

CHAPTER 1

INTRODUCTION

HAND PREFERENCES IN NONHUMAN PRIMATES

Handedness, or the preferential use of one hand over the other in most tasks and in most subjects in a group (McGrew and Marchant, 1993), was once believed to be a characteristic unique to humans (Warren, 1977; Warren, 1980). However, MacNeilage et al. (1987, 1989, 1990) challenged this hypothesis, reanalyzing a number of studies and revealing asymmetrical distributions, at the population level, of right and left-hand preferences in various nonhuman primate species. MacNeilage et al. (1987, 1989, 1990) proposed that handedness in nonhuman primates might be present for tasks sharing the same perceptual, cognitive and/or motor demands. They presented the 'Postural Origins hypothesis' as an initial attempt at a unified evolutionary explanation of how manual specialization (handedness) may have evolved in nonhuman primates. They proposed that handedness evolved first in the prosimians, the earliest primates, to overcome problems of postural control when feeding. Two specializations were said to have evolved in prosimians: a right hemisphere specialization (left-hand preference) for the control of simple, visually guided reaching and a left hemisphere specialization (right-hand preference) for postural control, these specializations being retained by the later evolving primates, both New and Old World species. MacNeilage et al. (1987, 1989, 1990) hypothesized further that the role of the right hand in postural control may have led to specialization of the left hemisphere for precise sequential limb positioning and thus fine somatic sensorimotor control. This may have predisposed later evolving primates, less dependent on vertical support, to prefer the right hand for manipulative tasks or tasks requiring fine sensorimotor control. In summary, MacNeilage et al.

(1987, 1989, 1990) postulated the presence of a left-hand preference for visually guided reaching tasks and a complementary right-hand preference for manipulative tasks in both New and Old World primate species, and suggested that the transition from left-hand preferences for simple, visually guided reaching to right handedness for fine manipulation may have occurred in the great apes along with increased bipedal locomotion. Finally, according to their hypothesis, with the advent of predominant bipedalism generalized right handedness may have evolved in humans.

Prosimians have been found to be left handed when picking up and holding food, supporting the Postural Origins hypothesis (Sanford et al. 1984; Forsythe and Ward, 1988; Masataka, 1989; Ward et al. 1990; Milliken et al. 1991a). However, the results of studies examining hand use during feeding in New and Old World primates are contradictory. Although some studies report left handedness in feeding (picking up and holding food) for some species (*Macaca mulatta*, Hauser et al. 1991; *Ateles geoffroyi*, Laska, 1996b), there is right handedness in others (*Presbytis*, Yuanye et al. 1986; *Saguinus oedipus*, Diamond and McGrew, 1994; *Cebus apella*, Westergaard et al. 1997), and either a symmetrical distribution of hand preferences within groups or no hand preferences in other studies (*Macaca mulatta*, Warren, 1953; *Callithrix jacchus*, Rothe, 1973; *Macaca mulatta*, Fagot et al. 1991; *Cebus apella*, Parr et al. 1997). In a number of studies of the great apes, mostly chimpanzees, a bias toward right lateral preferences has been found (Bard et al. 1990; Fagot et al. 1992; Hopkins, 1993; Hopkins et al. 1993; Colell et al. 1995; Hopkins and de Waal, 1995), possibly supporting the hypothesis of MacNeilage et al. (1987, 1989, 1990). However, some studies of hand use in orangutans and gorillas have found no handedness in feeding despite the existence of preferences at the individual level (Annett and Annett, 1991; Byrne and Byrne, 1991; Rogers and Kaplan, 1996). Thus, studies of handedness for feeding in nonhuman primates are contradictory. While there is convincing evidence that most prosimians are left handed, consistent with the hypothesis of MacNeilage et al. (1987, 1989, 1990), the data for hand preferences in apes are either inconsistent or possibly have a tendency for right handedness, at least in chimpanzees. The hand

preferences displayed by the New and Old World primates appear to vary between species and studies, and would not support the hypothesis of MacNeilage et al. (1987, 1989, 1990).

At the time the Postural Origins hypothesis was formulated there were very few studies of hand preferences in the New World species and MacNeilage et al. (1987) based their hypothesis on only 5 studies of the New World primates. MacNeilage et al. (1987) combined the evidence for the New World primates with that of the Old World primates generating the theory for the combined platyrrhine and catarrhine species, as discussed previously. However, as these species have evolved as geographically distinct populations, and thus different variables may have influenced the evolution of their hand preferences, it is suggested that New World species should be considered separately from Old World primates. Since the publication of MacNeilage et al. (1987), there has been a number of studies examining hand use in the platyrrhine species. As the aim of the experiments reported in this thesis is to examine the functional lateralization of a New World primate, *Callithrix jacchus*, the discussion in this chapter of this type of lateralization will focus on the platyrrhine species. However, the extensive literature on the prosimian species, the Old World primates and the ape species will be considered also

Hand Preferences in New World Primates when Reaching for and Holding Food

The studies of hand preferences in New World primates when reaching for and holding food are summarized in Table 1.1. The species, ages of the subjects and individual hand preferences are indicated where possible, but not all of the papers reported all of these variables. Lateralized hand use for reaching for and holding food has been recorded in a variety of platyrrhine species (Table 1.1), and lateralization for this function appears to be species-specific.

Table 1.1- Hand use for reaching for and holding food

Species	Study	Task Description	Number of Individuals	Age	Preference	Bias
<i>Callithrix jacchus</i>	Box (1977a)	Taking food	8	4A	3L 1R	-
				4J	3L 1A	
	Matoba et al. (1991)	Holding food	8	A	2L 4R 2A	-
		Taking food	46	A	20L 11R 15A	NS
			23	J	9L 8R 6A	NS
<i>Saguinus oedipus</i>	Hook-Costigan and Rogers (1995)	Holding food	8	8A	2L 4R 2A	NS
	Diamond and McGrew (1994)**	Holding food	20	10A 7S 3J	NA	Right (p≤0.001)
		Food carry	20	10A 7S 3J	NA	Right (p≤0.001)
		King (1995)**	30	A&J	7L 21R 2A	Right (p= 0.14)
<i>Saimiri sciureus</i>	Laska (1996a)	Taking food (objects)	12	8A 4J	3L 3R 3A	NS
<i>Ateles geoffroyi</i>	Laska (1996b)	Taking food	13	10A 3J	9L 1R 3A	Left (p<0.025)
<i>Brachyteles arachnoides</i>	Ades et al. (1996)	Holding, taking food	25-30	A, S & J	NA	Right (59%)
						Left (22%)
						Both (16%)
						Right (67%)
<i>Cebus capucinus</i>	Gomperts and Costello (1991)	Holding food	NA (Wild)	NA	NA	
<i>Cebus albifrons</i> <i>Cebus apella</i>	Masataka (1990)	Taking food	4	NA	1L 3R	-
		Taking food	3	NA	2R 1A	-
	Fragaszy and Mitchell (1990)	Taking food	24	NA	3L 20R 1A	Right (p≤ 0.01)
		Holding, taking food	7	A	3L 1R 3A	-
		Searching for food	7	A	3L 2R 2A	-
	Westergaard and Suomi (1993b)	Simple reach through holes	21	16A	3L 12R 1A	Right (p≤0.005)
				5J	5L	-
	Anderson et al. (1996)	Taking food	10	7A/ S 3J	NA	NS
	Westergaard and Suomi (1996b)	Taking food	34	19A 15J	15L 16R 3A	NS
	Parr et al. (1997)	Taking food (quadrupedal)	22	13A	3L 3R 7A	NS
				9J	1L 8A	
		Taking food (bipedal)	22	13A	6L 3R 4A	NS
	Westergaard et al. (1997)			9J	4L 5A	
		Taking food (quadrupedal)	28	20A 8J	13L 14R 1A	NS
		Taking food (bipedal)	28	20A 8J	7L 20R 1A	Right (p<0.01)

**These studies were conducted using the same colony of tamarins. Subjects were classified by age as A- adults, S-subadults, J-juveniles, I-infants. NA- Individual data was not reported. NS- Nonsignificant results (as reported in study or calculated using a chi square goodness-of-fit test), - insufficient data to reach conclusion about direction of bias. L- left preference, R- right preference, A- ambipreference

Marmosets (Callithrix jacchus, Callithrix penicillata)

Studies of hand use in the common marmoset (*Callithrix jacchus*) when taking and holding food reveal a symmetrical distribution of preferences at a group level. Two studies have recorded the hand preferences of marmosets for feeding. Box (1977a) reported that 6 of the 8 marmosets she tested were left handed when picking up food, and 5 displayed left-hand preferences when holding food. Matoba et al. (1991) have reported significant left handedness for 46 adult marmosets scored when picking up food (Table 1.1). However, a reanalysis of their data comparing their population distribution to chance using the chi square goodness-of-fit statistic failed to find significance ($\chi^2(2) = 2.65$, $p > 0.20$, Siegel and Castellan, 1988). In addition, analysis of the distribution of left and right-hand preferences in the male/female subgroups revealed no significant effects of gender on handedness in the marmoset (males, $n = 23$, $\chi^2(2) = 1.13$, $p > 0.5$; females, $n = 23$, $\chi^2(2) = 1.65$, $p > 0.30$). Reanalysis of the data of Matoba et al. (1991) also indicates that the juvenile marmosets tested did not display handedness. There was a symmetrical distribution of left and right-hand preferences at the group level (Table 1.1, $\chi^2(2) = 0.61$, $p > 0.70$). Despite the objections to the statistical analysis of Matoba et al. (1991), they do present convincing evidence suggesting that hand preferences of marmosets (*Callithrix jacchus*) are strongly influenced by the preferences of their mothers: there was correlation with preferences of their mothers but not their fathers. Matoba et al. (1991) propose that the infants' hand preferences may be genetically determined or may develop with experience, for example through imitation of the mother's hand use.

Overall, it appears that the common marmoset does not have a population bias toward either right or left handedness during feeding although there might be a slight, but nonsignificant, bias toward left-hand preferences.

Tamarins (Saguinus oedipus)

In contrast to the marmoset, the closely related tamarin species (*Saguinus oedipus*) is right handed at the group level when holding food and picking up small

objects including food and twigs (Table 1.1). Diamond and McGrew (1994) and King (1995) both used the same colony of tamarins (Diamond and McGrew (1994) tested 20 tamarins and King (1995) tested 30 tamarins) and both found right handedness (Table 1.1). Diamond and McGrew (1994) reported that age, gender and family membership did not affect the distribution of hand preferences during feeding. King (1995) also reported that the distribution of the tamarins' hand preferences was not related to age or gender, but he found a positive correlation between age and the degree of laterality displayed for taking food.

