CHAPTER 5

LEADING-LIMB (HAND AND FOOT) PREFERENCES IN WALKING, LEAPING AND LANDING

5.1   INTRODUCTION

The aim of the experiments reported in this chapter was to investigate whether marmosets have hand or foot preferences for initiating or terminating locomotion. Leading-limb (hand and foot) preferences were examined for walking, leaping and landing. A previous study of marmosets did not find handedness for the initiation of walking or climbing (Box, 1977a). Of the 8 marmosets that Box (1977a) examined, two subjects displayed significant preferences for initiating walking: one preferred the right hand and one the left. Only one subject displayed a right-hand preference for climbing and the remaining subjects were ambipreferent (Box, 1977a). These preferences deserve further examination with a larger sample size. It was considered important for the present study to compare them with hand preferences for simple food holding and visuospatial reaching.

There appear to be differences between species in leading-limb preferences, as other studies of nonhuman primate species have found leading-limb preferences for initiating walking and most report preferences for the right hand (foot). Forsythe and Ward (1987) found that 4 ruffled lemurs, *Varecia variegata*, displayed right-limb preferences for initiating quadrupedal locomotion. Group level biases for right handedness (footedness) have also been reported in captive chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), orangutans (*Pongo pygmaeus*) and gorillas

(*Gorilla gorilla*; Heestand, 1986, cited in Hopkins et al. 1993; Cunningham et al. 1989; Hopkins et al. 1993; Hopkins and deWaal, 1995). There was a total of 21 bonobos, 20 chimpanzees, 9 orangutans and 29 gorillas in these studies. Hopkins et al. (1993) also reported a significant positive relationship between the hand preferred for taking food and the hand preferred for initiating quadrupedal locomotion in bonobos. By contrast, Hopkins and deWaal (1995) found a significant negative correlation between the hand preferred for carrying food and the hand preferred for initiating locomotion in bonobos. Thus, bonobos appear to take food with the right hand, but to carry the food in the left hand when locomoting. Leading-limb preferences have been found in neonatal chimpanzees also: Hopkins et al. (1997) found a population level bias for the right hand in the initiation of crawling by neonates, although the neonatal chimpanzees did not have foot preferences for initiating stepping (Bard et al. 1990; Hopkins et al. 1997). Right footedness for kicking, stepping and stamping actions is also characteristic of humans (Horine, 1968; Seltzer et al. 1990; Gentry and Gabbard, 1995; Day and MacNeilage, 1996).

Only one study of adult chimpanzees, out of the four conducted, has not found right handedness, or a bias at the group level, during quadrupedal locomotion (Marchant and McGrew, 1996). The absence of handedness for initiating locomotion in the study of Marchant and McGrew (1996) might be related to their observation of wild chimpanzees, rather than captive apes as observed in the other studies. It is noted, however, that the chimpanzees displayed significant individual preferences for the initiation of locomotion (Marchant and McGrew, 1996), unlike the marmosets studied by Box (1977a).

There have been no previous investigations of limb preferences for leaping and landing in nonhuman primates. In fact, only one study has examined the lateralization of a nonhuman primate species during arboreal locomotion. Stafford et al. (1990) recorded the leading-limb preferences of gibbons (*Hylobates spp.*) during brachiation. They found no evidence of handedness for this behaviour (Stafford et al. 1990). In the present study it was proposed, however, that leaping and landing might demand even

higher levels of motor control and visuospatial processing than brachiation and thus may reveal hemispheric specializations for the control of arboreal locomotion. Leaping and landing would require higher amounts of visuospatial processing for the accurate assessment of the position and distance of a landing substrate, and therefore may reveal underlying asymmetries for spatial processing. Right hemisphere specialization for visuospatial processing has been found in a variety of other species (Chapter 4, p. 141) and thus it was considered that marmosets might display left handedness or footedness in leaping or in landing. It is noted that vertical clinging and leaping is characteristic of callitrichid locomotion (Stevenson and Rylands, 1988). Tamarins (*Saguinus geoffroyi*, *S. mystax*, *S. fuscicollis*) spend less than 10% of foraging time (for fruits) using walking and quadrupedal running modes of locomotion, in contrast to 40-50% of time climbing, grasping and jumping (Garber, 1993). Although the percentage of time marmosets spend walking and leaping is not known, it is likely to be very similar to the *Saguinus* species. Thus, as callitrichid locomotion is largely comprised of leaping and landing, marmosets may display leading-limb preferences for these behaviours even though they may not for walking (Box, 1977a), which is less commonly used by these species.

5.2   METHODS

5.2.1   Leading-Hand and Foot Preferences for Walking, Leaping and Landing

Seventeen adult marmosets (12 females, 5 males) were individually tested. Individual testing was necessary to correctly identify the subject being tested. The video camera recording their movements was placed underneath the subjects allowing both hands and feet to be seen simultaneously. The subjects were videotaped for 30 minutes per day as they walked on, leapt off and landed on a perspex platform (44cm x 44cm). The perspex platform was a lid on a wooden box (Figure 5.1). The wooden box was 44cm x 44cm x 94cm high (Figure 5.1). The video camera (Sony Hi 8) was attached to a steel mount inside the box and was focused on the perspex platform (Figure 5.1). The perspex platform was cleaned with hot water and disinfectant between testing sessions so that the video image was not obscured by scent marks of the subjects, and to prevent the scent of one individual affecting another individual's

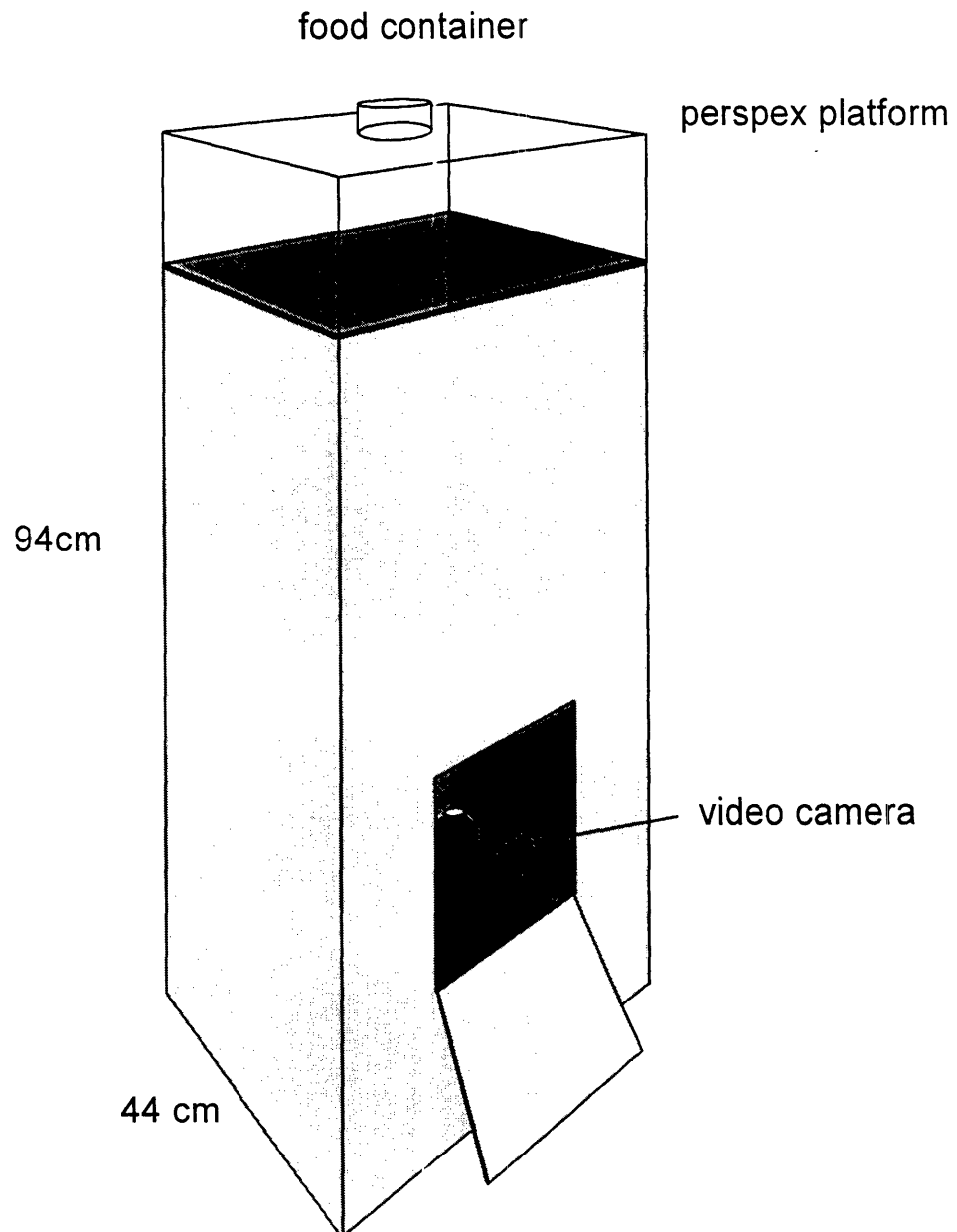food container

perspex platform

94cm

video camera

44 cm

Figure 5.1 Apparatus used for recording leading-limb preferences for walking, leaping and landing. As shown in the figure, a video camera was focused on the perspex platform and hand and foot movements were recorded as the marmosets leapt off, landed on and walked on the platform. The video camera was attached to a steel mount inside the wooden box. A small perspex bowl was attached to the perspex platform. Food was placed in the bowl.

behaviour. The box was placed into the subjects' home cages for testing, and was positioned so that it was at least 20 cm from other objects, ensuring that there was no obstruction for any direction of movement. Individual subjects were tested in one half of the home cage while their cagemates were held in the other half of the cage (Chapter 2, p. 58). Only one male (Blue) could not be tested in his home cage and was tested in one of the females' cages in the same room. He was habituated to being placed into the females' cage for one week prior to testing, so that he became familiar with the scents and objects in the cage.

Hand and foot movements in each locomotory behaviour were determined from *post hoc* frame-by-frame video analyses. The methods for scoring hand and foot preferences for walking, leaping and landing are described below. The hand and foot that moved first was scored. Unimanual hand preferences and unipedal preferences for the left or right foot were analyzed using z-score tests. During leaping and landing, bimanual hand use and bipedal foot use also occurred: that is, both hands or both feet moved at the same time. Bimanual hand use and bipedal foot use were scored. A minimum of 100 sequences of each locomotory behaviour (walking, leaping and landing) was scored (Appendix A, Table I). This total included bimanual and bipedal scores in leaping and landing.

