4	4
Mean	**7.27**	**7.27**	**6.55**	**4.73**	**2.36**	**5.36**	**5.82**	**1.45**	**5.18**
sem	0.98	1.01	0.77	0.75	0.61	1.22	1.09	0.39	0.70

	Marmoset	**Quoll/ marmoset food-directed calls**	**Marshmallow/ leopard growl**	**Cat faeces/ marmoset food-directed calls**	**Marshmallow odour/ leopard growls**	**Quoll/marshmallow**	**Quoll/marshmallow/ leopard growl**
Closest distance (cm)	Ness	45	0	-	-	40	20
	Bandit	116	0	-	-	15	20
	Mogwai	113	0	-	-	68	80
	Jade	148	0	-	-	15	0
	Mackybe	208	212	-	-	201	181
	Ash	143	0	-	-	150	191
	Smokey	20	0	-	-	20	20
	Ranger	94	0	-	-	20	20
	Gizmo	113	0	-	-	0	25
	Inca	93	0	-	-	82	82
	Aziz	90	0	-	-	15	20
	Mean	**107.55**	**19.27**	-	-	**56.91**	**59.91**
	sem	15.19	19.27	-	-	19.47	20.34
Latency to approach (secs)	Ness	40.56	6.31	-	-	11.79	1.31
	Bandit	120	2.72	-	-	0	3.6
	Mogwai	0	5.94	-	-	6.41	31.4
	Jade	120	4.75	-	-	2.91	11.75
	Mackybe	120	120	-	-	120	24.87
	Ash	120	1.32	-	-	120	120
	Smokey	5.63	4.34	-	-	5.72	2.47
	Ranger	48.91	4.35	-	-	0	17.5

	Gizmo	38.06	9.28	-	-	3.07	4.13
	Inca	92.54	6	-	-	13.5	13.97
	Aziz	3.22	6.75	-	-	0.84	2.18
	Mean	**64.45**	**15.61**	-	-	**25.84**	**21.20**
	sem	15.38	10.46	-	-	14.10	10.33
Latency to vocalise (secs)	Ness	6.48	19.22	41.55	12.86	10.87	1.98
	Bandit	14	33.47	29.41	9.36	5.22	4.93
	Mogwai	0	45.21	58.91	12.54	0.56	2.65
	Jade	53.61	4.44	5.56	4.42	5.02	1.52
	Mackybe	120	120	99.8	120	102.97	24.87
	Ash	120	79.58	120	120	120	120
	Smokey	1.06	3.84	36.28	2.43	3.24	1.76
	Ranger	16.46	1.1	74.25	6.05	0.32	1.09
	Gizmo	2.7	5.11	38.95	31.86	1.53	7.36
	Inca	2.95	30	10.85	25.82	0.89	9.8
	Aziz	8.95	9.96	120	120	4.38	2.84
	Mean	**31.47**	**31.99**	**57.78**	**42.30**	**23.18**	**16.25**
	sem	13.94	11.31	12.28	15.28	13.24	10.58
		Quoll/ marmoset food-directed calls	**Marshmallow/ leopard growl**	**Quoll/ marshmallow**		**Quoll/ marshmallow/ leopard growl**	
				Quoll	Marshmallow	Quoll	Marshmallow
Looks at stimulus per 2 mins	Ness	18	11	9	0	15	1
	Bandit	6	3	8	4	8	2
	Mogwai	10	13	12	0	20	0
	Jade	4	7	10	3	10	0
	Mackybe	9	1	4	0	6	0
	Ash	6	8	2	0	5	0
	Smokey	9	16	12	5	13	1
	Ranger	15	4	10	3	15	2
	Gizmo	12	6	16	2	13	1
	Inca	4	7	15	0	13	0

Aziz	6	10	10	2	10	2
Mean	**9.00**	**7.82**	**9.82**	**1.73**	**11.64**	**0.82**
sem	1.36	1.34	1.26	0.56	1.32	0.26

Appendix IX. Results of the statistical comparisons of the first and second minute of the test period of the experiment in which conflicting combinations were presented (Ch. 6).