Posture influenced the direction of hand preferences in tamarins. Diamond and McGrew (1994) found a shift away from right-hand preferences when the tamarins (*Saguinus oedipus*) adopted a vertical posture during feeding. The authors suggested that this trend away from right handedness may reflect a trade-off between using the more efficient forelimb for maintaining posture and the more efficient forelimb for performing the task. This result would appear to support the hypothesis of MacNeilage et al. (1987), as increased postural demands may have masked preferred hand use in the tamarins for picking up and holding food in a vertical posture if they were right-hand preferent and used the right side of the body in postural control. King (1995) found no group bias, toward either right or left handedness, for vertical suspension by one hand and arm in the group of 30 tamarins (*Saguinus oedipus*; Table 1.1). He recorded the hand used to grip when a subject suspended its entire weight from one forelimb. There was an increased incidence of left-hand preferences in the group (Table 1.1), but not a complete shift to left handedness, as MacNeilage et al. (1987) would have predicted for suspension.

Squirrel monkeys (Saimiri sciureus), Spider monkeys (Ateles geoffroyi) and Muriquis (Brachyteles arachnoides)

Studies of hand use in feeding for other New World species including squirrel monkeys, spider monkeys and muriquis also fail to support the Postural Origins hypothesis. Only the spider monkey (*Ateles geoffroyi*) appears to show left handedness during feeding. Laska (1996b) found a significant bias for left handedness in a group

of 13 spider monkeys when reaching from a tripedal posture for a raisin on the floor. However, on the same task Laska (1996a) found no evidence for handedness in a group of 12 squirrel monkeys (*Saimiri sciureus*). Instead, the hand preferences of the squirrel monkeys, as for the common marmoset, were symmetrically distributed at the group level. The hand preferences of the squirrel monkeys were not affected by age, gender, matriline or social rank (Laska, 1996a).

In contrast to both squirrel and spider monkeys, preliminary evidence indicates that wild muriquis (*Brachyteles arachnoides*) are right handed for taking and holding food (Ades et al. 1996; Table 1.1). The distribution of hand preferences of the muriquis did not appear to be influenced by age or gender but it was influenced by the posture assumed during feeding. Ades et al. (1996) recorded whether muriquis were feeding in sitting, standing or suspensory postures. In contrast to the tamarins, they found that right handedness was strongest when the muriquis fed in a standing posture, least when the subjects fed in a suspensory posture and intermediate when they fed in a sitting posture ($\chi^2(6) = 67.9$, $p < 0.01$). Ades et al. (1996) suggest that these results demonstrate intensification of pre-existing hand preferences when feeding in a more unstable standing posture.

Capuchins (Cebus spp.)

Westergaard et al. (1997) have reported that posture influences hand use in tufted capuchins (*Cebus apella*). The capuchins exhibited right handedness when they reached for food from a bipedal posture but not from a tripedal posture (Table 1.1) in which they kept both hindlimbs and one forelimb on the cage floor while reaching. There was an effect of age on the distribution of hand preferences during bipedal feeding: the right-hand preferences in adults were stronger than those of immatures. Increased right-hand use with increasing age has also been found in prosimians (Ward et al. 1993). There were no effects of either age or gender on directional hand preferences during feeding in a tripedal posture. Westergaard and Suomi (1993a) found right handedness in adult capuchins (*Cebus apella*) reaching for peanuts inside a container, but found left handedness in juvenile subjects (Table 1.1). The container the

capuchins were required to reach into was 10 cm in diameter and only one type of food was presented; therefore it is suggested that this task did not demand high levels of visuospatial processing (Westergaard and Suomi, 1993a). Other studies have also found that capuchins (*Cebus apella*, *Cebus albifrons*, *Cebus capucinus*) are right handed when collecting small pieces of food scattered on the floor (Masataka, 1990, see Table 1.1). The species *Cebus capucinus* also uses the right hand twice as many times as the left when holding food (Gomperts and Costello, 1991; Table 1.1).

Parr et al. (1997) found no handedness in a group of 22 capuchins scored when they reached for food from both tripedal and bipedal postures (Table 1.1). More than 50% of subjects were ambipreferent in each of the postural conditions. They did, however, report that the number of lateralized subjects almost doubled when the capuchins were required to reach from a bipedal rather than tripedal posture (Table 1.1). Parr et al. (1997) concluded that the assumption of a bipedal posture may strengthen individual hand preferences in capuchins, although group level biases may not be influenced by bipedalism.

Three other studies of hand use in *Cebus apella* have not found right handedness. Anderson et al. (1996) report a mean percentage of left-hand use of 50% for a group of 10 capuchins scored when they adopted a tripedal posture to pick up food pellets from the floor. Unfortunately, this study did not report individual hand preferences. Frigaszy and Mitchell (1990) observed hand use in 7 capuchins when they were feeding in a seated position and searching for food in a tripedal posture. They found no evidence of a group bias for hand preference in either of these tasks (Table 1.1). Westergaard and Suomi (1996b) also found no evidence of handedness in a group of 34 capuchins taking food from a pipe (Table 1.1). They did not report the posture that subjects adopted while reaching.

Overall, there appears to be a tendency toward increased right-hand preferences in feeding in *Cebus apella*, with 3 out of 7 studies reporting significant group biases. The 3 studies reporting right handedness in *Cebus apella* also had the largest number of

subjects ($n > 20$; Table 1.1). Yet two studies did not find handedness with a sample size of more than 20 subjects (Westergaard and Suomi 1996b; Parr et al. 1997). The differences in handedness found across studies of capuchins, which all used similar methods to score hand preferences in feeding, suggest that other factors such as individual experience, familial relationships and housing conditions may influence lateralization in this species. Further research of hand preferences taking these variables into consideration is needed for all of the New World species.

Visuospatial Reaching Preferences

Visuospatial reaching tasks require subjects to assess visually the spatial position of an object while reaching. Although hand use in feeding may require some degree of visuospatial processing, the tasks referred to as visuospatial are dependent on this form of processing. As neurophysiological evidence suggests that different neural pathways are involved in the perception of form and motion (Van Essen and Gallant, 1994), the visuospatial tasks used with New World primates were divided into two categories: 1) reaching for a static object (Table 1.2), and 2) reaching for a moving object (Table 1.3). Visual monitoring of moving objects also requires the analysis of the temporal aspects of the stimulus and thus may be more spatially complex than reaching for static objects.

1. Reaching for static objects

Rothe (1973) found right handedness in marmosets (*Callithrix jacchus*) required to perform reaching tasks in tripedal and upright standing postures (Table 1.2). Unfortunately, Rothe (1973) did not report the results obtained in the different tasks and hand use in the two postures separately, but rather lumped the data into a category referred to as "handedness during the test series". Rothe (1973) seemed to have reported the results of his first test, requiring subjects to take a mealworm from a tube, independently of the other tests, but contradiction between his statement of methods, in which he indicates that he did not test juveniles, and the apparent results, in which

Table 1.2- Visuospatial reaching for static objects

Species	Study	Task Description	Number of Individuals	Age	Preference	Bias
<i>Callithrix jacchus</i>	Rothe (1973)	Pooled visuospatial reach (quadrupedal/ bipedal)	21	13A	5L 8R 1A	Group-Right ($p \leq 0.05$)
	Hook-Costigan and Rogers (1995)	Reach through holes	8	8J S	1L 6R 1A 6L 1R 1A	NS
		Vertical cling reach with extended arm	8	S	3L 3R 2A	NS
<i>Saguinus oedipus</i>	King (1995)	Extended reach	22	A&J	11L 11 R	NS
		Ceiling suspended reach	22	A&J	8L 14R	NS
<i>Saimiri sciureus</i>	Roney and King (1993)	Vertical cling reach	14	A	6L 8R	NS
	King and Landau (1993)	Reach through pipe (quadrupedal/ bipedal)	30	NA	12L 11R 7A	NS
		Vertical cling reach	37	NA	7L 24R 6A	Right ($p = 0.004$)
	Roney and King (1993)	Reach through holes (horizontal/vertical cling)	30	A, S&J	14L 15R 1A	NS
		Vertical reach	12	8A 4J	6L 4R 2A	NS
<i>Ateles</i>	Kounin (1938)	Extended reach	1	J	1R	-
<i>Ateles geoffroyi</i>	Laska (1996b)	Vertical reach	13	10A 3J	10L 1R 2A	Left ($p < 0.01$)
<i>Cebus</i>	Kounin (1938)	Extended reach	3	S	1L 2R	-
<i>Cebus apella</i>	Lacreuse and Fragaszy (1996)	Reach through holes	17	12A 4J 1I	2L 3R 7A 2L 1R 1A 1A	NS
		Reach through holes	10	7A/ S 3J	NA	NS
		Vertical cling reach	10	7A/ S 3J	NA	NS
	Anderson et al. (1996)	Extended reach (vertical)	10	7A/ S 3J	NA	NS
		Visually guided prehension	7	A	3L 4R	-
		Bimanual visually guided prehension (hand used to lift lid on box)	7	A	4L 2R 1A	-
	Fragaszy and Mitchell (1990)	Visually guided prehension	7	A	3L 4R	-
		Bimanual visually guided prehension (hand used to lift lid on box)	7	A	4L 2R 1A	-
		Visually guided prehension	7	A	3L 4R	-
		Bimanual visually guided prehension (hand used to lift lid on box)	7	A	4L 2R 1A	-

Symbols as in Table 1.1

juvenile preferences on the test are reported, does not allow us to elucidate exactly what was found. Five of six tasks employed by Rothe (1973) required reaching for static objects and one test required the subjects to retrieve food from a swinging piece of string and from a moving platform. Overall, it can be concluded that these six tests, cumulated by Rothe (1973), required visuospatial processing. The right handedness reported may have been due to the assumption of a standing posture (no details given) as Hook-Costigan and Rogers (1995) did not find handedness for visuospatial reaching when marmosets reached for a static object in a tripedal posture or suspended posture.