As can be seen in Figure 5.1, a plastic food bowl was fixed in the centre of the perspex platform and 10-15 small pieces of food were placed into the bowl at the beginning of each testing session. This encouraged the marmosets to leap onto the box and also allowed the experimenter to record hand preferences for simple food holding in the first 8-10 days of testing. On most occasions the marmosets remained on the perspex platform while eating the food. However, if the subjects did initiate walking or leaping while carrying food in the hands, hand and foot movements were not scored. Subjects could carry food in the mouth during walking and leaping. The procedure for scoring acts of food holding is described in Chapter 3 (pp. 68-70). One hundred incidences of simple food holding were recorded for each individual. The nonparametric statistics used in this chapter are described in Chapter 2 (pp. 62-64).

Leading-hand and leading-foot preferences in walking

The hand and foot used to initiate walking were recorded after a subject had been stationary for a minimum of 0.5 seconds with all four limbs on the perspex substrate. Scores were taken if the subjects then walked in a frontal direction (Box, 1977a). No score was taken if a subject turned 45^0 or more to step. Hand and foot movements were scored when the subjects used a crossed diagonal gait, with one hand followed by the contralateral foot, and when subjects moved the two hands prior to moving the two feet. Three limbs were in contact with the perspex substrate at all times, with one limb moving, in each of the sequences that was scored.

Leading-hand and leading-foot preferences in leaping

Leaping was scored when all four limbs were lifted off the perspex for at least 2.5 milliseconds (1 frame; Figure 5.2). Leaping was not scored if it was initiated from a tripedal posture. Scores were taken only when subjects initiated the leap from a quadrupedal or bipedal posture with each of the limbs in the same horizontal plane. However, when subjects initiated leaping from a bipedal posture no hand use scores were collected (see Table 5.1, p. 169). Also, it was not always possible to record the first hand to move during leaping (no data, see Table 5.1, p. 169). In some sequences the definition of the video recording and the subject's posture before leaping precluded the accurate assessment of hand movements. Leaping was not scored when foot movements could not be accurately assessed.

Leading-hand and leading-foot preferences in landing

Hand preferences in landing may be independent of those found for leaping and thus the two modes of locomotory activity were analyzed separately. The marmosets displayed *quadrupedal landing* on most occasions. The leading hand and leading foot were recorded as they contacted the perspex substrate following leaping (Figure 5.2).

a. Leaping

b. Landing

Figure 5.2 Marmosets leaping and landing. These photographs show a marmoset leaping (a) and landing (b). Leaping was recorded when the 4 limbs were lifted off the surface for at least 1/24 of a second (i.e. 1 video frame). In landing, the leading hand and foot were scored as each limb contacted the perspex platform.

5.2.2 Effect of Type of Locomotory Behaviour on Lateral Preferences

Spearman rank correlations were used to examine the relationships between leading-hand preferences (expressed as percentage left) displayed for walking, leaping and landing. Foot preferences found for walking, leaping and landing were also correlated.

The Friedman statistic was used to compare the strength of leading-limb preferences, or the absolute preference for one limb regardless of the direction of the bias (Chapter 2, pp. 62-63), displayed for each of the behaviours measured. Comparisons were made between the strength of leading-hand preferences displayed for walking, leaping and landing. Similarly, the strength of leading-foot preferences in walking, leaping and landing were compared.

5.2.3 Influences of Gender, Family Group and Early Experience on Lateral Preferences in Locomotion

The percentage of left-limb (hand and foot) preference displayed by female and male subjects in walking, leaping and landing were compared. The strength of preferences displayed by female and male subjects were compared also. Comparisons were made between the percentage left-limb preferences and the strength of preferences displayed by subjects belonging to the different Family Groups (Chapter 2, p. 47) and to the two Experience Groups (Chapter 2, pp. 47-48).

5.2.4 Comparisons Between Hand Preferences for Locomotory Behaviours and Hand Preferences for Simple Food Holding and Visuospatial Reaching

Spearman rank correlations were used to examine the relationships between leading-hand preferences (expressed as percentage left) in walking, leaping and landing and percentage left-hand use for simple food holding (measured on the same test). Leading-hand preferences during locomotion were also correlated with hand preferences for visuospatial reaching.

5.3   RESULTS

5.3.1   Leading-Hand and Foot Preferences for Walking, Leaping and Landing

Unimanual/ bimanual hand use and Unipedal/bipedal foot use in leaping and landing

Most subjects displayed a preference for initiating leaping using one hand or foot to push off from the surface, rather than using the two front or two hindlimbs together (Table 5.1). In most sequences one hand pushed off from the platform first followed by the other hand, and then one foot pushed off from the platform followed by the other foot (Figure 5.3a). Use of one hand to push off from the platform first, rather than both hands together (Figure 5.3b) occurred in a mean of 54.5± 4.2% of sequences (Table 5.1). Only one subject (Gold) did not prefer to leap with one foot leaving the

Table 5.1 Hand and foot movements in leaping sequences

Subject	N	% of hand use				% of foot use	
		Unimanual	Bimanual	No hand use	No data	Unipedal	Bipedal
L. Blue	100	58	13	21	8	82	18
Gold	101	28	4	56	12	58	42*
Red	100	71	4	7	18	83	17
Blue	100	57	8	6	29	79	21
Black	101	66	8	3	23	88	12
Silver	101	57	2	0	41	83	17
Sage	102	24	5	50	21	84	16
Coco	101	20	6	74	0	70	30
Maylin	103	51	5	26	18	88	12
Sunga	101	40	9	20	31	82	18
Snap	101	67	12	6	15	82	18
Crackle	101	75	4	0	21	88	12
Pop	102	74	5	11	10	90	10
Crassus	100	65	4	18	13	82	18
Pompey	100	62	11	11	16	84	16
Ash	100	49	7	30	14	83	17
Wattle	100	63	10	15	12	76	24
Mean	100.8	54.5±	6.9±	20.8±	17.7±	81.3	18.7
±SEM	±0.2	4.2	0.8	5.1	2.3	±1.9	±1.9

N is the total number of sequences analyzed. Unimanual and unipedal indicate that one hand or foot was used to initiate leaping, while bimanual and bipedal mean that both hands, or both feet, moved together. Leaping was also initiated from a bipedal posture (no hand use). The no data column indicates that the movements of hands could not be seen. * indicates that the subject did not display a preference for unipedal or bipedal foot use in the initiation of leaping.
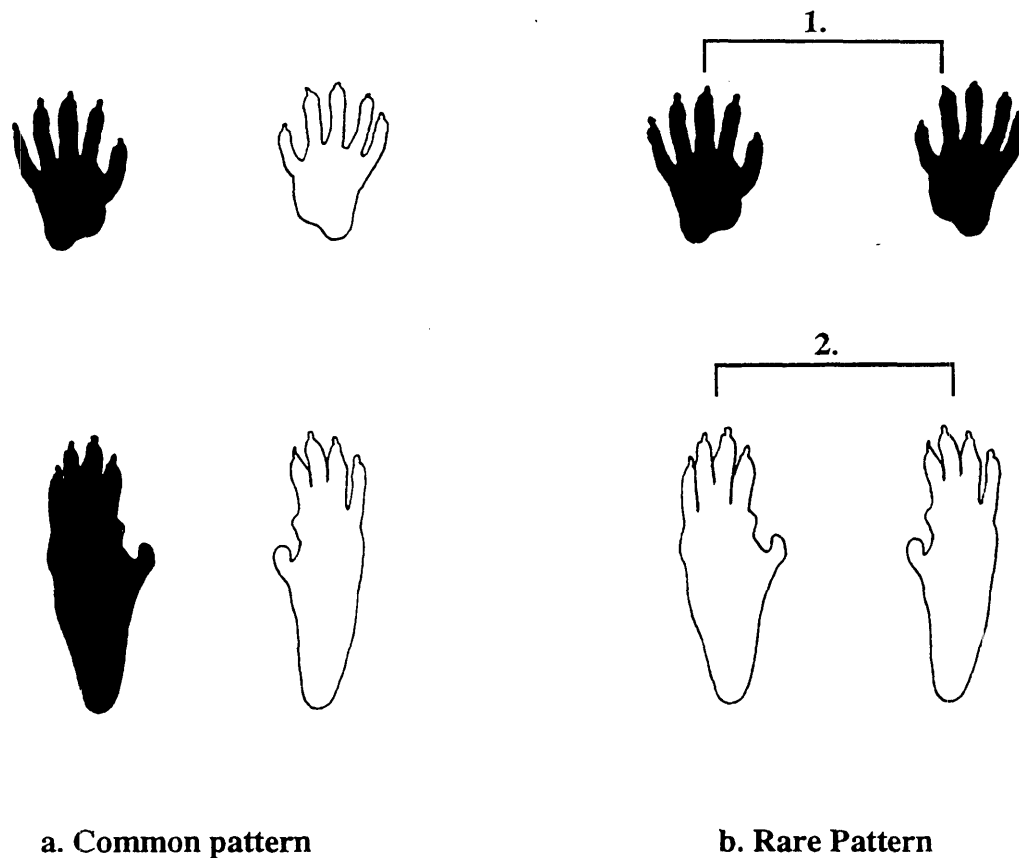
Figure 5.3 Unimanual/bimanual hand use and unipedal/bipedal foot use in leaping and landing.
Figure 5.3a represents unimanual hand use and unipedal foot use in leaping and landing. The white hand and the white foot leave the platform before the black hand and the black foot. The sequence in which hand and foot movements occur is indicated by the numbers. The leading-hand (1) is followed by the other hand (2) and then the leading-foot (3) is followed by the other foot (4). Figure 5.3b depicts bimanual hand and bipedal foot use. In these sequences both of the hands move together (1). Both of the feet move together when bipedal foot use occurs (2). Note that bimanual hand use is not usually followed by bipedal foot use, or vice versa.

the platform before the other. This aberrant subject leapt with one foot leaving the platform before the other for approximately the same number of sequences as he leapt with both feet leaving the platform at the same time (bipedal; as illustrated in Figure 5.3b). The rest of the marmosets preferred to initiate leaping with one foot leaving the platform first.

Similarly, as shown in Table 5.2, most of the subjects landed with one hand contacting the surface before the other hand (Figure 5.3a), rather than with both together (Figure 5.3b), in most sequences. The two hands always contacted the perspex substrate before the feet landed. One foot also contacted the surface before the other

Table 5.2 Hand and foot movements in landing sequences

| Subject | N | % of hand use | | % of foot use | |
		Unimanual	Bimanual	Unipedal	Bipedal
L. Blue	101	71	29	81	19
Gold	101	63	37	58	42*
Red	100	75	25	90	10
Blue	100	74	26	78	22
Black	100	78	22	91	9
Silver	103	64	36	85	15
Sage	101	72	28	74	26
Coco	101	64	36	48	52*
Maylin	101	73	27	86	14
Sunga	100	70	30	69	31
Snap	101	62	38	89	11
Crackle	101	54	46*	84	16
Pop	102	82	18	81	19
Crassus	100	79	21	88	12
Pompey	100	73	27	87	13
Ash	100	70	30	82	18
Wattle	100	70	30	88	12
Mean	100.7	70.2	29.8	79.9	20.1
±SEM	±0.2	±1.7	±1.7	±2.9	±2.9

See Table 5.1. * indicates that the subject did not display a preference to land with one hand/foot first or with both hands/feet together.

foot (Figure 5.3a). Of the 17 subjects tested, 16 preferred to land with one hand first rather than with both together, and one subject did not show a significant preference for either landing pattern (Table 5.2). Fifteen subjects preferred to land with one foot before the other, and two subjects did not show a significant difference between the number of sequences in which they landed with one foot first or both feet together (Table 5.2).