	Quoll/marmoset food-directed calls	**Marshmallow/ leopard growl**	**Cat faeces/ food-directed calls**	**Marshmallow odour/leopard growl**	**Quoll/ marshmallow**	**Quoll/marshmallow/ leopard growl**
Mean distance (cm)	$Z = -0.71$ $p = 0.48$	**$Z = -2.67$** **$p = 0.01$**	-	-	$Z = -1.78$ $p = 0.08$	**$t = -2.41$** **$p = 0.04$**
Closest distance (cm)	$Z = -0.36$ $p = 0.72$	$Z = -1.60$ $p = 0.11$	-	-	$Z = -0.84$ $p = 0.40$	$t = -0.53$ $p = 0.61$
Activity per min	$t = 0.00$ $p = 1.00$	$t = 0.19$ $p = 0.85$	$Z = -1.71$ $p = 0.09$	$t = -0.13$ $p = 0.90$	$t = -0.70$ $p = 0.50$	$t = -1.00$ $p = 0.34$
Contact calls per min	$Z = -0.38$ $p = 0.71$	$Z = -1.00$ $p = 0.32$	$Z = -1.41$ $p = 0.16$	$t = -0.41$ $p = 0.69$	$t = -0.69$ $p = 0.51$	$Z = -0.37$ $p = 0.71$
Mobbing/alarm calls per min	$Z = -0.85$ $p = 0.40$	$Z = -1.16$ $p = 0.25$	$Z = -1.00$ $p = 0.32$	$Z = -0.63$ $p = 0.53$	**$Z = -2.67$** **$p = 0.01$**	**$Z = -2.67$** **$p = 0.01$**
Food-related calls per min	-	$Z = -1.83$ $p = 0.07$	-	$Z = -1.34$ $p = 0.18$	$Z = -1.00$ $p = 0.32$	$Z = -1.00$ $p = 0.32$
Looks upwards per min	$Z = -0.07$ $p = 0.94$	$t = -1.17$ $p = 0.27$	$t = 0.21$ $p = 0.84$	$Z = -0.63$ $p = 0.53$	$Z = -0.58$ $p = 0.56$	$Z = -1.00$ $p = 0.32$
Looks downwards per min	$t = -0.80$ $p = 0.44$	$t = 2.06$ $p = 0.07$	$t = -1.96$ $p = 0.08$	**$t = -3.09$** **$p = 0.01$**	$Z = -0.47$ $p = 0.64$	$Z = 0.00$ $p = 1.00$
Looks at stimulus (visual) per min	$t = 0.79$ $p = 0.45$ (quoll)	$t = 0.88$ $p = 0.40$ (marshmallow)	-	-	**$t = 3.09$** **$p = 0.01$** **(quoll)** $Z = -0.37$ $p = 0.71$ (marshmallow)	$t = 1.47$ $p = 0.17$ (quoll) $Z = -0.38$ $p = 0.71$ (marshmallow)

Appendix X. Statistical comparisons of scores collected in the pre- and post-test periods in each conflicting combination (Ch. 6) and the relevant individually-presented stimuli (Ch. 4). 'Comb' refers to 'combination'.