Hook-Costigan and Rogers (1995) scored the hand used by marmosets (*Callithrix jacchus*) when adopting a tripedal posture and reaching through holes in a clear perspex lid for assorted pieces of food in a bowl (Table 1.2). The subjects were required to assess spatial restrictions of hand holes while reaching and they also visually assessed the position of desired foods (i.e. they looked for banana and cherries and avoided other pieces of fruit). [Note that this experiment differs from the previously mentioned one of Westergaard and Suomi (1993a), in which the subjects were required to reach for only one type of food and did not have to visually assess the spatial restrictions of hand holes. The latter study involved simple reaching.] In the study of 8 marmosets, tested on the visuospatial bowl task, there was no evidence of a bias toward right or left-hand preferences (Table 1.2). Next the visuospatial and postural demands of this task were increased by requiring the marmosets to reach for food on a plate held approximately 5 cm outside the cage while they maintained the suspended posture, hanging on the wire mesh with one hand and two feet. Arm extension would increase the visuospatial demands by requiring visually guided movement using the proximo-distal musculature. Again, there was no evidence of handedness in this task (Table 1.2). It is recognized that this sample size would be too small to make conclusions on the presence or absence of handedness for these tasks.

However, absences of handedness have been reported for tamarins tested in tasks requiring them to adopt a suspensory posture to reach for static objects. King (1995) scored hand preferences in the tamarins (*Saguinus oedipus*) while suspending

their entire weight from the ceiling (upside down) to reach for food. He found no evidence of a group bias in this task (Table 1.2). Nor did he find handedness when the tamarins were required to reach for a piece of food set on a disc outside their cage (Table 1.2), although all of the subjects tested displayed significant hand preferences on both tasks (Table 1.2). Next King (1995) introduced novel postural demands by requiring the subjects to reach for a static object when standing on stable and unstable platforms, which were alternated between testing sessions. Neither postural condition resulted in handedness in the group (King, 1995). Similarly, Roney and King (1993) did not find a bias for right or left handedness, or an effect of posture on visuospatial reaching preferences, in 14 tamarins (*Saguinus oedipus*) required to reach for food with an extended arm. They found that 6 tamarins were left-hand preferent and 8 were right-hand preferent when reaching for food from both tripodal and suspended postures (Table 1.2).

King and Landau (1993) did not find handedness in squirrel monkeys (*Saimiri sciureus*) reaching for a static food object when they were adopting a bipedal or tripodal posture (Table 1.2), but they did find right handedness when the squirrel monkeys were required to maintain a suspended posture while reaching (Table 1.2). These results were not replicated in subsequent tests requiring suspension even though 24 of the same subjects were tested (Roney and King, 1993). Instead, a bimodal distribution of hand preferences was found (Table 1.2). Roney and King (1993) argued that the different distributions of hand preferences in the two experiments may have been due to alternation between reaches from a tripodal and vertical posture, a condition introduced in the second experiment. Laska (1996a) reported an increased incidence of individual hand preferences when squirrel monkeys were required to reach from an unsupported bipedal posture for food placed above them, compared to hand preferences when feeding in a tripodal posture, although there was no handedness within the group for either task (Tables 1.1 and 1.2). Overall, these results suggest that squirrel monkeys may display right handedness when reaching for static objects from a suspended posture and are ambipreferent when they reach from tripodal or bipedal postures.

As for hand preferences in feeding activities, spider monkeys (*Ateles geoffroyi*) display left handedness when reaching from an erect bipedal posture for a raisin placed outside the cage (Table 1.2). The spider monkeys were able to support themselves with one hand on this task. Ten of the 11 subjects that displayed significant preferences on this task were left handed. Laska (1996b) found that the hand use of the spider monkeys on this task did not differ significantly from that displayed during feeding activities.

Studies of capuchins on tasks requiring simple reaching through holes to retrieve food have not found handedness (Lacreuse and Frigaszy, 1996; Anderson et al. 1996). However, Anderson et al. (1996) reported an increase in strength of individual preferences when subjects assumed a clinging posture while reaching, rather than a sitting position. Employing more difficult visually guided prehension tests, Frigaszy and Mitchell (1990) found that no handedness occurred in capuchins, although they acknowledged that their sample size of 7 subjects was too small to draw conclusions (Table 1.2).

Overall, these data indicate that either a bimodal distribution of hand preferences or right handedness occurs during static reaching tasks in the New World species. Arm extension does not appear to influence handedness, but the posture assumed while reaching does influence the strength and, possibly, direction of individual preferences in squirrel monkeys and capuchins. As for hand use in feeding, the effect of posture on hand preferences scored when reaching for static objects is species-specific.

2. Reaching for a moving object

Hook-Costigan and Rogers (1995) conducted two tasks requiring common marmosets to reach for a moving object (Table 1.3). Postural demands and arm extension were required in a task that involved reaching to catch a swinging piece of string (approximately 5 cm outside the cages) while maintaining a suspended posture. As for the static reaching tasks, there was no evidence of a group bias in this task

Table 1.3- Visuospatial reaching for moving objects

Species	Study	Task Description	Number of Individuals	Age	Preference	Bias
<i>Callithrix jacchus</i>	Hook-Costigan and Rogers (1995)	Extended reach to grasp swinging string	8	S	4L 3R 1A	NS
		Rotating disc task	8	A	5L 2R 1A	NS
<i>Saguinus oedipus</i>	King (1995)	Rotating disc task	21	A&J	8L 8R 5A	NS
<i>Saimiri sciureus</i>	King and Landau (1993)	Fishing from bowls	16	NA	11L 3R 2A	NS
		Fishing from wading pools	10	NA	8L 2A	Left (p= 0.013)

Symbols as in Table 1.1

Table 1.4- Hand use in haptic exploration and tactually guided tasks

Species	Study	Task Description	Number of Individuals	Age	Preference	Bias
<i>Saimiri sciureus</i>	Laska (1996a)	Vertical reach	12	8A 4J	6L 6R	NS
	Laska (1996a)	Tactual vertical reach	12	8A 4J	5L 6R 1A	NS
<i>Ateles geoffroyi</i>	Laska (1996b)	Tactual reach	13	10A 3J	10L 1R 2A	Left (p<0.025)
<i>Cebus apella</i>	Parr et al. (1997)	Haptic exploration (objects in pine-shavings)	22	13A 9J	11L 2R 4A	Left (p<0.01)
		Haptic exploration (objects in water)	22	13A 9J	15L 2R 5A	Left (p<0.01)
	Lacreuse and Fragaszy (1996)	Haptic exploration	21	12A 6J 3I	7L 2L 3L 2R 2A	Group-Left (p<0.05)

Symbols as in Table 1.1

(Table 1.3). Similarly, neither marmosets (*Callithrix jacchus*) nor tamarins (*Saguinus oedipus*) demonstrate handedness when required to retrieve food from rotating discs (Hook-Costigan and Rogers, 1995; King, 1995). Both species display bimodal distributions of hand preferences (Table 1.3).

Only one test of visuospatial reaching for moving objects has demonstrated left handedness, as proposed by MacNeilage et al. (1987). King and Landau (1993) reported left handedness in a group of 10 squirrel monkeys (*Saimiri sciureus*) required to catch live fish from wading pools (Table 1.3).

There have been too few studies of hand use when reaching for moving objects to determine whether New World primate species have manual specialization for these tasks. To date, to the author's knowledge, there have been no studies investigating hand preferences of capuchins when reaching for moving objects. Although Westergaard and Suomi (1996a) have scored the hand preferences of 4 capuchins throwing stones (Table 1.6), there has been no examination of catching behaviour in this species.

Hand Preferences for Haptic Exploration and Tactually Guided Reaching

Only four studies have examined hand preferences for haptic discrimination and tactually guided reaching in the New World primates. These studies tested capuchins (*Cebus apella*), spider monkeys (*Ateles geoffroyi*) and squirrel monkeys (*Saimiri sciureus*). Lacreuse and Frigaszy (1996) scored 21 capuchins in a task requiring the subjects to explore, without visual guidance, clay objects of different shapes (e.g. star, sphere) in order to find sunflower seeds embedded in them. They found significant left handedness in the group (Table 1.4) and there was no effect of object shape on the hand preferences. Lacreuse and Frigaszy (1996) found an effect of gender on hand preferences in this task: females showed significant handedness at a group level but males did not. They suggest that this effect was primarily due to the adult male subgroup (n=3) in which two subjects were right-hand preferent and one was ambipreferent. No similar shift in handedness was found in the female subjects.

Parr et al. (1997) found left handedness for the performance of a haptic discrimination task by capuchins. However, they found no effect of age or gender on the hand preferences of the subjects. Fourteen of 22 individuals preferred to use the left hand to locate food hidden in pine-shavings (Table 1.4). Moreover, 15 of the subjects displayed left-hand preferences when required to locate food in water and there was a significant shift toward stronger left-hand preferences. The increased left-hand use may have been caused by increased difficulty during prehension of an object in a water substrate or, as the authors suggest, may have been due to decreased visual cues in the second condition. In the first condition the subjects were able to view the contents of the box of pine-shavings through the hand hole before they reached, whereas they could not see objects in the water through the arm hole.

Laska (1996b) found evidence of left handedness in spider monkeys during tactually guided reaching (Table 1.4). The subjects were required to locate a raisin at the bottom of an opaque tube without visual guidance. The subjects had to assume a squatting bipedal posture to reach into the tube. Eleven of the 13 subjects tested displayed significant left-hand preferences on this task and 2 were right-handed. It is interesting to note that Laska (1996b) found no significant differences between hand preferences displayed in feeding activities, visually guided reaching and tactually guided reaching.

However, Laska (1996a) found no evidence of handedness for tactually guided reaching in a group of 12 squirrel monkeys on a similar task to that used with the spider monkeys (Table 1.4). The squirrel monkeys were required to reach into a tube to grasp a raisin while maintaining an erect bipedal posture. The hand preferences displayed by the squirrel monkeys were, however, stronger in the tactually guided reaching tasks than in the visually guided tasks performed with the same subjects (Table 1.2). There were no effects of age, gender or family membership on hand preferences in the tactually guided reaching task. It would appear that the postural demands in this task affected the hand preferences of the squirrel monkeys.

Therefore, capuchins, and perhaps spider monkeys, appear to have specialization of the right hemisphere (left hand) for the fine digital exploration of objects while squirrel monkeys have no specialization for this type of hand use. Alternatively, manual specialization for haptic exploration may not emerge when subjects are required to grasp a single object, such as a raisin, perhaps using a power grip, as in the task used for the squirrel monkeys. Tactual exploration may be necessary to elicit handedness for this type of manual function. Whether the left handedness displayed by the group of spider monkeys, tested on a task similar to that used for the squirrel monkeys, is indicative of a right hemisphere specialization for haptic exploration remains to be discerned. To evaluate hemispheric differences the movement of the digits needs to be noted in haptic discrimination tasks.