The mean percentage unimanual (±SEM) hand use and foot use in leaping and landing is presented in Figure 5.4a. The marmosets leapt with both hands leaving the substrate at the same time significantly less often than they landed with both hands touching the substrate simultaneously (Wilcoxon, $T^+= 0$, p= 0.0003; Figure 5.4a).
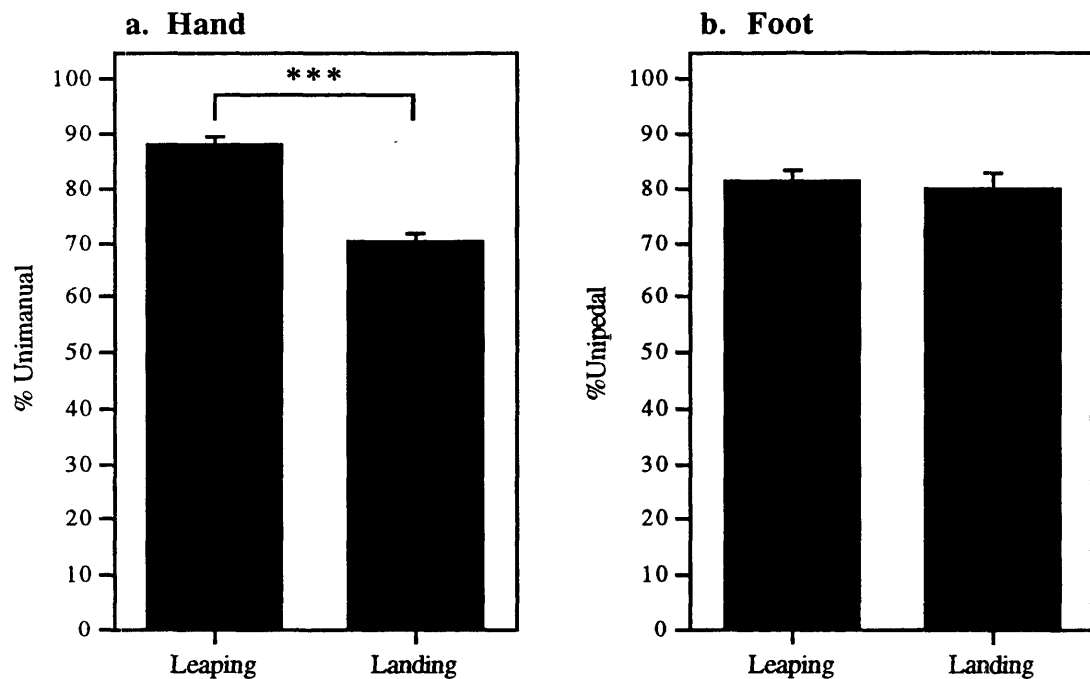
a. Hand

b. Foot

Figure 5.4 Comparison between the percentage use of one or both limbs during leaping and landing. Bimanual hand use was observed significantly more often in landing than in leaping (***p< 0.001). The percentage of unipedal, versus bipedal, foot use did not differ for leaping and landing. Data on unimanual/unipedal versus bimanual/bipedal limb use for the individual subjects are shown in Tables 5.1 and 5.2 respectively.

There was no difference between the percentage of bipedal foot use in leaping and landing (Wilcoxon, $T^+= 7$, p= 0.72; Figure 5.4b).

Leading-hand and leading-foot preferences in walking

As can be seen in Figure 5.5, only 2 of the 17 subjects displayed leading-hand and leading-foot preferences when initiating walking (see also Appendix A; Tables G and H). One subject (Red) preferred to walk with the right hand first, followed by the left foot, while the other subject (Snap) preferred to initiate walking with the left hand followed by the right foot (Figure 5.5). As the remaining 15 subjects did not display significant preferences for either the left or right limbs (Figure 5.5), ambipreference was characteristic of the group for initiating walking (χ^2 (2) = 9.94, p<0.01).
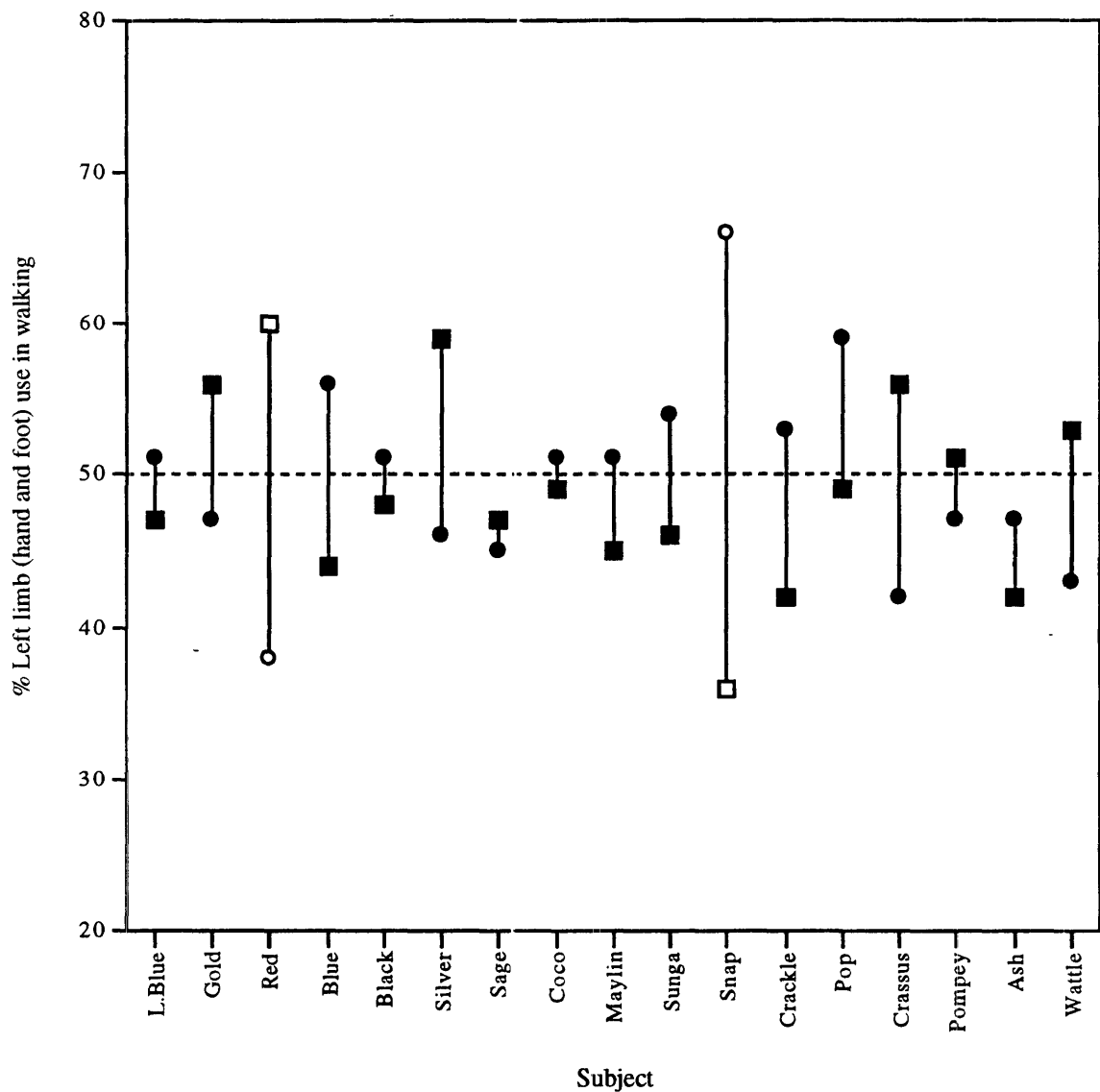
Figure 5.5 Limb preferences of the individual subjects during walking. The percentage left-hand (O or ●) and foot (□ or ■) use of individuals in walking are presented. Subjects are presented on the x axis and their percentage left-limb (hand and foot) use is shown on the y axis. The white symbols indicate a significant preference, and the black symbols represent ambipreference. Significance was tested using the z-score test. Only two subjects displayed significant limb preferences for walking. The lines are used to connect the hand and foot preferences of an individual.

There was a significant negative correlation between percentage left-hand preference and percentage left-foot preference for initiating walking (Spearman rank, $r_s = -0.70$, $p < 0.005$; Figure 5.6a), indicating use of a crossed diagonal gait (Figure 5.6b). Thus, in most cases subjects used the left hand followed by the right foot, or vice versa, rather than the left hand followed by right hand or the left foot (Figure 5.6b). There was no difference between the strength of preferences displayed for a leading hand or leading foot in walking (Wilcoxon, $T^+ = 7$, $p = 0.68$).

The distribution of hand and foot preferences at the group level is summarized in Figure 5.7, and can be compared with the distribution of percentage left leading-limb preferences for leaping and landing. The hand and foot preference data for the locomotory behaviours can also be compared with the distribution of hand preferences for simple food holding, which is also shown in Figure 5.7.

a. Correlation between hand and foot
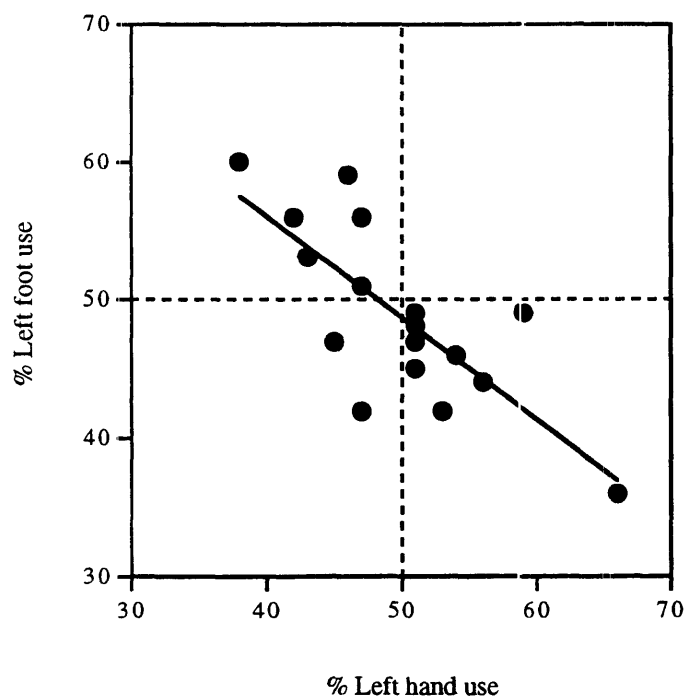
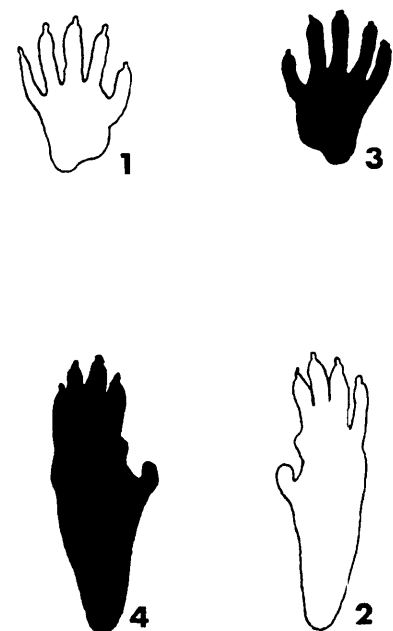**b. Pattern of hand and foot movement in walking**