Pre-test	**Quoll/ marmoset food-directed calls**	**Marshmallow/ leopard growl**	**Cat faeces/ marmoset food-directed calls**	**Marshmallow odour/ leopard growls**	**Quoll/ marshmallow**	**Quoll/marshmallow/ leopard growl**
Mean distance (cm)	$t = 2.17$ $p = 0.06$	$t = 0.69$ $p = 0.51$	$t = 1.46$ $p = 0.18$	$t = 1.19$ $p = 0.26$	$X^2 = 2.18$ $p = 0.34$	$X^2 = 4.91$ $p = 0.09$
Activity per 2 mins	$F_{(2,20)} = 0.08$ $p = 0.93$	$F_{(2,20)} = 1.45$ $p = 0.26$	$F_{(2,20)} = 0.21$ $p = 0.81$	$F_{(2,20)} = 0.57$ $p = 0.58$	$F_{(2,20)} = 0.57$ $p = 0.58$	$F_{(3,30)} = 2.28$ $p = 0.10$
Contact calls per 2 mins	$F_{(2,20)} = 0.82$ $p = 0.46$	$F_{(2,20)} = 0.42$ $p = 0.67$	$F_{(2,20)} = 0.05$ $p = 0.95$	$F_{(2,20)} = 1.08$ $p = 0.36$	$F_{(2,20)} = 0.87$ $p = 0.43$	$F_{(3,30)} = 0.17$ $p = 0.92$
Mobbing/alarm calls per 2 mins	$X^2 = 0.48$ $p = 0.79$	$X^2 = 2.11$ $p = 0.35$	$X^2 = 2.95$ $p = 0.23$	$X^2 = 0.00$ $p = 1.00$	$X^2 = 0.25$ $p = 0.88$	$X^2 = 0.33$ $p = 0.96$
Food-related calls per 2 mins	-	-	$X^2 = 2.00$ $p = 0.37$	-	-	-
Looks upwards per 2 mins	$X^2 = 2.05$ $p = 0.36$	**$X^2 = 6.14$** **$p = 0.05$** Comb vs marshmallow: $Z = -1.65$ $p = 0.10$ Comb vs leopard growl: $Z = -0.36$ $p = 0.72$	$X^2 = 3.60$ $p = 0.17$	$X^2 = 2.15$ $p = 0.34$	**$X^2 = 5.85$** **$p = 0.05$**	$X^2 = 0.83$ $p = 0.84$
Looks downwards per 2 mins	$X^2 = 5.19$ $p = 0.08$	**$F_{(2,20)} = 3.75$** **$p = 0.04$** Comb vs marshmallow: $p = 0.75$ Comb vs leopard growl: $p = 0.79$	$F_{(2,20)} = 1.30$ $p = 0.29$	$F_{(2,20)} = 2.78$ $p = 0.09$	**$F_{(2,20)} = 4.23$** **$p = 0.03$** Comb vs quoll: $p = 0.29$ Comb vs marshmallow: $p = 0.08$	**$F_{(3,30)} = 4.19$** **$p = 0.01$** Comb vs quoll: $p = 1.00$ Comb vs marshmallow: $p = 0.22$ Comb vs leopard growl: $p = 1.00$

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Post-test	**Quoll/ marmoset food-directed calls**	**Marshmallow/ leopard growl**	**Cat faeces/ marmoset food-directed calls**	**Marshmallow odour/ leopard growls**	**Quoll/ marshmallow**	**Quoll/marshmallow/ leopard growl**
Mean distance (cm)	$t = 1.41$ $p = 0.19$	$Z = -1.51$ $p = 0.13$	$Z = -1.51$ $p = 0.13$	$Z = -1.68$ $p = 0.09$	$F_{(2,20)} = 2.04$ $p = 0.16$	**$F_{(3,30)} = 4.84$** **$p = 0.02$** **Comb vs quoll:** **$p = 0.05$** Comb vs marshmallow: $p = 0.06$
Activity per 2 mins	$F_{(2,20)} = 0.43$ $p = 0.66$	$F_{(2,20)} = 0.31$ $p = 0.74$	$F_{(2,20)} = 0.27$ $p = 0.76$	$X^2 = 2.28$ $p = 0.32$	$F_{(2,20)} = 1.62$ $p = 0.22$	$X^2 = 1.47$ $p = 0. 24$
Contact calls per 2 mins	$F_{(2,20)} = 0.05$ $p = 0.96$	$X^2 = 1.27$ $p = 0.53$	$F_{(2,20)} = 0.04$ $p = 0.96$	$X^2 = 1.72$ $p = 0.42$	$F_{(2,20)} = 0.05$ $p = 0.95$	$X^2 = 0.78$ $p = 0.86$
Mobbing/alarm calls per 2 mins	$X^2 = 1.5$ $p = 0.47$	$X^2 = 0.26$ $p = 0.88$	$X^2 = 1.50$ $p = 0.47$	$X^2 = 1.90$ $p = 0.39$	$X^2 = 2.10$ $p = 0.35$	$X^2 = 2.75$ $p = 0.43$
Food-related calls per 2 mins	-	$X^2 = 2.00$ $p = 0.37$	-	$X^2 = 1.00$ $p = 0.61$	-	-
Looks upwards per 2 mins	**$F_{(2,20)} = 3.43$** **$p = 0.05$** Comb vs quoll: $p = 0.42$ Comb vs marmoset food-directed calls: $p = 0.08$	$X^2 = 4.00$ $p = 0.14$	$X^2 = 3.27$ $p = 0.20$	$F_{(2,20)} = 0.69$ $p = 0.52$	$F_{(2,20)} = 0.91$ $p = 0.42$	$X^2 = 2.24$ $p = 0.52$
Looks downwards per 2 mins	$X^2 = 4.00$ $p = 0.14$	$F_{(2,20)} = 0.01$ $p = 0.99$	$F_{(2,20)} = 0.10$ $p = 0.91$	$F_{(2,20)} = 1.0$ $p = 0.38$	$X^2 = 2.65$ $p = 0.27$	$F_{(3,30)} = 0.38$ $p = 0.77$