Manipulative Hand Use and Tool Use Preferences

Tool using was once believed to be a characteristic unique to humans, but there is increasing evidence of tool using by other species, including nonhuman primates, elephants and birds (Beck, 1980; Westergaard and Frigaszy, 1985, 1987; Frigaszy, 1986; Rogers and Kaplan, 1993; Chevalier-Skolnikoff and Liska, 1993; Petit and Thierry, 1993; Nishida and Nakamura, 1993; Tokida et al. 1994; Hunt, 1996). However, capuchins are the only New World species so far reported to use tools. Capuchins are also the only species so far reported to use a precision grip (Frigaszy et al. 1990). Westergaard and Suomi (see Table 1.5) have scored hand preferences during the use of hammering, sponging and probing tools by captive capuchins (*Cebus apella*). They reported a bias toward right-hand preferences for adults during sponging activity (Westergaard and Suomi, 1993a). They also suggested that right handedness may increase with age, as 7 of the 9 adult subjects tested displayed right-hand preferences when using sponges, while 3 of 5 juveniles displayed left-hand preferences and 2 were ambipreferent (Table 1.5). The adults displayed a stronger mean lateral bias than the juvenile subjects.

Table 1.5- Hand preferred during use of tools

Species	Study	Task Description	Number of Individuals	Age	Preference	Bias
<i>Cebus apella</i>	Westergaard et al. (1993a)	Sponging task	14	9A	2L 7R	Adults toward Right
	Westergaard et al. (1993b)	Nut cracking	14	5J	3L 2A	Toward left
				7A	3L 3R 1A	
				7J	5L 1R 1A	
	Westergaard (1991)	Probing: Insert probe	5	4A	3L 1R	-
		Probing: Remove probe	5	4A	2L 1R 1A	-
		Probing: Feed from probe	5	1J	1L	-
				4A	3L 1R	
	Anderson et al. (1996)	Probing: Insert probe (sitting, standing)	10	7A/ S 3J	NA	NS
		Probing: Insert probe (vertical cling)	10	7A/ S 3J	NA	NS
				1J	1L	

Symbols as in Table 1.1

Table 1.6- Other measures of hand preferences

Species	Study	Task Description	Number of Individuals	Age	Preference	Bias
<i>Callithrix jacchus</i>	Stellar (1960)	Displace an object	8	NA	2L 4R 2A	-
<i>Saimiri sciureus</i>	Costello and Fragaszy (1988)	Unimanual grasp (object in view/ out of view, embedded)	6	A	4L 2R	-
<i>Ateles</i>	Kounin (1938)	Open box, hold lid and take food with one hand	1	J	1R	-
<i>Cebus</i>	Kounin (1938)	Retrieve food with a rake	1	J	1L	-
		Open box, hold lid and take food with one hand	3	S	1L 2R	-
		Retrieve food with a rake	3	S	1L 2R	-
<i>Cebus apella</i>	Costello and Fragaszy (1988)	Unimanual grasp (object in view/ out of view, embedded)	6	A	2L 4R	-
	Westergaard and Suomi (1996b)	Stone throwing	4	3A 1J	2L 1R 1A	-

Symbols as in Table 1.1

Westergaard and Suomi (1993b) found that juvenile capuchins (*Cebus apella*) used bimanual striking actions more than adults when they were required to use nut cracking tools, although they found no significant differences in the strength or direction of hand preferences between the age groups (Table 1.5). On this task they found a tendency toward left-hand preferences in the group as a whole and proposed that this bias may be due to increased spatial processing which would be necessary to hit a nut accurately. They also reported that, when striking nuts, female capuchins displayed stronger right-hand biases than males. This contrasts with the absence of gender differences in other studies of capuchins during feeding activities and use of sponging and probing tools (Westergaard, 1991; Masataka, 1990; Westergaard and Suomi, 1993a).

Westergaard and Suomi (1994) reported an increased incidence of unilateral hand use during probing behaviour in adult capuchins (*Cebus apella*) compared to juveniles. They found that unimanual manipulation emerged in capuchins between 3 and 5 years of age. Regrettably, however, these authors did not report the direction of hand preferences in this particular study.

Westergaard (1991) reported that 4 out of 5 capuchins were left-hand preferent and one was right-hand preferent for inserting and feeding from a probe (Table 1.5). He suggested that the tendency toward left-hand preferences in this study might be indicative of specialization of the right hemisphere for spatial processing, a proposal needing to be confirmed with a larger sample. A later study by Anderson et al. (1996) reported stronger left-hand use, compared to hand preferences measured during feeding and in visuospatial tasks (Tables 1.1 and 1.2), in a group of 10 *Cebus apella* observed when inserting a baton through a hole and into a tube to obtain honey, although they found no significant bias for handedness at the group level. These authors did not report individual hand preferences. Anderson et al. (1996) also reported postural effects on handedness in the probing task, demonstrating that increased left-hand use was evident only when the capuchins were required to maintain a vertical clinging

posture.

Costello and Frigaszy (1988) reported that, in a group of 6 capuchins (*Cebus apella*), 4 subjects displayed right-hand preferences when reaching for and grasping objects and 2 displayed left-hand preferences (Table 1.5). When using a precision grip 3 of the 4 subjects that had displayed overall right-hand preferences for reaching and grasping again displayed right-hand preferences and the fourth subject displayed more right than left-hand use, but this subject's preference was not significant. The two subjects that displayed left-hand preferences for reaching and grasping did not show a significant hand preference when using a precision grip. Costello and Fragaszy (1988) also reported that the subjects that preferred the right hand in reaching were more likely to take an object using a precision grip, rather than a power grip, while left-handed subjects did not favour either a precision or power grip when prehending an object. Costello and Fragaszy (1988) suggested that these results may be indicative of increased right-hand use in capuchins when fine sensorimotor control is required. Aye-ayes (*Daubentonia madagascariensis*) prefer to use the slender third finger on the right hand for extracting larvae or grubs from holes (Milliken et al. 1991b; Milliken, 1995), a task that would require fine sensorimotor control.

At present, results for the different types of tool-using tasks employed with capuchins suggest left hemisphere specialization for manipulative tool-using tasks. This may, possibly, be the case in sponging, which may require precise finger positioning and grip strength in order to absorb a fluid and to squeeze it into the mouth, although this has not been scored. There is also evidence for increased right-hand use when capuchins grasp objects with precision grips (Costello and Fragaszy, 1988). The right hemisphere may be specialized for tasks demanding high levels of spatial processing, such as nut cracking and probing (Westergaard, 1991; Westergaard and Suomi, 1993a, 1993b). Further research with larger samples is needed to confirm the biases reported. However, the findings that capuchins display tool use and have manipulative ability indicates that tool using and right handedness may have evolved before bipedalism, and well before the apes and, indeed, humans evolved.

Hand Use in Routine Activities Other than Feeding

Hand use in routine activities such as grooming, object exploration and play, have been referred to as "spontaneous hand use" by a number of researchers (eg. Diamond and McGrew, 1994; Rothe, 1973). However, these activities should be distinguished from hand use in feeding, as they might require different levels of manipulative control.

Rothe (1973) found no evidence for handedness in marmosets, most of the subjects being ambipreferent, but he lumped into a single category hand using behaviours as diverse as food holding, grooming, play and object exploration (Table 1.7). The predominance of ambipreference in Rothe's (1973) study may have been the result of cumulating the data across this variety of hand use behaviours. In fact, Box (1977a) reported that more than 50% of individuals were ambipreferent when she scored hand use in climbing, walking and hitting other subjects (Table 1.7). Differences in hand preferences displayed across simple acts of hand using have also been reported for orangutans: orangutans (*Pongo pygmaeus pygmaeus*) display left handedness when touching the face but no handedness for food holding (Rogers and Kaplan, 1996).

The consistency of hand preference across routine manual activities may be another way in which marmosets and tamarins differ. Diamond and McGrew (1994) found that tamarins are significantly right handed for retrieving food, holding food, carrying food, self grooming, grooming others and hitting other individuals (Tables 1.1 and 1.7). In fact, the tamarins displayed ambipreference only when scratching themselves. Age, gender and family membership did not affect the hand preferences of the tamarins in any of the activities. However, as for the feeding activities, there was a shift away from right-hand preferences in the tamarins when they performed routine tasks, other than feeding, while adopting a vertical posture. In the vertical posture right handedness was maintained only for hitting other individuals.

Table 1.7- Hand preferred in routine activities other than feeding

Species	Study	Task Description	Number of Individuals	Age	Preference	Bias
<i>Callithrix jacchus</i>	Rothe (1973)	Simple hand use (pooled)	21	13A	1L 4R 8A	NS
				8J	1L 2R 5A	
	Box (1977a)	Reaching up	8	4A	1R 3A	-
		Reaching down	8	4J	1L 1R 2A	-
				4A	4A	
		Walking	8	4J	4A	-
				4A	1R 3A	
		Climbing up	8	4J	1L 3A	-
				4A	1R 3A	
		Hit	8	4J	4A	-
				4A	1L 3A	
<i>Saguinus oedipus</i>	Diamond and McGrew (1994)**	Self groom	20	10A 7S 3J	2R 2A	Right ($p \leq 0.001$)
		Social groom	20	10A 7S 3J	NA	Right ($p \leq 0.001$)
		Scratch	20	10A 7S 3J	NA	NS
		Hit	20	10A 7S 3J	NA	Right ($p \leq 0.001$)
		One arm suspension	30	A&J	17L 10R 3A	NS
<i>Saimiri sciureus</i>	King (1995)	Self touching (body)	13	A	2R 11A	NS
<i>Cebus apella</i>	Arguette et al. (1992)	Social grooming	3	A	2L 1A	-
	Fragaszy and Mitchell (1990)					

Symbols as in Table 1.1

Arguette et al. (1992) found that only 2 individuals, in a group of 13 squirrel monkeys (*Saimiri sciureus*), had significant right-hand preferences for self-directed touches (Table 1.7), but all of the subjects did, in fact, perform more touches with the right hand than the left, indicating a tendency for right-hand use in the group as a whole. It is interesting to note that the preferred hand for self-touching may be opposite in orangutans and squirrel monkeys.