Figure 5.6 **Correlation between hand and foot preferences in walking.** A strong negative correlation was found between percentage left-hand use for initiating walking and percentage left-foot use for initiating walking (Figure 5.6a). Most subjects used a crossed diagonal gait for walking (Figure 5.6b). In Figure 5.6b the white hand and foot represent the leading hand and the leading foot. The numbers 1 through 4 also show the sequence of movement of each of the limbs. The movement of one hand (1), was followed by the movement of the contralateral foot (2), and then the second hand moved (3) followed by the contralateral foot (4).
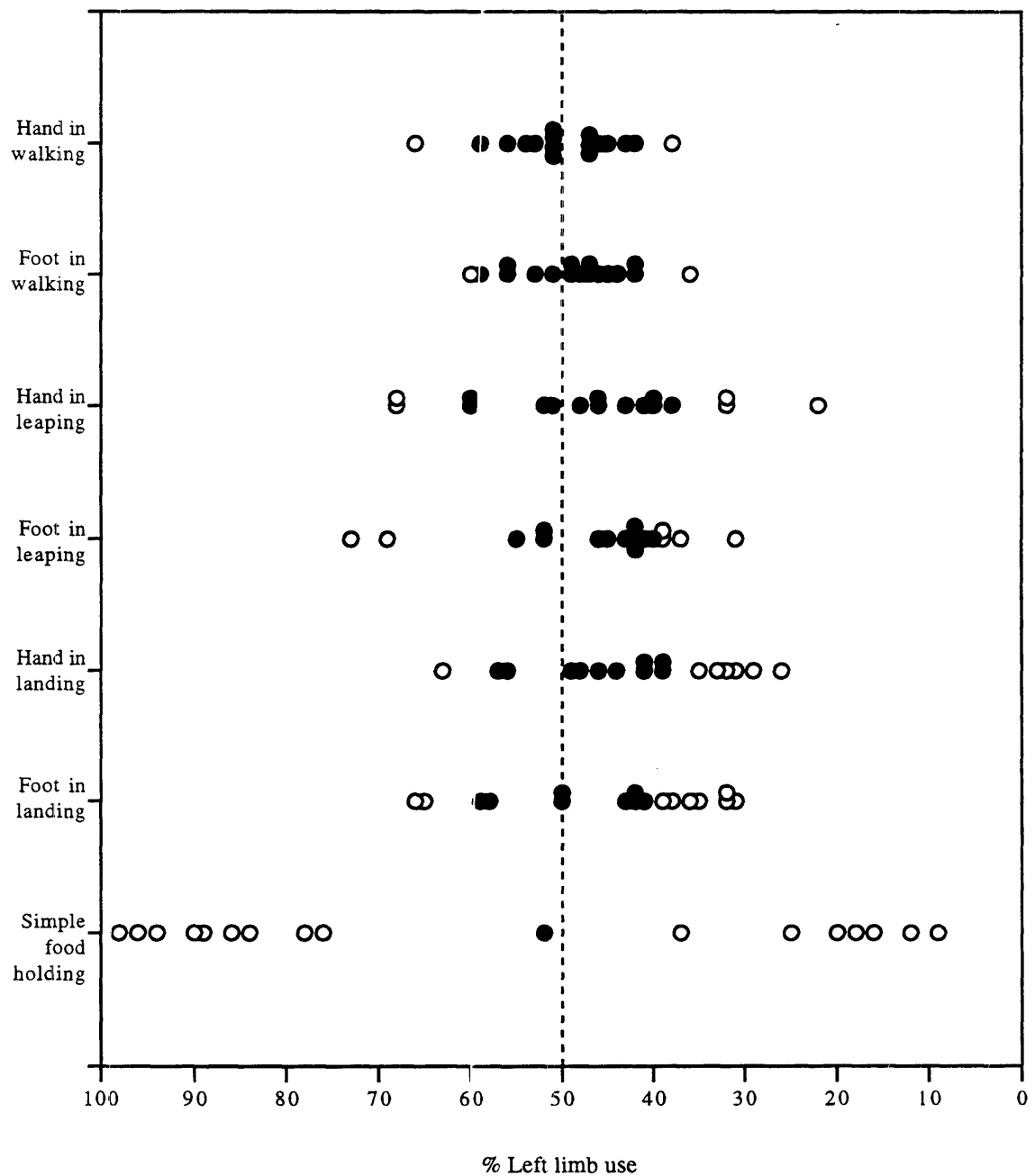
Figure 5.7 The distribution of leading-limb preferences. The percentage left-hand and foot use for each individual (O) on each test of locomotion is plotted (y axis). The white circles (O) indicate that scores were significant at p≤ 0.05, and the black (●) circles represent nonsignificant scores. Significance was tested using the z-score test. Also, note that the x axis has been reversed so that subjects with a left-limb bias are on the reader's left and those with a right-limb bias are on the right side of the graph.

Leading-hand and leading-foot preferences in leaping

Despite preferences for initiating leaping with one hand leaving the substrate slightly (1/24 second) before the other hand, only five marmosets displayed significant leading-hand preferences in leaping (Figure 5.8). As can be seen in Figure 5.8, two subjects (Black and Silver) preferred the left hand and three subjects (Red, Ash and Wattle) preferred the right hand (Figure 5.8). The two left-hand preferent subjects and
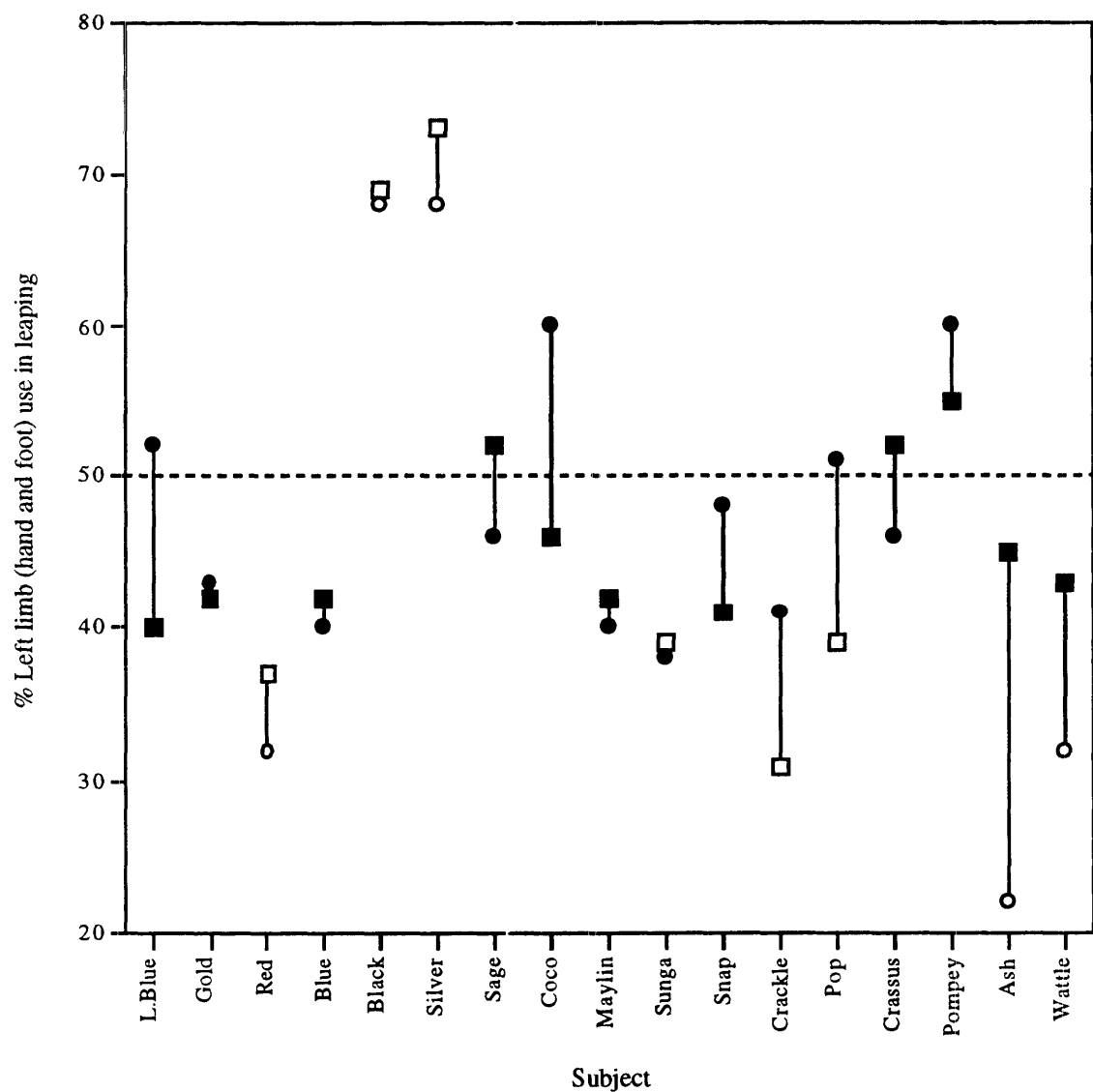

Figure 5.8 Leading-limb preferences of the individual subjects for leaping. Hand (O or ●) and foot (□ or ■) preferences in leaping are shown. Subjects are presented on the x axis and the percentage left-limb (hand and foot) preference is shown on the y axis. The white symbols indicate a significant preference, and the black symbols represent ambipreference. These data are also summarized in Figure 5.7, which compares the distribution of leading-limb preferences across tasks. The lines connect the hand and foot preferred by an individual.

one of the right-hand preferent subjects (Red) also displayed significant preferences to use the ipsilateral foot in leaping (Figures 5.8). In total, two subjects preferred to leap with the left foot first and 3 subjects preferred to initiate leaping with the right foot (Figure 5.8). Subjects were not evenly represented across the left, right and ambipreferent categories for hand use in leaping (χ^2 (2)= 10.71, p<0.01). The ambipreferent subjects (n=12) significantly outnumbered the subjects with hand preferences (ambipreferent versus left, χ^2 (1)= 7.14, p<0.05; ambipreferent versus right, χ^2 (1)= 5.40, p= 0.02).