Appendix XI. Individual and mean (± sem) scores for each behavioural response scored in the pre-test, test and post-test periods of the snake hiss, red-shouldered hawk call and leopard growl (Ch. 7). The pre- and post-test periods are shown divided by two so as to be comparable with the test period (i.e. pre- and post-test periods were two minutes long while the test period was only conducted for one minute).

		Pre-test/2			**Test**			**Post-test/2**		
	Marmoset	**Snake hiss**	**Hawk call**	**Leopard growl**	**Snake hiss**	**Hawk call**	**Leopard growl**	**Snake hiss**	**Hawk call**	**Leopard growl**
Activity per min	Ness	2.75	1.5	4	3.5	0.5	2.0	1.5	1.25	2.25
	Bandit	4.25	6.75	5.5	3.5	7	4.5	3.5	5	6.75
	Mogwai	2	2.25	1	2.5	0.5	0.5	1.75	0.75	1.75
	Jade	2.75	5.75	4.5	3.5	6	6.0	3	5.75	3.25
	Mackybe	2.25	0.75	0.75	0.5	0	0.0	0.5	0	0.5
	Ash	1.5	1	1.75	0	1.5	2.0	0	0.75	1.25
	Smokey	4	7	5.5	3.5	7.5	0.5	3.75	5	2.75
	Ranger	1.25	1.25	2.75	1	1	3.0	0	2.5	0.75
	Gizmo	1.75	0.5	2.25	1.5	1	0.0	0	2	1.5
	Flint	2.25	1.25	2.75	3	2.5	4.0	2.75	2.5	3
	Inca	2.5	3.5	4.25	0.5	2.5	4.5	2.5	2	5
	Aziz	3.5	6.5	7	5	6	4.0	5.25	4	3.75
	Mean	**2.56**	**3.17**	**3.50**	**2.33**	**3.00**	**2.58**	**2.04**	**2.63**	**2.71**
	sem	0.27	0.75	0.56	0.46	0.81	0.59	0.49	0.55	0.53
Latency to move (secs)	Ness	-	-	-	6.17	55.42	20.67	-	-	-
	Bandit	-	-	-	35.18	2.27	3.39	-	-	-
	Mogwai	-	-	-	10.58	30.00	39.84	-	-	-
	Jade	-	-	-	7.55	9.46	3.28	-	-	-
	Mackybe	-	-	-	42.88	44.91	60.00	-	-	-
	Ash	-	-	-	59.88	22.41	32.99	-	-	-
	Smokey	-	-	-	22.66	8.62	14.14	-	-	-
	Ranger	-	-	-	31.69	33.83	36.11	-	-	-
	Gizmo	-	-	-	41.03	30.00	39.75	-	-	-