Overall, the lack of data on the different forms of routine manual activities makes it impossible to postulate whether handedness is present for these behaviours in the New World species.

Comparisons with Prosimians, Old World Species and Apes

Handedness in the New World primates

The reported hand preferences in the New World species do not support the hypothesis proposed by MacNeilage et al. (1987). Instead, some of the platyrrhine species demonstrate right handedness during feeding activities and others, including the common marmoset (*Callithrix jacchus*) and squirrel monkeys (*Saimiri sciureus*), do not display handedness in feeding. Only one New World species, the spider monkey (*Ateles geoffroyi*), displays the left handedness predicted by the Postural Origins hypothesis (MacNeilage et al. 1987).

In addition, while there is some evidence of left handedness for tasks demanding high levels of spatial processing when reaching for a moving object (King and Landau, 1993), hand use appears to be task specific. The limited number of studies reporting this type of hand use makes it difficult to discern the factors affecting the expression of this type of manual asymmetry. In studies reporting visuospatial reaching for static objects, the New World primates appear to display right handedness, a symmetrical distribution of preferences at a group level, or left handedness for spider monkeys, which resembles the results for hand use in feeding more than those for reaching for moving objects.

There is evidence that capuchins, and perhaps spider monkeys, display left handedness for haptic discrimination (Lacreuse and Frigaszy, 1996; Laska, 1996b; Parr et al. 1997). Left handedness for haptic discrimination has also been reported for rhesus monkeys (Fagot et al. 1991) and for humans (Hermelin and O'Connor, 1971; Flannery and Balling, 1979). Capuchins display right handedness in tasks requiring fine motor control and manipulation (Costello and Frigaszy, 1988; Westergaard et al. 1993a) and an increased incidence of left-hand use on tasks with increased spatial demands such as probing (Westergaard, 1991; Anderson et al. 1996). Overall, like humans, capuchins appear to be right handed for most tasks but left handed for haptic discrimination and complex spatial tasks.

Effects of age on hand preferences

Several variables may affect the distribution and strength of hand preferences in the New World primates. These are age, gender and posture, but the effects of age on the development of manual preferences in primates are still unclear. In studies of prosimians, Old World primates and great apes, some researchers have found increases in strength of manual preference with increasing age (Lehman, 1978; Brooker et al. 1981; Forsythe and Ward, 1988; Mason et al. 1995; Toonoka and Matsuzawa, 1995), others suggest shifts in hand preferences with age (Sugiyama et al. 1993; Hopkins et al. 1993; Rogers and Kaplan, 1996) and yet others report no effect of age on hand preferences (Vauclair and Fagot, 1987; Fagot and Vauclair, 1988; Fagot et al. 1991; Hopkins, 1993; Colell et al. 1995).

Similarly, the influence of age on hand preferences in the New World primates varies. Some of the studies of hand use in the platyrrhine species report no effect of age on lateralization (Diamond and McGrew, 1994; Ades et al. 1996), whereas others have found that age affects hand preferences in these species (Westergaard and Suomi, 1993a; King, 1995; Lacreuse and Frigaszy, 1996; Westergaard et al. 1997). An increase in right handedness with age has been found for capuchins in a variety of tasks including hand use when feeding in a bipedal posture (Westergaard et al. 1997), hand use when reaching for a static object (Westergaard and Suomi, 1993a) and hand use

while using sponges to absorb juice (Westergaard and Suomi, 1993a). Lacreuse and Fragaszy (1996) reported increased right handedness in adult male capuchins in a test of haptic exploration. Conversely, they found no shift to right handedness with age in females but, in fact, adult females displayed stronger left-hand preferences than juvenile females. By contrast, Parr et al. (1997) found that neither age nor gender influenced hand preferences of capuchins on their haptic discrimination task. Overall, while age may increase handedness in capuchins, there do not appear to be consistent effects of age on lateralization across tasks or groups of subjects in the other New World primates. Consideration of other variables in addition to age, such as individual history or experience, familial relationships, housing conditions (Deuel and Dunlop, 1980) and the disposition of the subjects at the time of testing may allow for more conclusive analyses of developmental effects on lateralization. Clearly, age is a variable that needs to be stated in all studies of handedness.

Effects of gender on hand preferences

The gender composition of a population has also been suggested as a variable that may affect handedness distributions (Ward et al. 1993). Overall, however, very few studies have reported an effect of gender on hand preferences in nonhuman primates. Most of the reports of gender effects on handedness are for prosimians, with increased left-hand preferences occurring in males compared to females (Milliken et al. 1989; Milliken et al. 1991a; Mason et al. 1995). A study of hand use during feeding in Old World species *Rhinopithecus* and *Presbytis* suggests that males display right handedness while there is a symmetrical distribution of hand preferences in females (Yuanye et al. 1986). Yet, the majority of studies of Old World primates and the great apes have reported no relationship between gender and hand preference distributions (Brooker et al. 1981; Vauclair and Fagot, 1987; Annett and Annett, 1991; Fagot et al. 1991; Hopkins, 1993; Hopkins et al. 1993; Colell et al. 1995; Tonooka and Matsuzawa, 1995).

As is the case for Old World primates, most studies of the New World primates have reported no influence of gender on the distribution of hand preferences (Masataka,

1990; Westergaard, 1991; Westergaard and Suomi, 1993a; Diamond and McGrew, 1994; King, 1995; Ades et al. 1996; Westergaard et al. 1997). Only two studies with capuchins have reported gender effects on hand preferences (Lacreuse and Frigaszy, 1996; Westergaard and Suomi, 1993b). Westergaard and Suomi (1993b) reported stronger lateralization in female than male capuchins during a nut cracking task, while Lacreuse and Fragaszy (1996) found differential effects of age according to the gender of the subjects on haptic discrimination preferences as discussed above. It may be argued that effects of gender on hand preference are secondary to other variables such as social status and age.

Posture and hand preferences

There is evidence that increasing postural instability increases handedness across tasks, but postural effects appear to be species-specific. Right handedness decreased in tamarins when they performed daily hand-using activities in a bipedal stance (Diamond and McGrew, 1994) and when they reached from suspended postures (Roney and King, 1993; King, 1995). Squirrel monkeys display stronger hand preferences when reaching from a suspended posture than they do from tripedal or bipedal postures (King and Landau, 1993; Roney and King, 1993). Ades et al. (1996) reported that wild muriquis display a stronger right-hand bias for feeding when standing than when sitting or suspended. Capuchins also display stronger handedness when stability is decreased during feeding, reaching and tool using (Anderson et al. 1996; Westergaard et al. 1997). This strong effect of posture is not limited to the New World species; there is also evidence of postural effects on hand preferences in other primates, including prosimians, Old World species and apes (Sanford et al. 1984; Larson et al. 1989; Forsythe and Ward, 1988; Milliken et al. 1991a; Fagot et al. 1991; Hopkins et al. 1992; Dodson et al. 1992; Ward et al. 1993; Hopkins, 1993; Devleeschouwer et al. 1995). Unstable postures appear to intensify hand preferences in most primate species, perhaps by increasing arousal (Ward et al. 1993) or the spatiotemporal requirements of a task (Fagot and Vauclair, 1991).

Conclusions

Overall, posture appears to be a very important influence on the expression of hand preferences, as MacNeilage et al. (1987) suggested. In fact, in accordance with the hypothesis of MacNeilage et al. (1987), the assumption of a vertical posture appear to increase right-hand use in squirrel monkeys (King and Landau, 1993), muriquis (Ades et al. 1996) and capuchins (Wesiersgaard et al. 1997). However, these reports are contradicted by evidence suggesting an opposite effect of vertical posture in tamarins (Diamond and McGrew, 1994). It is agreed that, as Parr et al. (1997) have suggested, if bipedalism does increase handedness in a species it intensifies pre-existing specializations. This would suggest that specialization of the left hemisphere for manual tasks that do not demand high levels of visuospatial or haptic processing may be present in some arboreal New World primates, contradicting the hypothesis of MacNeilage et al. (1987).

The predominance of right handedness among the New World primates is contrasted by reports of left handedness in prosimian populations (Sanford et al. 1984; Forsythe and Ward, 1988; Masataka, 1989; Ward et al. 1990; Milliken et al. 1991a). Adaptation to the New World environment and the evolution of manipulative feeding strategies may have led to an evolutionary shift in hemispheric dominance.

LATERALIZATION OF OTHER MOTOR FUNCTIONS IN NONHUMAN PRIMATES: FOOT AND SIDE-OF-MOUTH PREFERENCES

While there is extensive literature on the hand preferences of nonhuman primates in a variety of tasks, very few studies have examined the lateralization of other motor functions including foot preferences in locomotion and mouth use asymmetries. There is evidence that foot preferences in humans may be better indicators of lateralization for language functions than hand preferences (Searleman, 1980; Day and MacNeilage, 1996), possibly because they are less subject to social pressures (Peters, 1988a). Foot preferences, in humans, are measured in tasks such as kicking, stepping and stamping, and most studies report a right-foot bias for these behaviours (Searleman, 1980; Brown and Taylor, 1988; Seltzer et al. 1990; Gentry and Gabbard,

1995; Day and MacNeilage, 1996; Gabbard and Iteya, 1996; Porac, 1996).

Foot and hand preferences in nonhuman primates are often recorded during the initiation of locomotory activities. Marchant and McGrew (1996) found no evidence for footedness in the initiation of quadrupedal locomotion in wild chimpanzees (*Pan troglodytes schweinfurthii*), with 12 individuals displaying left-foot preferences and 14 right-foot preferences. Bard et al. (1990) also report no evidence of a group bias for stepping in infant chimpanzees (*Pan troglodytes*), and as discussed above, there was no evidence for a leading hand during walking or climbing in 8 common marmosets (Box, 1977a; see Table 1.7). It has also been shown that gibbons (*Hylobates syndactylus*, *H. concolor* and *H. lar*) do not have a group bias for one limb in the initiation of brachiation (Stafford et al. 1990).