As shown in Figure 5.9a, most subjects used the ipsilateral hand and foot for the initiation of leaping (Figure 5.9b), but the correlation between hand and foot preferences in leaping was not quite significant at the stringent level of p≤ 0.01 adopted for this research (Spearman rank, r_s= 0.50, p= 0.05). Although most subjects did not display significant hand and foot preferences for initiating leaping, it can be seen in Figure 5.9a that the majority of subjects used the right hand and foot to initiate leaping in more than 50% of sequences. Comparison between the bottom left hand corner and the top right hand corner of Figure 5.9a shows that while 8 subjects used the right hand and right foot in more than 50% of sequences to initiate leaping, only 3 subjects used the left hand and left foot to initiate leaping in more than 50% of sequences. Thus, in leaping there was a tendency for the right side of the body to push off from the surface first in leaping. There was no difference between the strength of leading-hand preferences and the strength of leading-foot preferences displayed for leaping (Wilcoxon, T+= 10, p= 0.65).

Leading-hand and leading-foot preferences in landing

In most sequences of landing the leading-hand and the leading-foot were on the same side of the body. Most subjects preferred to land with one hand (or one foot) before the other hand (or foot) but, although a greater proportion of subjects displayed significant lateral biases for landing in comparison to leaping and walking (Figures 5.7 and 5.10), approximately 50% of subjects were ambipreferent. During landing, one of

a. Correlation between hand and foot
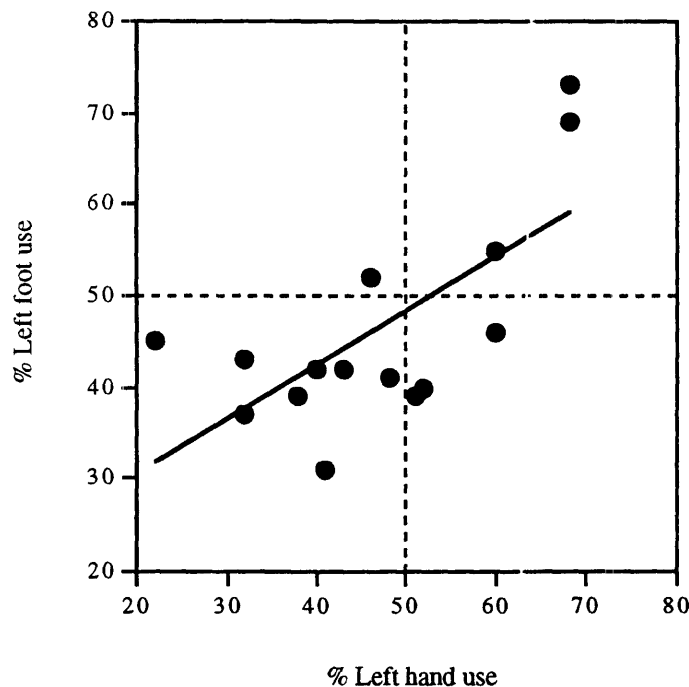
b. Pattern of hand and foot movement in leaping
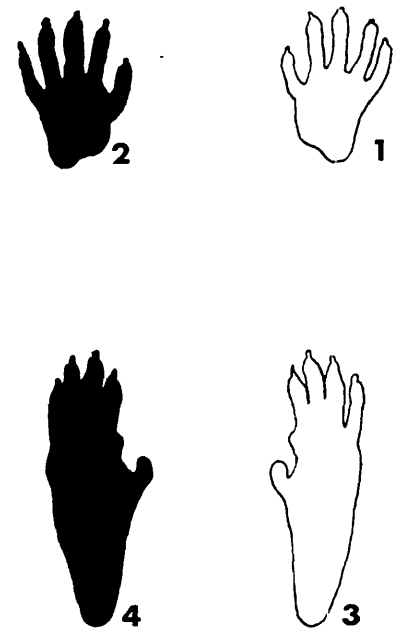

Figure 5.9 Correlation between hand and foot preferences in leaping. In Figure 5.9a, percentage left-hand use in leaping is presented on the x axis and percentage left-foot use is shown on the y axis. Note that there was a positive relationship between percentage left-hand use and percentage left-foot use in leaping, but it was not quite significant. The graph is divided into quadrants so that the number of subjects displaying increased use of the right hand and right foot in leaping can be shown. There are 8 subjects in the bottom left quadrant and only 3 subjects in the top right quadrant. Thus, 8 subjects initiated leaping with the right hand and the right foot in more than 50% of sequences and only 3 subjects used the left hand and the left foot to initiate leaping in more than 50% of sequences. The pattern of limb movement in leaping is shown in Figure 5.9b. The white hand and foot represent the leading-hand and the leading-foot. The numbers 1 through 4 also show the dominant sequence of movement of each of the limbs. The movement of one hand (1), was followed by the movement of the other hand (2), and then the first foot moved (3) followed by the second foot (4). In most cases the leading hand and leading foot were on the same side of the body.

the 17 subjects (Black) preferred to land with the left hand first, 6 subjects preferred to land with the right hand first and 10 subjects were ambipreferent (Figure 5.10). The subjects were not equally represented in the left, right and ambipreferent categories for hand use in landing (χ^2 (2) = 7.18, p<0.05; Figure 5.7). The number of subjects that did not show a preferred hand (n=10) significantly outnumbered the single subject with a left-hand preference (χ^2 (1) = 7.36, p<0.01).
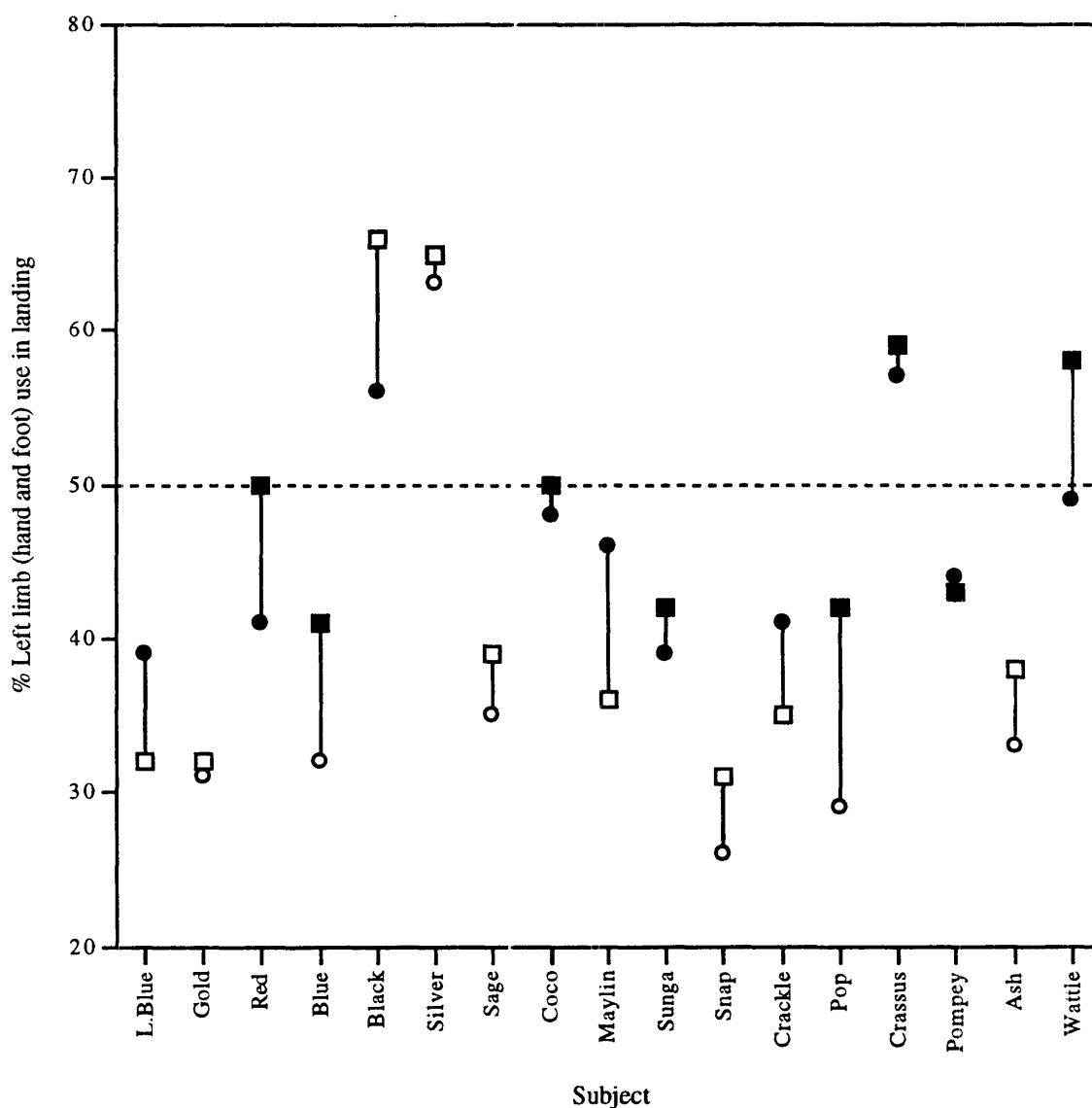
Figure 5.10 Leading-limb preferences of the individual subjects for landing. Individual's hand (O or ●) and foot (□ or ■) preferences in landing are plotted in the same way as in Figures 5.6 and 5.8. Subjects are presented on the x axis and their percentage left leading-limb (hand and foot) preference for landing is shown on the y axis. The white symbols indicate a significant hand or foot preference, and the black symbols represent ambipreference. Almost 50% of the subjects displayed significant hand or foot preferences in landing.

No group bias for left or right footedness was found. Subjects were evenly distributed across the three categories of foot preference (χ^2 (2) = 3.65, p>0.10; Figure 5.7). Nine of the 17 subjects displayed significant foot preferences in landing: 2 preferred to land with the left foot first, 7 preferred to land with the right foot first and 8 subjects did not have a foot preference (Figure 5.10).