	Flint	-	-	-	7.83	30.00	9.58	-	-	-
	Inca	-	-	-	31.30	22.64	20.68	-	-	-
	Aziz	-	-	-	4.38	3.45	3.36	-	-	-
	Mean				**25.09**	**24.42**	**23.65**			
	sem				5.20	4.75	5.24			
Contact calls per min	Ness	4	3.25	2	0.5	0	1	4.25	3	2.75
	Bandit	2.5	5	4.25	2	3	2	1.5	4.5	2.75
	Mogwai	2.75	1.75	3.25	1	0	1.5	2.25	1	2.5
	Jade	3.5	3	0.75	2	0	1	2	3.25	2.5
	Mackybe	2.25	3.5	3.5	1	0	1	2.75	2.75	1.5
	Ash	2	0	2.5	0	1	0. 5	1.25	1	1
	Smokey	2.5	4.75	3.25	2	3	0	2.5	5	0.75
	Ranger	1.5	1	0.75	0	0.5	0	0.25	1.5	0.75
	Gizmo	5.25	4.75	5.5	2	1.5	1	4	2.75	3.5
	Flint	2.5	0.5	1.5	0	0	0	1.25	0.75	0.75
	Inca	1.5	2.75	8.25	1	2.5	7	1.25	4.75	7
	Aziz	3	4.25	2.25	0.5	2	2	3.25	5.25	2.5
	Mean	**2.77**	**2.88**	**3.15**	**1.00**	**1.13**	**1.42**	**2.21**	**2.96**	**2.35**
	sem	0.31	0.50	0.61	0.24	0.35	0.55	0.35	0.48	0.50
Mobbing/alarm calls per min	Ness	0	0	0.25	0	0.5	0	0	5.25	6.25
	Bandit	6.25	0	12.25	0	0	37	0	0	0
	Mogwai	0	0	0	0	0	0	0.25	0	1.25
	Jade	1.25	2	0	0.5	0	0	0.75	3.5	1
	Mackybe	0	0	0	0	0	0	0	0	0
	Ash	0	0	4	0	0	1	0	0	1.25
	Smokey	0	0.25	0	4.5	0	0	0	0.5	0

	Ranger	0	0	0	0	0	0	0	0	0
	Gizmo	6.25	0	0	0	0	0	0	6.5	0
	Flint	0	0	0	0	0	0	8.25	0	0.17
	Inca	0	0	0	0	0	0.5	0	0	0
	Aziz	0	0	0	0	0	0	0	0	0
	Mean	**1.15**	**0.19**	**1.38**	**0.42**	**0.04**	**3.21**	**0.77**	**1.31**	**0.83**
	sem	0.70	0.17	1.04	0.37	0.04	3.07	0.68	0.68	0.52
Latency to vocalise (secs)	Ness	-	-	-	44.79	39.11	43.64	-	-	-
	Bandit	-	-	-	40.17	15.29	16.57	-	-	-
	Mogwai	-	-	-	27.35	31.09	23.09	-	-	-
	Jade	-	-	-	9.25	60.00	28.58	-	-	-
	Mackybe	-	-	-	49.02	60.00	47.36	-	-	-
	Ash	-	-	-	60.00	51.06	53.00	-	-	-
	Smokey	-	-	-	27.30	20.91	35.40	-	-	-
	Ranger	-	-	-	60.00	35.26	60.00	-	-	-
	Gizmo	-	-	-	41.11	40.77	49.04	-	-	-
	Flint	-	-	-	60.00	60.00	60.00	-	-	-
	Inca	-	-	-	34.53	14.61	5.51	-	-	-
	Aziz	-	-	-	57.30	35.42	36.79	-	-	-
	Mean				**42.57**	**38.63**	**38.25**			
	sem				4.62	4.80	4.98			
Looks upwards per min	Ness	1	0.5	1.75	0.5	1	0	1.25	0.75	1
	Bandit	2	0.75	2	1.5	2	1	1.25	3.75	0.5
	Mogwai	0.75	1	1.25	0.5	3.5	0	1.5	2	0.5
	Jade	0	1	0.5	1.5	2.5	0	0.25	1	2
	Mackybe	0	0.25	1.5	1	0.5	1.5	4	2	2