Although infant chimpanzees do not show footedness for stepping (Bard et al. 1990; Hopkins et al. 1997), it appears that they do have right handedness for initiating crawling behaviours (Hopkins et al. 1997). In fact, all of the nonhuman primate studies that have found lateral asymmetry in the initiation of locomotory activities report right-side biases. Right-limb preferences for initiation of terrestrial locomotion were found for 4 ruffed lemurs, *Varecia variegata* (Forsythe and Ward, 1987). Bonobos (*Pan paniscus*) also prefer to lead locomotion with the right limb (hand or foot). Hopkins et al. (1993) found that 6 of 10 bonobos used the right hand to lead quadrupedal locomotion significantly more often than the left. Moreover, they found stronger right-side preferences when bipedal locomotion was examined and subjects initiated walking with the right foot. These results were replicated in a further study with another group of bonobos by Hopkins and deWaal (1995). Right-hand preferences for initiating quadrupedal locomotion have also been reported for gorillas, chimpanzees and orangutans (Heestand, 1986, cited in Hopkins et al. 1993). Thus, when a lateral bias is present for the initiation of locomotion in nonhuman primates it is for the right limb, as in humans. There is no evidence of left sidedness for the initiation of locomotion in nonhuman primates, but of course there remains a majority of species that have not been examined for lateralization of this function.

It has also been suggested that side-of-mouth preferences in chewing might be related to the evolution of left hemisphere dominance for speech (Peters, 1988b; MacNeilage, 1997). In fact, MacNeilage (1997) suggested that jaw movements during chewing might have been the precursors of mouth movements in speech production. Humans do have a tendency to chew with the right side of the mouth (Hoogmartens, 1986). As it has been suggested that the hands may be subordinate to the mouth in nonhuman primates (Peters, 1988b), these species would be ideal for studying the evolutionary relationship between language, handedness and mouth use asymmetries. Yet, there have been only three studies of side-of-mouth use during chewing in nonhuman primates, and two of these were conducted with prosimian species.

Stafford et al. (1993) examined lateralized mouth use in 11 *Hapalemur griseus* scoring the side-of-mouth used to chew a bamboo shoot. They found that six subjects preferred to chew with the left side of the mouth, three preferred the right side and two subjects did not display significant side-of-mouth preferences (Stafford et al. 1993). Side-of-mouth preferences in chewing in the gentle lemurs were directionally congruent with the preferred hand in feeding (Stafford et al. 1993), but there was no evidence that side-of-mouth preferences were more strongly lateralized than hand preferences measured during feeding.

Bennett et al. (1995) considered that the food type might affect the side-of-mouth preferred when chewing. Subsequently, Bennett et al. (1995) recorded side-of-mouth preferences when *Lemur catta* chewed either primate chow or fruit. Both types of food elicited significant preferences for one side of the mouth during chewing. Of the total 21 subjects, 20 displayed a significant preference for one side of the mouth, but only 10 subjects displayed the same side-of-mouth preferences for chewing both types of food: six preferred the right side of the mouth and four the left. In contrast to the findings of Stafford et al. (1993) it was suggested that in the ring-tailed lemur side-of-mouth preferences in feeding might not be related to the preferred hand.

Side-of-mouth preferences were also measured in 8 members of the marmoset

(*Callithrix jacchus*) colony at the University of New England. There was no evidence of a bias for a left or right side-of-mouth preference for chewing in this small group (Hook-Costigan and Rogers, 1995). As for *Hapalemur griseus*, however, there was a strong positive correlation between side-of-mouth preferences for chewing and hand use for holding food in this group (Hook-Costigan and Rogers, 1995). The results with the marmoset subjects will be discussed in more detail in Chapter 4.

Conclusions

Thus, both foot preferences in locomotion and side-of-mouth preferences in chewing have been proposed as lateralized functions that might have led to the evolution of specializations for language processing and speech production in humans. Yet, there are insufficient data on the lateralization of these motor functions in nonhuman primates to test these hypotheses. On the basis of the few studies that have been conducted it could be suggested only that chimpanzees, gorillas and orangutans might have right leading-limb preferences for quadrupedal locomotion and that prosimians and, possibly, marmosets do not have mouthedness for chewing. Moreover, the absence of a leading-limb bias for climbing and brachiating in marmosets and gibbons, respectively, suggests that hemispheric specializations might not have evolved for the performance of arboreal forms of locomotion. As most primate species do spend significant proportions of their time in an arboreal habitat, lateralization of locomotion in these conditions must be investigated further. Leaping and landing might be better indicators of the lateralization of arboreal primates, particularly if the evolutionary advantage of lateralization is to be considered. Further research on the lateralization of foot and mouth use is needed. Also, the relationships between motor preferences and communication functions should be examined before further hypotheses on the evolution of hemispheric specializations are proposed.

VISUAL LATERALIZATION: EYE PREFERENCES IN NONHUMAN PRIMATES

Eye preference refers to the consistent choice of one eye over the other in the monocular viewing situation. Porac and Coren (1976) distinguish 3 forms of eye preference in humans: sighting dominance, sensory dominance and acuity dominance. Studies of eye preferences in nonhuman primates have measured sighting dominance. Porac and Coren (1976) argue that sighting dominance is the only significant form of eye preference; humans show approximately 67% right eyedness on sighting dominance tasks (Porac and Coren, 1976).

Eye preference, or sighting dominance, in nonhuman primates has been determined in studies that require subjects to look through a peephole or down a tube. There have been two studies of eye preference in prosimians (Rogers et al. 1994; Ward and Cantalupo, 1997), both measuring preferences in the small-eared bushbaby (*Otolemur garnettii*). Rogers et al. (1994) found that five subjects, tested looking through slits in a grid, displayed left-eye preferences when viewing food. However, when three of the bushbabies were presented with a more arousing stimulus (their babies held in the experimenter's hand) their eye preferences changed; two subjects displayed equal use of both eyes, while a third subject displayed a weaker left-eye preference (Rogers et al. 1994). These results indicate that eye preferences are affected by arousal and/or the stimulus being viewed.

Ward and Cantalupo (1997) tested eye preference in bushbabies (*Otolemur garnettii*) when viewing stimuli through a transparent slit in a plexiglass door. Of 26 subjects tested, 16 subjects fixated the stimuli for longer when viewing with the left eye, 9 favoured the right eye and one subject did not display an eye bias for this measure. Although more than half of the lemur subjects spent significantly longer viewing the stimuli with the left eye than with the right eye, the distribution of subjects across the preference categories was not significantly different from chance (Ward and Cantalupo, 1997). When frequency of left and right-eye monocular looking was compared, 13 subjects displayed a left-eye preference, 7 subjects preferred the right eye

and 6 subjects had no bias. Again, this result demonstrated that more subjects preferred to look with the left eye.

There have been some studies examining eye preference in Old World primates but there is no clear information as to whether these species have left or right eyedness. Cole (1957) found a tendency toward right preferences in a group of seven adult macaques, *Macaca nemestrina*, tested by scoring monocular looking through a tube. By contrast, Kruper et al. (1966) found left eyedness in a group of 19 naive immature macaques, *Macaca mulatta*. Smith (1970) and Kounin (1938) also reported left-eye preferences, each testing one immature rhesus macaque. When Kruper et al. (1966) tested a group of seven adult macaques, however, they found no bias for either eye at the group level. Kruper et al. (1966) noted, comparing the responses of the juvenile and adult macaque subjects, that there was no evidence to suggest that the degree of eye preference changed with age. They suggested that differences in the directional eye use of the two groups might not simply be due to maturation, and wrote that they were unaware of any experimental variables that would selectively reinforce use of one eye. Perhaps, as in *Otolemur garnettii*, arousal in the novel testing situation influenced the distribution of eye preferences in the experimentally naive subjects. The macaques' level of arousal in the testing situation may have changed with age and experience.

There have been four studies of eye preference in the platyrrhine species and these studies have also produced inconsistent results. Kounin (1938) measured eye preferences in three immature New World primates (*Cebus* spp.). When the subjects heard a 'slight' noise they were required to look through a tube at a piece of food. The capuchins displayed right-eye preferences on this task. McFerran (1992) investigated eye preference in a group of 38 cotton-top tamarins (*Saguinus oedipus*) also looking monocularly at food through a viewing hole. Only seven of the 38 subjects tested displayed significant eye preferences, six preferring the left eye and one the right. Westergaard and Suomi (1996b) tested 40 capuchins (*Cebus apella*) when looking through a pipe at a grape. They found a symmetrical distribution of eye preferences in the group: 13 subjects displayed right-eye preferences, 14 subjects preferred the left eye

and 7 did not display a bias (Westergaard and Suomi, 1996b). Hook-Costigan and Rogers (1995) reported a bias for right-eye preferences in a group of 8 marmosets when looking through a monocular viewing hole. These subjects were not rewarded for monocular viewing and were not able to use their hands in the task. In this preliminary study it was noted that when 4 of the marmosets were aroused, following a dominance battle, they displayed a shift away from right-eye preferences.

Although these results may indicate inconsistency in the presence and direction of lateral bias for eye preference among New World primates, methodological differences between the experiments may also have affected the results. For example, the introduction of an auditory cue may have influenced the results of Kounin (1938) by indirectly conditioning the subjects' responses. In McFerran's study, testing in a group situation may have induced arousal through competition between subjects at the peephole. In fact, McFerran (1992, p. 38) states that interest in the peephole was high with several animals jostling for an opportunity to view. Arousal does affect eye preferences in bushbabies (Rogers et al. 1994) and might affect eye use in New World primates (Hook-Costigan and Rogers, 1995). Unfortunately, Westergaard and Suomi (1996b) do not give details on the procedures that they used to test eye preferences in the capuchins. For example, they do not indicate whether subjects were tested in groups or individually or whether the subjects were able to hold the pipe that they looked through. It is implied, however, that they were not able to use the wire mesh for postural support during viewing (Westergaard and Suomi, 1996b). The lack of methodological details given by Westergaard and Suomi (1996b) makes it impossible to speculate on factors that might have led to differences between the results of this study and the other studies of New World primates.

The significance of eye preferences is not known. Eye preferences could reflect underlying motor or perceptual processes. Relationships between eye preferences and motor behaviours have been found in bushbabies (Ward and Cantalupo, 1997), capuchins (Westergaard and Suomi, 1996b) and humans (Harris and Lovegrove, 1984; Metalis and Niemic, 1984; Brown and Taylor, 1988). However, a number of other

studies of nonhuman primates have not found relationships between eye preferences for monocular viewing and motor lateralizations (Cole, 1957; Kruper et al. 1966; Rogers et al. 1994; Hook-Costigan and Rogers, 1995). Moreover, in studies of other species with laterally placed eyes, it has been suggested that eye preferences are indicative of underlying hemispheric specializations for perceptual functions and emotional control (eg. Andrew, 1991; Deckel, 1995; Cantalupo et al. 1995). Thus, it is possible that eye preferences in primate species also reflect asymmetries of perceptual processing, rather than simply being a product of lateralized motor control. Although both eyes project to both hemispheres in nonhuman primates it has been suggested that morphological asymmetries of ganglion cell and photoreceptor distribution in the nasal and temporal hemiretinas of primate species might result in a more detailed cortical representation of a visual stimulus in the hemisphere contralateral to a viewing eye (Rowe, 1991; Weisz et al. 1994). The morphology of the retina in primates and the evidence suggesting that sensory information transmitted to the hemispheres during monocular viewing might be asymmetrical is discussed in detail in Chapter 6.