As shown in Figure 5.11a, most subjects used the left hand and left foot for approximately the same percentage of landing sequences. A significant and strong positive correlation was found between hand and foot preferences in landing (Spearman rank, r_s= 0.80, p<0.001; Figure 5.11a). Figure 5.11a also shows a clear tendency for subjects to land with the right hand and the right foot contacting the substrate before

a. Correlation between hand and foot
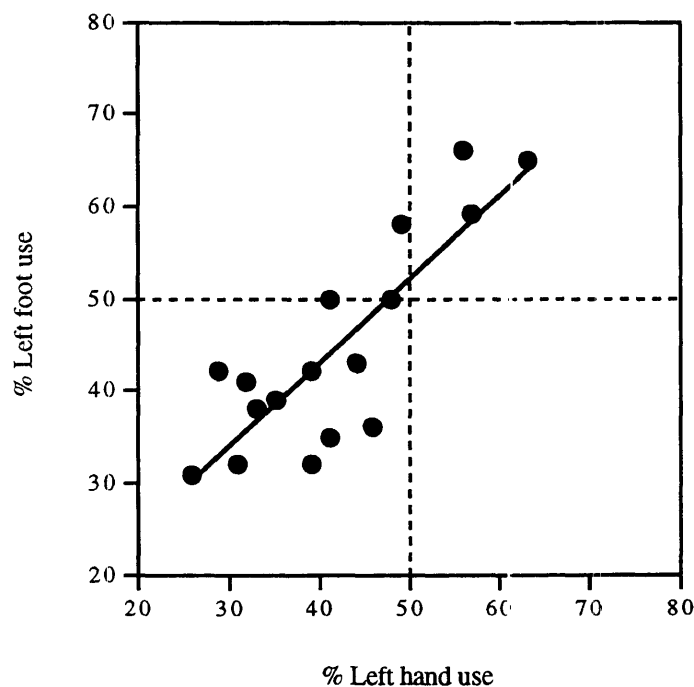
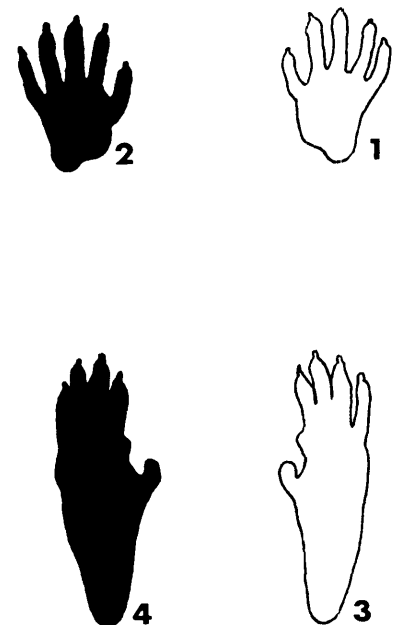**b. Pattern of hand and foot movement in landing**

Figure 5.11 **Correlations between hand and foot preferences for landing.** A significant positive correlation was found between hand and foot preferences in landing. Thus, the hand that subjects tended to use to land first was generally on the same side of the body as the foot that landed first (Figure 5.11b). Note that 11 subjects preferred to use the right hand and foot in more than 50% of sequences (bottom left quadrant), whereas only 3 subjects preferred to land with the left hand and foot contacting the perspex first in more than 50% of sequences (top right quadrant). In Figure 5.11b the white hand and foot represent the leading-hand and the leading-foot. As in Figure 5.7 and 5.9, the numbers 1 through 4 also show the dominant sequence of movement of each of the limbs.

the left hand and left foot, respectively (Figure 5.11b). In the bottom left quadrant it

can be seen that 11 of the subjects landed with the right hand and right foot contacting

the substrate first in more than 50% of the sequences analyzed, whereas only 3 subjects

landed with the left hand and foot contacting the substrate before the right hand and

foot (top right quadrant, Figure 5.11a). There was no difference between the strength of

preferences displayed for the leading hand or leading foot in landing (Wilcoxon, $T^+= 9$,

p= 0.89).

Hand preferences for simple food holding

Hand preferences for simple food holding, measured during the observations of

locomotory behaviours, were bimodally distributed (Figure 5.7). Of the 17 subjects

tested, 9 subjects displayed left-hand preferences for simple food holding, 7 subjects

displayed significant right-hand preferences and one subject was ambipreferent (Figure

5.7). As can be seen in Figure 5.12, 15 of the 17 subjects displayed the same hand

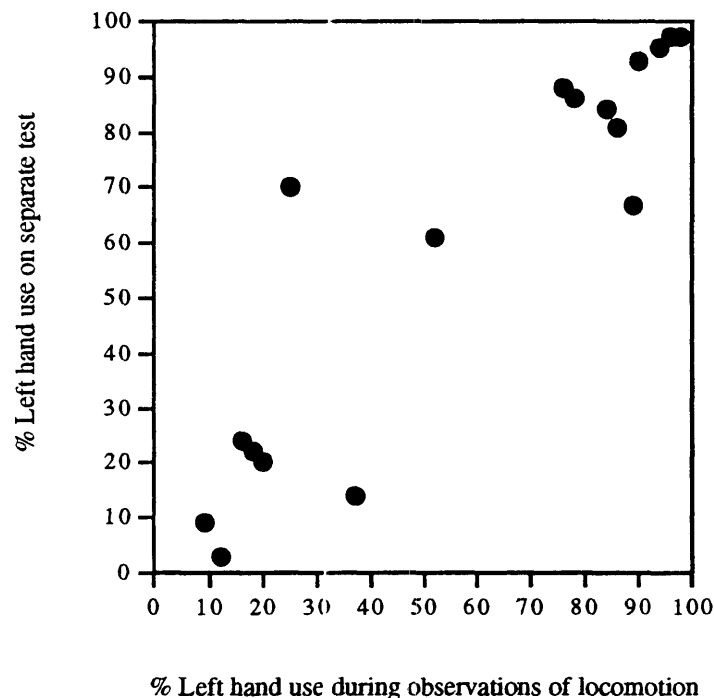% Left hand use during observations of locomotion

Figure 5.12 Comparison between hand preferences for simple food holding displayed on the tests of locomotory behaviours and those displayed on separate tests. Percentage left-hand use displayed for simple food holding during the period of observation of locomotory behaviours is presented on the x axis and percentage left-hand use for simple food holding found on separate tests conducted within 6 months of the experiments reported in this chapter is shown on the y axis. The two clusters of data indicate that most subjects displayed the same hand preferences in the separate tests.

preferences in this test of simple food holding as they displayed for simple food holding measured within 6 months of the observations of locomotory behaviours. One of the remaining two subjects, both in Experience Group 1, had displayed a left-hand preference on the previous test and a right-hand preference during the tests of locomotory behaviour (Figure 5.12). The second subject did not display a significant hand preference for simple food holding during the tests of locomotory behaviour, but she displayed a significant left-hand preference on a separate test conducted only 3 months earlier (Figure 5.12).

5.3.2   Testing for Effects of Type of Locomotion on Lateral Preferences

Relationships between leading-limb (hand and foot) preferences

Comparisons were made between leading-hand preferences (expressed as percentage left) displayed for the different modes of locomotory behaviour. As shown in Figure 5.13a, there was a tendency for a negative correlation between percentage left-hand use for walking and percentage left-hand use for landing, but it was not significant at the $p \leq 0.01$ criterion chosen in this thesis (Spearman rank, $r_s = -0.53$, $p = 0.03$). There was no correlation between percentage left-hand use for initiating walking and percentage left-hand use for initiating leaping (Spearman rank, $r_s = 0.16$, $p = 0.52$) or between percentage left-hand preferences for leaping and landing (Spearman rank, $r_s = 0.28$, $p = 0.27$).

There was a significant positive relationship between percentage left-foot use for walking and percentage left-foot use landing (Spearman rank, $r_s = 0.63$, $p < 0.01$; Figure 5.13b). Thus, the first foot to move in walking was the same as the foot that landed first. There was also a positive correlation between foot preferences for leaping and landing, but it was not quite significant (Spearman rank, $r_s = 0.55$, $p = 0.03$; Figure 5.13c). There was no correlation between foot preferences for walking and leaping (Spearman rank, $r_s = 0.31$, $p = 0.22$).
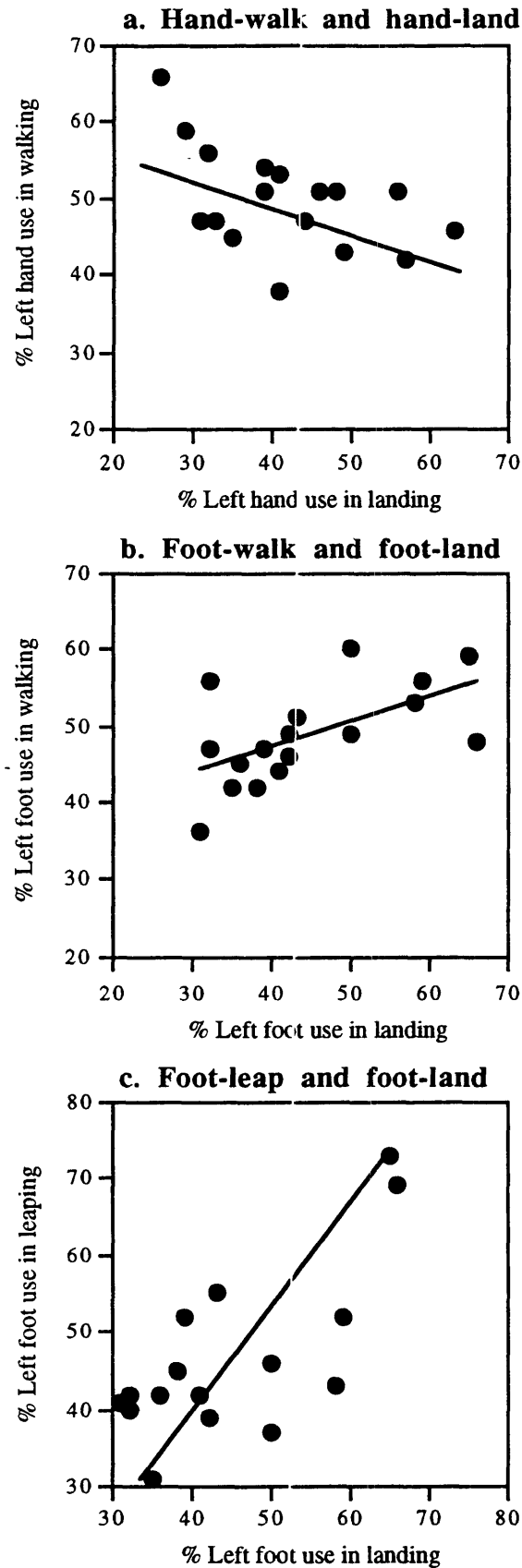
a. Hand-walk and hand-land

% Left hand use in walking

% Left hand use in landing

b. Foot-walk and foot-land

% Left foot use in walking

% Left foot use in landing

c. Foot-leap and foot-land

% Left foot use in leaping

% Left foot use in landing

Figure 5.13 Correlations between limb preferences found for the separate modes of locomotion. The negative relationship, though not significant, between hand preferences in walking and landing is shown in Figure 5.13a. Figure 5.13b presents the significant positive correlation between foot preferences in walking and landing. Figure 5.13c shows the tendency for a positive relationship between foot preferences in leaping and landing, but it was not significant.