	Ash	0.5	1.5	0.75	2.5	1	0	1.75	1	1
	Smokey	0	0	0.75	1	1.5	0	1.25	0.25	0
	Ranger	0	0.75	0.25	0.5	2	0.5	0.5	1.5	0.25
	Gizmo	0.5	0.5	0.5	0.5	2	0	0	1	1.25
	Flint	1	0.5	1.25	0.5	2.5	1.5	0.75	1.5	1
	Inca	0	0	0.5	0.5	0.5	0.5	0.25	0.5	0.25
	Aziz	1.25	2	1.5	1.5	3	2.5	1	2	0.5
	Mean	**0.58**	**0.73**	**1.04**	**1.00**	**1.83**	**0.63**	**1.15**	**1.44**	**0.85**
	sem	0.19	0.17	0.17	0.18	0.28	0.24	0.30	0.27	0.19
Looks downwards per min	Ness	2	3.25	2	5	5.5	2	4.5	5.75	3.25
	Bandit	1.75	2	0.75	3.5	3	1	2.25	3	1
	Mogwai	2	3.75	2.5	3	0.5	1.5	3.5	3.5	2.25
	Jade	1.75	3.25	4	5.5	1.5	1.5	4.25	2.5	3.25
	Mackybe	3.75	3	2.25	2.5	4.5	0.5	2.5	3.25	3.25
	Ash	3.5	3.5	3.25	6	2	4.5	4.5	1.5	4.5
	Smokey	4	2.75	2.5	1	3	2	3.75	2	6.25
	Ranger	4	6.25	4.75	6	3.5	3.5	0.75	5.5	2.75
	Gizmo	4	2	2.5	2	2	4.5	3.25	4	1.75
	Flint	2	4.75	4.5	3.5	3.5	5	3.75	4.25	3.75
	Inca	2.5	2.5	1.25	5	3	3.5	5.75	1.5	3.5
	Aziz	0.75	1.75	0.25	0.5	0.5	1.5	1.5	3.25	1.5
	Mean	**2.67**	**3.23**	**2.54**	**3.63**	**2.71**	**2.58**	**3.35**	**3.33**	**3.08**
	sem	0.32	0.37	0.41	0.55	0.43	0.44	0.41	0.40	0.41
Hiding scores per min	Ness	0	0	2.75	0	0.5	0	0	0	0.5
	Bandit	0	0	0	7	1.5	0	6.75	0	1.75
	Mogwai	0	0	0	0	0	0	1	0.25	0.75

	Jade	0	0	0	5	1.5	2	0.75	0.5	1
	Mackybe	0	0	0	0	0	0	0	0	0
	Ash	0	0	0	0	2.5	0	0	0	0
	Smokey	0.25	0	0	3.5	1	0	0.25	0.25	0.25
	Ranger	0	1.25	0	0	0	0	0.25	5.25	0
	Gizmo	0	0	0	0	3	0	0	1	1.25
	Flint	0	0	0	0.5	1.5	0.5	0.5	0	0.5
	Inca	0	0	0	0	0	3.5	0	0.25	0
	Aziz	0	0.25	0	1.5	0	1	0	0	0
	Mean	**0.02**	**0.13**	**0.23**	**1.46**	**0.96**	**0.58**	**0.79**	**0.63**	**0.50**
	sem	0.02	0.10	0.23	0.69	0.30	0.32	0.55	0.43	0.17
Freezing scores per min	Ness	0	0	0	0.5	1	0	0	0	0
	Bandit	0	0	0	0.5	0.5	0	0	0	0
	Mogwai	0	0	0	0.5	5	0	0	0	0
	Jade	0	0	0	0.5	0	0	0	0	0
	Mackybe	0	0	0	0.5	0.5	5.5	0	0	0
	Ash	0	0	0	0	1	1	0	0	0
	Smokey	0	0	0	1	2	0	0	0	0.75
	Ranger	0	0	0	0.5	0.5	3.5	0	0	2.5
	Gizmo	0	0	0	1	1	0	0.25	0	0
	Flint	0	0	0	0	1	0.5	0	0	0
	Inca	0	0	0	0	0.5	0.5	0	0	0
	Aziz	0	0	0	0	0	0	0	0	0
	Mean	**0.00**	**0.00**	**0.00**	**0.42**	**1.08**	**0.92**	**0.02**	**0.00**	**0.27**
	sem	0.00	0.00	0.00	0.10	0.39	0.51	0.02	0.00	0.21