Conclusions

Although there has been considerable research on hand preferences in nonhuman primates, literature on sensory asymmetries is sparse. Further research on eye preferences in nonhuman primates is needed to determine the significance of this functional lateralization. At present, the data on eye preferences in nonhuman primates indicate inconsistency in the presence and direction of lateralization among, and within, species. Whether the different results of the studies of nonhuman primates are indicative of species or environmental differences, or are simply a product of methodological differences between studies, is unknown. There are indications that arousal and age might influence eye preferences in these species, but further examination of these possibilities is needed to determine whether these variables caused the inconsistencies found in the studies that have been conducted so far. Also, greater attention must be paid to the relationships between eye preferences and lateral biases found on other tests of motor and cognitive function.

PERCEPTUAL ASYMMETRIES FOR PROCESSING VISUAL STIMULI

Initial evidence of hemispheric asymmetries in nonhuman primates for processing visual stimuli was presented by Hamilton and Lund (1970). They tested 4 split-brain macaques, in whom the corpus callosum and optic chiasm was severed, and 4 control macaques, in which only the optic chiasm was cut, on a task that required them to discriminate between the directions of movements of fields of dots (i.e. up-down, left-right). They found that learning was significantly faster when the subjects used the left hemisphere in 13 of the 16 discrimination tasks presented. Yet, there was no cerebral dominance when subjects were required to discriminate between a field of stationary and a field of moving dots. Therefore, Hamilton and Lund (1970) proposed that the left hemisphere superiority revealed in this task was due to differences in the orientational aspects of the stimuli.

Jason et al. (1984) also found evidence for left hemisphere specialization for the perception of spatial cues. They trained nine male rhesus macaques (*Macaca mulatta*) to perform simultaneous discriminations between dots differing in their relative vertical positions on a square background. Following training, four of the macaques received a left-sided occipital lobectomy and the splenium of the corpus callosum, which transfers visual information between the hemispheres, was severed. The remaining five subjects received a right-sided occipital lobectomy combined with splenial transection. Pre and post-operative discrimination thresholds were determined for each individual. Discrimination thresholds were defined as the minimal distance of displacement of a dot from the centre of a square which could be discriminated. The results indicated that subjects with lesions of the left hemisphere were impaired on the task while those with right hemisphere lesions were not affected.

A recent study by Dépy et al. (1996) indicates that baboons (*Papio papio*) and humans may also have specialization of the left hemisphere for discriminating distance cues. Dépy et al. (1996) compared the performance of humans and baboons on a test that required them to judge if a dot was near to or far from a horizontal line. Both species displayed a left hemisphere advantage for classifying stimuli close to the

boundary separating the two responses (Dépy et al. 1996).

Hamilton and Vermeire (1988) found that 22 of 25 split-brain macaques, *Macaca mulatta*, displayed left-hemisphere superiority for discriminating between the spatial orientation of lines differing in slope by 15°. Subjects were required to indicate which of two lines was more vertical. In the task used by Hamilton and Vermeire (1988), however, only one line was presented to the subjects at a time, thus requiring the subjects to remember the initial line orientation in order to perform the task. It has been proposed that the memory component of this task might have influenced the macaques' responses (Bradshaw and Rogers, 1993). In humans, there is usually right hemisphere superiority for the processing of spatial cues (Atkinson and Egeth, 1973; Taylor and Warrington, 1973). However, on tasks that require spatial memory, damage to the left hemisphere appears to impair performance (Mehta and Newcombe, 1991). Thus, the macaques may be lateralized in the same way as humans, and may be like food-storing birds (*Parus palustris*, Clayton and Krebs, 1993; Clayton and Krebs, 1994) and female Sprague-Dawley rats (Adelstein and Crowne, 1991), but for spatial memory rather than for the processing of spatial cues.

Visuospatial processing in apes, like humans, is lateralized to the right hemisphere. Two language-trained chimpanzees (*Pan troglodytes*) were taught a visual discrimination task that required them to determine the shorter of two lines contained within a geometric form (Hopkins and Morris, 1989). Stimuli were presented randomly to the left, right and central fields and the subjects were forced to use the left and right hands equally to manipulate the cursor. Both of the chimpanzees displayed a left visual field advantage for processing the visual stimulus, indicating right hemisphere dominance for the discrimination of spatial cues, similar to the results found for human subjects.

Fagot and Deruelle (1997) have shown that baboons may be lateralized for processing global and local information in the same way as humans. Specialization of the right hemisphere, left visual field, appears to be present in both species for

matching objects according to global characteristics, and a nonsignificant right visual field advantage for processing objects differing in local cues has been determined (Fagot and Deruelle, 1997). Despite this similarity in lateralization, however, Fagot and Deruelle (1997) found differences in the processing strategies used by the baboons and humans. Humans performed the matching tasks faster and with increased accuracy using global stimuli, whereas the baboons demonstrated improved performance for both speed and accuracy when matching stimuli according to the local information (Fagot and Deruelle, 1997). The possibility that experimental tasks may not elicit hypothesized processing strategies and may subsequently reveal different lateralizations from those expected should be considered.

Conclusions

There have been very few studies on the lateralization of perceptual (e.g. visual) processing in nonhuman primate species. This is despite evidence of hemispheric specializations for perceptual processing in species that evolved prior to the evolution of primates, such as fish, birds, rats and mice (e.g. Bradshaw and Rogers, 1993; Cantalupo et al. 1995). The lack of evidence makes it impossible to speculate on whether nonhuman primate species have hemispheric specializations similar to humans, or other nonprimate species, for these functions. As perceptual processing is important in all aspects of behaviour, knowledge of the lateralization of these functions in species that inhabit very different environments would be of benefit to our understanding of factors influencing the development and evolution of hemispheric specializations. Moreover, the intriguing possibility that species, and perhaps individuals, might process tasks using different cognitive or perceptual processing strategies should be considered in all studies of lateralization.

LATERALIZATION OF VISUAL AND VOCAL COMMUNICATION PROCESSES

Hamilton and Vermeire (1988) found that the specialization of the left hemisphere for spatial memory in rhesus macaques, *Macaca mulatta*, was

complemented by a right hemisphere advantage for distinguishing between faces. Asymmetries in the processing of facial characteristics were tested using eight coloured photographs; four depicted two different macaques displaying the same expression and four were based on the discrimination of two different facial expressions displayed by an individual macaque. There was a right hemisphere advantage in 18 of the 25 macaques tested on this task. Twenty-two of the same macaques were tested again 6 months later and 18 immediately performed better with the right hemisphere. The addition of 20 novel photographs did not impair the discriminatory abilities of the subjects and in some cases was shown to enhance lateralization.

Similarly, Ifune et al. (1984) reported that split brain macaques, *Macaca mulatta*, made significantly more facial expressions when viewing coloured video recordings of monkeys, people, other animals and scenery with their right eye, and thus right hemisphere, than when they viewed with the left eye. The macaques also spent significantly longer viewing the stimuli with the right eye than with the left. Ifune et al. (1984) suggest that these findings may reflect right hemisphere dominance for perception of emotional stimuli and specialization of the right hemisphere for producing emotional responses in the macaques.

Dittrich (1990) found evidence of hemispheric specialization in macaques, *Macaca fascicularis*, for the recognition of faces. In fact, Dittrich (1990) found that the macaques were able to recognize a schematic drawing of the right hemiface of a conspecific with a 'slandering' emotional expression (invitation for other individuals to interact with the sender: Dittrich, 1990) significantly more often than they recognized the left hemiface. The macaques were trained to select the 'slandering' face from four emotional expressions presented on a screen. When left or right hemiface chimeras of the emotional expressions were presented, the macaques recognized the right slandering hemiface chimera on 70-80% of trials but recognized the left hemiface chimera on 20-30% of presentations only. Unfortunately, Dittrich (1990) has not made it clear whether the left or right hemifaces of the chimeras were presented on the left or right sides of the macaques. That is, when Dittrich (1990) refers to the chimeras it is

not clear whether he is discussing them from the image or from the perceiver's perspective. It is presumed that the right chimera would be presented on the macaques' left side, thus indicating a right hemisphere advantage for the perception of the image, but this is not known.

In contrast to these results, Overman and Doty (1982) reported no hemispheric dominance for perception or production of facial expressions in another macaque species, *Macaca nemestrina*. Overman and Doty (1982) tested the macaques on a task that required them to indicate whether a left-left hemiface chimera or a right-right hemiface chimera more closely resembled a nonchimeric face presented simultaneously. The macaques did not show any bias for selection. Thus, Overman and Doty (1982) concluded that macaques do not have hemispheric specialization for processing facial stimuli. However, in the experiments conducted by Overman and Doty (1982) only 'emotionally neutral' faces were presented as stimuli, whereas in the other studies emotional expressions were used (Hamilton and Vermeire, 1988; Dittrich, 1990). The lack of emotional information may have biased the macaques' responses. Indeed, some studies also indicate that there is no consistent bias for the perception and production of a neutral facial expression in humans (Sackeim et al. 1984; Kowner, 1995). Thus, the absence of asymmetries in the perception, and possibly production, of facial expressions by macaques might be due to use of 'emotionally neutral' facial expressions (Overman and Doty, 1982).

Recent studies of the production of emotional expressions by rhesus macaques (*Macaca mulatta*) suggest that there are asymmetries between the two sides of the face. Like humans, rhesus macaques appear to have specialization of the right hemisphere for the production of fear expressions. Analysis of left-right hemiface differences revealed that the left side of the mouth opened first in the production of fear expressions (Hauser, 1993). Moreover, left-left hemiface chimeras of the macaques producing the fearful expression were perceived by human judges as more 'expressive' (Hauser, 1993). Thus, the majority of studies with various macaque species provide evidence that the right hemisphere is specialized for the perception and production of

emotional facial expressions.