Comparison between the strength of limb (hand and foot) preferences displayed for walking, leaping and landing

To determine whether motor complexity might influence the strength of leading-limb preferences, comparisons were made between preferences found for the three types of locomotory activity. There were significant differences in the strength of leading-hand preferences displayed (Friedman statistic, $F_r= 9$, p= 0.01). As can be seen in Figure 5.14a, the marmosets displayed stronger hand preferences for initiating leaping than they displayed for walking (Wilcoxon, $T^+= 13$, p= 0.03). They also displayed stronger leading-hand preferences for landing compared to walking (Wilcoxon, $T^+= 14$, p= 0.003; Figure 5.14a). There was no difference between the strength of leading-hand preferences displayed for leaping and landing (Wilcoxon, $T^+= 9$, p= 0.88; Figure 5.14a).
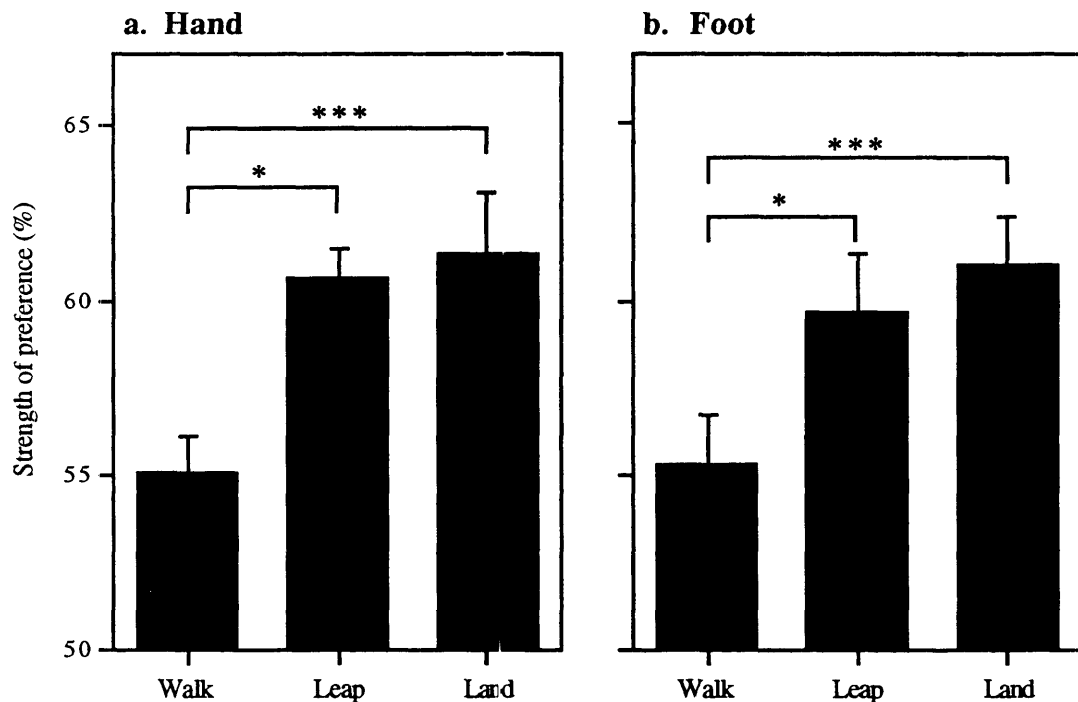

Figure 5.14 Comparisons between the strength of hand and foot preferences in walking, leaping and landing. In each graph the mean strength of preference (±SEM) displayed for each locomotory behaviour is shown. The strength of leading-hand preferences for walking, leaping and landing are compared in Figure 5.14a and the strength of leading-foot preferences are compared in Figure 5.14b. Leading-hand and leading-foot preferences in leaping and landing were significantly stronger than those displayed for initiating walking (* p≤0.03, ***p<0.005).

The strength of leading-foot preferences also differed for the separate locomotory behaviours (Friedman statistic, $F_r=$ 11.4, p= 0.003). Leading-foot preferences found for leaping and landing were significantly stronger than foot preferences in walking (Wilcoxon tests; leap versus walk, $T^+=$ 13, p= 0.02; land versus walk, $T^+=$ 15, p= 0.004; Figure 5.14b). There was no difference between the strength of foot preferences displayed for leaping and landing (Wilcoxon, $T^+=$ 7, p= 0.42; Figure 5.14b).

5.2.3 Influences of Gender, Family Group and Early Experience on Lateral Preferences in Locomotion

Gender did not influence either percentage left-hand or percentage left-foot use displayed for walking (Mann Whitney U, p>0.56 in both cases), leaping (Mann Whitney U, p>0.49 in both cases) or landing (Mann Whitney U, p>0.83 in both cases). There was also no difference in the strength of preferences displayed by female and male subjects in walking, leaping or landing (Mann Whitney U, p>0.39 in all comparisons; see Figure 5.15).

It should be noted that only offspring from Family Groups 1 and 2 were compared on the locomotory tasks, as members of Family Group 3 did not participate in these tests. Family Group membership did not appear to influence percentage left-limb use in leaping or landing (Figure 5.16). However, as shown in Figure 5.16, subjects in Family Group 1 used the left hand to initiate walking significantly more often than the subjects in Family Group 2 (Mann Whitney U, U= 2, p= 0.02). As only one of these subjects displayed a significant hand preference for walking, the significance of this difference between Family Groups is not clear. There was no difference between the strength of hand preferences displayed by subjects in the two Family Groups for walking, leaping or landing (Mann Whitney U; walk, U= 13, p= 0.85; leap, U= 6.5, p= 0.15; land, U= 9, p= 0.34). The strength of foot preferences also did not differ between Family Groups (Mann Whitney U, p≥0.15 in all comparisons).
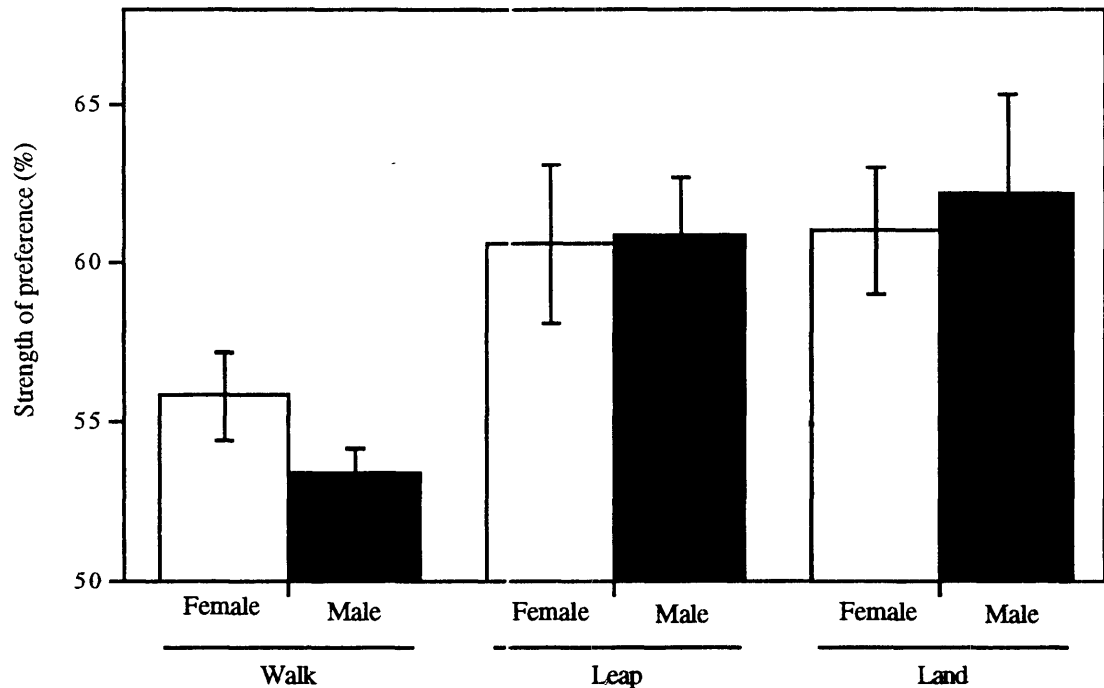
Figure 5.15 Comparison between the strength of hand preferences displayed by female and male subjects. The mean strength of hand preferences (±SEM) displayed by female (white bars) and male (black bars) subjects were compared for walking, leaping and landing. The mean strength of preferences (±SEM) is shown on the y axis and the behaviour measured and subgroup represented are shown on the x axis. There were no differences between the strength of hand preferences displayed by female and male subjects during walking, leaping or landing.
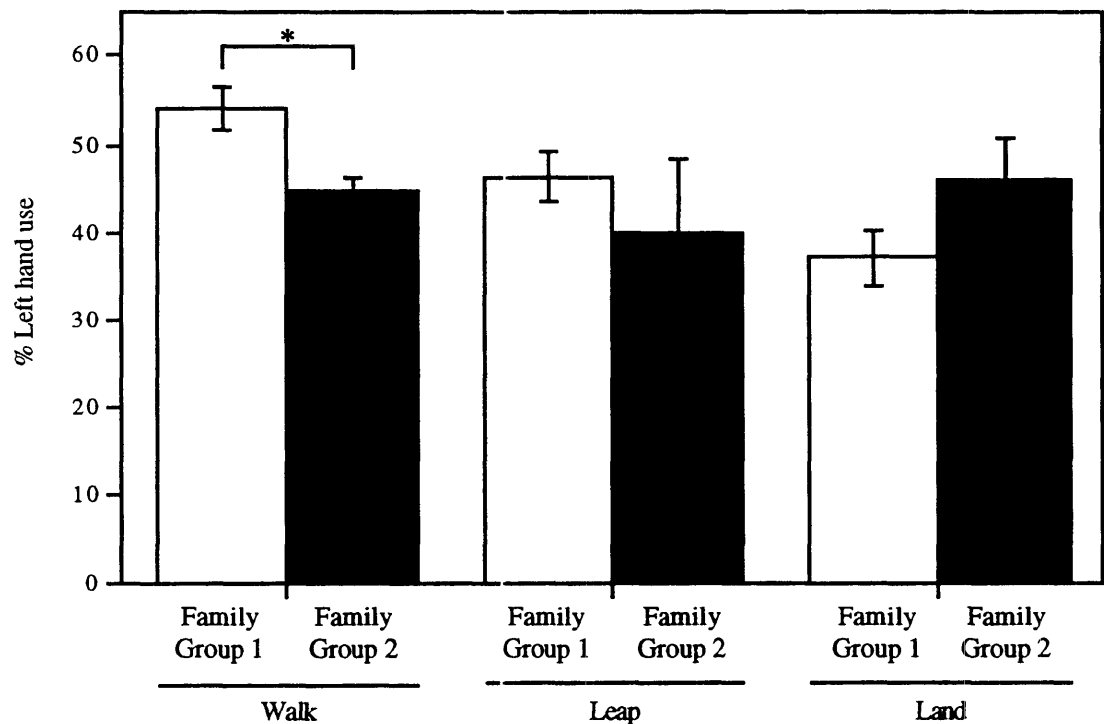

Figure 5.16 Comparison between the percentage left-hand use displayed by subjects in Family Group 1 and Family Group 2. The mean percentage left-hand use (±SEM) displayed by subjects in Family Group 1 (white bars) and Family Group 2 (black bars) is shown on the y axis. Subjects in Family Group 1 displayed significantly more left-hand use in walking than subjects in Family Group 2 (*p=0.02). There was no difference between the percentage left-hand use displayed by subjects in Family Groups 1 and 2 in leaping and landing.