Not only do macaques show right hemisphere specialization for the control of emotional responses, they also have specialization of the left hemisphere for the perception of species-specific vocalizations. In a preliminary study, Dewson (1977) trained five crab-eating macaques (*Macaca fascicularis*) to form conditional associations between acoustic and visual stimuli in an auditory discrimination task. Subjects were trained to discriminate between two monaurally presented sounds (a pure tone and a burst of white noise) and were then subjected to lesions of the left or right temporal gyrus (thought to be homologous to Wernicke's area in humans: Cowey and Dewson, 1972). Performance on this task was impaired in the four macaques in which the left superior temporal gyrus had been lesioned. Two macaques with lesions of the right superior temporal gyrus and one macaque with a lesion of the primary auditory cortex of the left hemisphere did not show effects of impaired discrimination or auditory memory deficits. Heffner and Heffner (1984) also reported that Japanese macaques with lesions of the left superior temporal gyrus and auditory cortex were initially impaired on auditory discrimination tasks requiring subjects to differentiate between species-specific vocalizations ('coo' vocalization subtypes). By contrast, lesioning of the same areas of the right hemisphere did not impair discriminatory performance. In this study it was found that the right hemisphere assumed control in left-lesioned macaques when they were retrained on the discrimination task. After bilateral lesions, however, the macaques were unable to perform the discrimination task. Thus, the results of Heffner and Heffner (1984) concur with those of Dewson (1977) demonstrating that the left superior temporal gyrus plays the predominant role in discrimination of the coo vocalizations. They also suggest that the right hemisphere can mediate discrimination in the absence of the left hemisphere.

Petersen et al. (1978) tested the discriminatory abilities of 10 Old World primates (5 *Macaca fuscata*; 2 *Macaca nemestrina*; 2 *Macaca radiata*; 1 *Ceropithicus aethiops*) on a task similar to that used by Heffner and Heffner (1984). The subjects were required to discriminate between two 'coo' vocalization subtypes produced by

Japanese macaques (*Macaca fuscata*). The two subtypes used in the tests were 'smooth early high' coos (SE) and 'smooth late high' coos (SL). All 5 of the Japanese macaques tested displayed a right-ear, left hemisphere advantage, for the discrimination task, whereas the 4 other macaque subjects, for whom the signals were communicatively irrelevant, did not show evidence of hemispheric lateralization. In a later study, Petersen et al. (1984) repeated their previous results with two Japanese macaques and two comparison macaque subjects (*Macaca nemestrina* and *Macaca radiata*). They found a right-ear advantage for the Japanese macaques and no advantage for either ear in the comparison macaques. Thus, Petersen et al. (1984) concluded that the left hemisphere advantage demonstrated by the Japanese macaques in these studies might reflect a species-specific neural or perceptual mechanism for the processing of communicatory signals. They suggested that other species may have similar mechanisms involved in the perception of their own species-specific signals.

Hauser and Andersson (1994) have conducted playback experiments with wild rhesus macaques in which they assessed lateralization by recording the ear that the subjects oriented towards a speaker. They found that adult macaques displayed a right-ear, left hemisphere preference when species-specific vocalizations were played, but infant macaques did not show a preference for either ear. This result was consistent despite use of aggressive, fearful and affiliative calls. The authors argued that left hemisphere dominance for species-specific calls reflects processing of the communicative information in the calls, regardless of the emotional content. However, a right hemisphere advantage for processing the emotional aspects of speech is found in humans (Haggard and Parkinson, 1971; Ley and Bryden, 1982; Bryden and McRae, 1989). Hauser and Andersson (1994) found a significant left-ear preference when the macaques heard the alarm call of a sympatric bird species. It is possible that some of the macaques may have been processing the task used by Hauser and Andersson (1994) like an auditory localization task, which might have influenced hemispheric asymmetries. Some studies of humans have found a right hemisphere advantage for localization of auditory cues (Burke et al. 1994; Butler, 1994), although the results of

other studies do not concur with this hypothesis. Despite the possibility that task type may have influenced lateralization, Hauser and Andersson (1994) raise an important point concerning the influence of age on lateralization of perceptual functions. They suggest that infant subjects may not show lateralization as they may not comprehend the call meaning. It is suggested that comprehension, and lateralization, may emerge with experience in rhesus macaque infants. Although age is considered as a factor that may influence lateralization for motor functions in nonhuman primate studies (MacNeilage et al. 1987; Fagot and Vauclair, 1991), very few studies have considered this variable when examining perceptual asymmetries.

As for humans, the right hemisphere is specialized for some aspects of vocal perception in nonhuman primates. Right hemisphere advantages for discriminating between voicing contrasts, such as 'ba-ja' have been found for rhesus macaques (Morse et al. 1987). The electrophysiological indices used to measure lateralization in this study indicated that the macaques, like humans, were using categorical processes to discriminate between the stimuli (Morse et al. 1987). Similarly, Pohl (1983) found that three of four baboons (*Papio cynocephalus*), tested on a task that required them to discriminate between sets of vowels and consonant-vowel syllables, displayed a left-ear advantage. Humans have also been shown to prefer the right hemisphere for processing vowels heard out of a language context (Spellacy and Blumstein, 1970).

Bernston et al. (1993) found right hemisphere dominance in a juvenile chimpanzee for the perception of vocalizations with affective significance. They recorded ERP (event-related potential) responses during perception of conspecific threat, alarm and scream vocalizations, and when a primary caregiver (human) spoke the subject's name. They found right lateral dominance for perception of the threat and human vocalizations and suggested that this asymmetry might be related to the affective significance of the two sounds (Bernston et al. 1993). Studies of humans also suggest that affective sounds such as laughing, shrieking, crying and sighing may be processed by the right hemisphere (Carmon and Nachson, 1973). The possibility that the right hemisphere may process or produce affective vocalizations in humans and

nonhuman species should be examined further.

Conclusions

The majority of studies on the lateralization of communication functions in macaques suggest that these species have specialization of the right hemisphere for the production and perception of negative emotional expressions and have specialization of the left hemisphere for the perception of species-specific vocalizations. To date, however, there have been no studies on the lateralization of production of species-specific vocalizations in these species. Moreover, there is a distinct lack of research on the lateralization of communication functions in other nonhuman primate species. To the author's knowledge, there has been only one study of the lateralization of perception of species-specific vocal signals in a nonhuman primate species that is not *Macaca*, and only one chimpanzee was studied. There have been no studies on the perception or production of facial expressions in other primate species. As the evidence suggests that macaques are lateralized in the same way as humans for these functions, it is considered important to determine how other nonhuman primate species are lateralized. It is possible that asymmetries of communication function led to the evolution of hemispheric specializations for speech production and language perception in humans, rather than handedness, or other motor functions, as has been proposed (Hewes, 1976; Kimura, 1976; Lieberman, 1985; Corballis, 1991; Day and MacNeilage, 1996; MacNeilage, 1997).

AN OVERVIEW OF THE PRESENT STUDY

The aim of the present study was to examine the functional lateralization of the common marmoset (*Callithrix jacchus*). It was aimed to conduct a detailed analysis of the lateralization of individual marmosets by examining lateralization for both motor and perceptual functions in individual subjects. As shown in the review of the literature, the lateralization of a number of motor and perceptual functions has been investigated in a variety of nonhuman primate species. Of the many lateralization studies that have been conducted with nonhuman primates, however, very few have

examined the lateralization of individual subjects on a variety of tasks. Moreover, there is limited evidence on the lateralization of individual species for a variety of functions. It is proposed that information on the lateralization of individual species for motor, perceptual and cognitive functions is necessary for further understanding of the evolution of hemispheric specialization. Apart from adding more data on lateralization in nonhuman primates, the potential links between different types of motor and sensory functions and the influences of environmental variables on lateralization of different species needs to be examined. Thus, rather than examining a large group of marmosets on a few tasks, or a number of species on one type of task, the experiments reported in this thesis aimed to examine the lateralization of a small group of marmosets (N= 21) on a variety of tasks and to investigate the relationships between motor and sensory functions.

In addition, the lateralization of marmosets at a group level, which is indicative of hemispheric specialization, has previously been assessed for hand use only (Stellar, 1960; Rothe, 1973; Box, 1977a; Matoba et al. 1991; Guerra and Da Silva, 1996). It is not known whether marmosets have hemispheric specializations for perceptual processing or communication functions. Therefore, in this study the lateralization of marmosets on different types of tasks was examined at the group level and the influences of variables including age, gender, experience and state of arousal on lateralization were determined. Thus, lateralization was examined at two levels: at the individual and at the group level.

Marmosets have been described as ideal research subjects for a number of practical and economic reasons (Box, 1995), but their position in phylogeny is possibly the most compelling reason for the study of the lateralization of this species. A number of researchers have argued that marmosets and tamarins are among the most primitive of living primates, representing the evolutionary ancestors of both New and Old World primate species (Stellar, 1960; Herschkovitz, 1977). Indeed, the morphology of the brain and hands in the callitrichidae species does suggest that in many ways they might represent an intermediate form between prosimians and *Cebine* New World primates.

It has been proposed that the brain of the callitrichidae is more advanced than that of the prosimian species, but less advanced than other New World primates (Beattie, 1927). Like that of the *Tarsiers*, the cerebral cortex of marmosets and tamarins are unconvoluted, with only four fissures: the Sylvian fissure, the superior temporal gyrus, the calcarine fissure and the hippocampal fissure (Beattie, 1927; Saavedra and Mazzuchelli, 1969). Cerebral control of motor functions in callitrichidae species may also be more similar to the prosimians than to other New World primates, with simple differentiation of the somatosensory cortex and parietal and temporal lobes in these species (Penden and Von Bonin, 1942; Zhang et al. 1996). However, cortical areas controlling the production and perception of auditory signals and those for perceiving visual stimuli in callitrichidae species resemble those of other New World primates. The occipital lobe and visual system in marmosets shows as high a degree of differentiation as in other New World primate species examined (Woolard, 1926; Penden and Van Bonin, 1942; Shyue et al. 1995; Fritsches and Rosa, 1996). The primary auditory cortex of the marmoset has been clearly identified (Aitken et al. 1986), and an area homologous to Broca's area in humans has been found (Penden and Von Bonin, 1942). As the callitrichidae species may, in some ways, represent a transitional form between the prosimian primates and the other New World primate species, comparative studies between prosimians, marmosets and other New World primates may further understanding of the evolution of hemispheric specializations.