No differences were found between the Experience Groups for percentage left-limb use during any of the locomotory activities (Mann Whitney U, p≥0.16 in all comparisons). Also, as can be seen in Figure 5.17, there was only one significant difference between the strength of foot preferences displayed by subjects in the two Experience Groups. It was found that subjects in Experience Group 1 displayed stronger foot preferences for leaping than subjects in Experience Group 2 (Mann Whitney U; U= 13.5, p= 0.05; Figure 5.17). There were no other differences between Experience Groups in the strength of leading-limb preferences displayed (Mann Whitney U, p>0.21 in all comparisons).
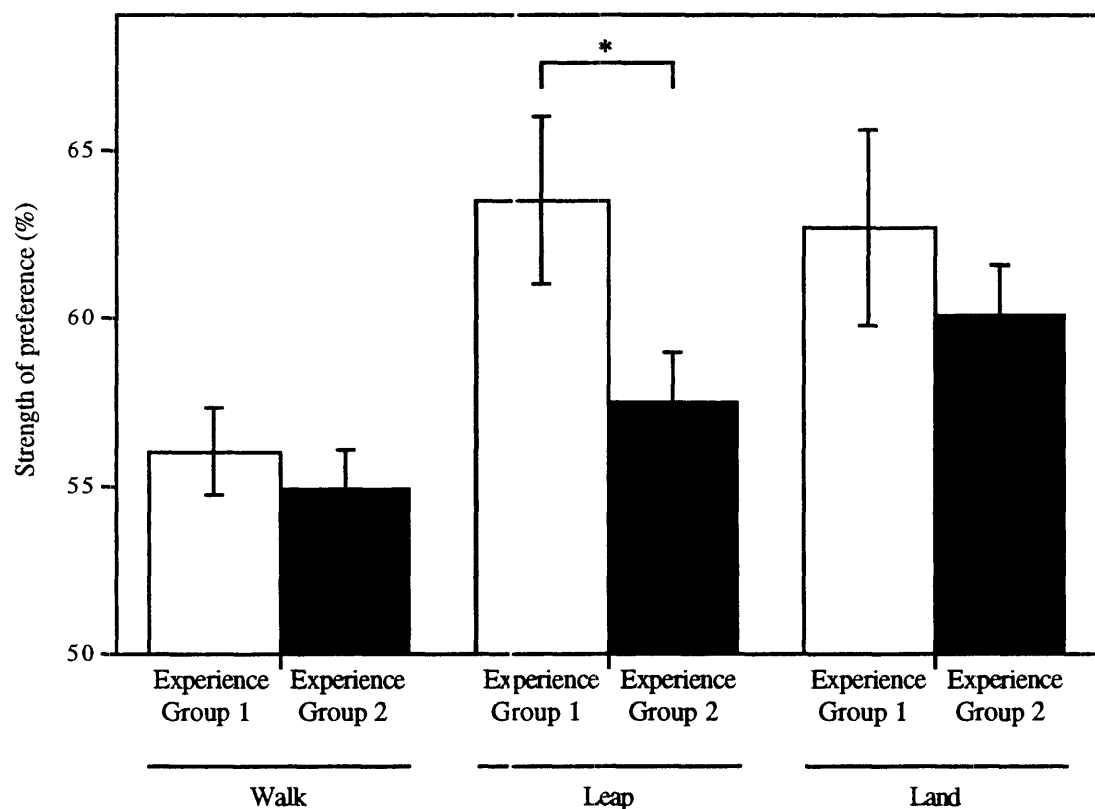
Figure 5.17 The effects of early experience on strength of foot preferences in initiating and terminating locomotion. Presented on the x axis are the Experience Groups being compared. The strength of foot preferences (±SEM) displayed by subjects belonging to the two Experience Groups during leaping is shown on the y axis. Subjects in Experience Group 1 (white bars) displayed significantly stronger foot preferences than subjects in Experience Group 2 (black bars). * p=0.05.

5.3.4 Comparisons Between Hand Preferences for Locomotory Behaviours and Hand Preferences for Simple Food Holding and Visuospatial Reaching

Leading-hand preferences for locomotory behaviours and hand preferences for simple food holding

To determine whether leading-hand preferences might be related to hand preferences for other manual tasks, percentage left-hand use for each type of locomotory function was correlated with percentage left-hand use for simple food holding, measured during the same testing period. As the data were clustered bimodally, correlations with simple food holding were determined separately for left and right-hand preferent subjects. The subjects were divided into groups according to the hand preferences they displayed for simple food holding, as most subjects did not display hand preferences in walking, leaping or landing.

There was no correlation between percentage left-hand use for initiating walking and percentage left-hand use for simple food holding (Spearman rank; left, r_s= 0.44, p= 0.19; right, r_s= -0.67, p= 0.10) There was also no relationship between hand preferences for initiating leaping and hand preferences for simple food holding (Spearman rank; left, r_s= -0.13, p= 0.69; right, r_s= -0.52, p= 0.20). Leading-hand preferences in landing were not related to hand preferences for simple food holding (Spearman rank; left, r_s= -0.29, p= 0.39; right, r_s= -0.32, p= 0.43).

Leading-hand preferences for locomotory behaviours and hand preferences for visuospatial reaching

As leaping and landing would require high levels of spatial processing for the accurate assessment of the position of a landing substrate, it was considered important to see whether leading-hand preferences might be related to hand preferences for visuospatial reaching. No correlation was found between hand preferences for reaching into the bowl (Chapter 4, pp. 116-119) and hand preferences for initiating walking (Spearman rank, r_s= 0, p= 0.96), leaping (Spearman rank, r_s= 0, p= 0.96) or landing (Spearman rank, r_s= -0.20, p= 0.38). Also, there was no correlation between hand preferences for taking food from the rotating disc and leading-hand preferences in locomotion (Spearman rank, p≥0.07 in all comparisons).

As hand preferences for taking food from the plate and grasping the string were clustered bimodally, correlations with leading-hand preferences for locomotion were calculated for the left and right-hand preferent subgroups separately. The subjects were grouped according to the hand preferences they displayed on each of the two visuospatial reaching tasks. No correlation was found between hand preferences for taking food from the plate and percentage left-hand preferences for walking, leaping or landing in either the left or right-hand preferent subgroups (Spearman rank; r_s between -0.27 and 0.21, $p \geq 0.42$). There were also no relationships between percentage left-hand preferences for grasping the string and percentage left-hand preferences for walking, leaping or landing in either the left (Spearman rank; r_s between -0.08 and 0.21, $p \geq 0.54$) or right-hand preferent subgroups (Spearman rank; r_s between -0.17 and 0, $p \geq 0.67$).

It was considered possible that the hand preferences of shifters might be correlated with leading-hand preferences in locomotory behaviours and that hand preferences displayed by nonshifters might not be correlated. The shifters were the marmosets that displayed opposite hand preferences for simple food holding and taking food from the plate, whereas nonshifters displayed the same hand preferences for both tasks (Table 4.2, p. 133). It was reasoned previously that shifters may have processed the visuospatial tasks primarily according to the spatial demands, whereas nonshifters may have been attending more to the motor demands of the tasks (Chapter 4, pp. 140-141). Thus, the hand preferences displayed by the shifters for visuospatial reaching were indicative of their lateralization for the control of visuomotor actions, and may be related to their leading-limb preferences for leaping and landing. The hand preferences for the nonshifters may not be indicative of their lateralization for visuospatial reaching and may have affected the correlation for the total group. Correlations were determined for the shifter subgroup separately. No correlations could be calculated for the nonshifter subgroup as the data were clustered in all comparisons.
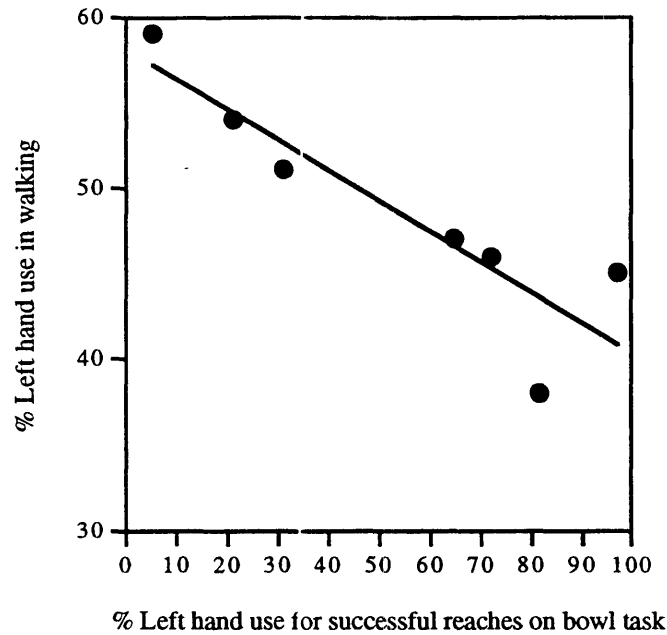
% Left hand use for successful reaches on bowl task

Figure 5.18 Relationships between hand preferences for initiating and terminating locomotion and hand preferences for visuospatial reaching. A strong negative correlation was found between percentage left-hand use for initiating walking and percentage left-hand use for successful reaches into the covered bowl, a visually guided reaching task. This correlation was present in the shifter subgroup only, and these are the data plotted.

Only hand preferences on the bowl task could be correlated with leading-hand preferences displayed by shifter subjects as the remaining sets of data were clustered. There was a tendency only for a negative correlation between percentage left-hand use on the bowl task and percentage left-hand use for initiating walking, but it was not significant at the $p \leq 0.01$ criterion (Spearman rank, $r_s = -0.79$, $p = 0.05$). A significant and strong negative correlation was found in the shifter subgroup, however, when percentage left-hand use for successful reaches on the bowl task was compared to percentage left-hand use for initiating walking (Spearman rank, $r_s = -0.96$, $p = 0.005$; Figure 5.18). Thus, the marmosets in the shifter subgroup tended to use one hand to initiate walking and preferred the other for visually guided reaching.

There was no significant correlation between percentage left-hand use for unsuccessful reaches on the bowl task and percentage left-hand use for initiating walking (Spearman rank, $r_s = -0.64$, $p = 0.12$). Leading-hand preferences for leaping

were not related to hand preferences on the bowl task (Spearman rank, r_s between -0.54 and -0.17, $p \geq 0.19$). There was also no correlation between leading-hand preferences in landing and hand preferences on the bowl task (Spearman rank, r_s between -0.43 and 0.32, $p \geq 0.29$).

Comparisons between the strength of preferences found for locomotory activities and those found for other motor functions

The subjects displayed significantly weaker preferences during locomotory activities, for both hand and foot use, than they displayed for simple food holding (Wilcoxon tests, $p < 0.0003$ in all comparisons). This can be seen in Figure 5.7 (p. 175). Subjects displayed a mean strength of preference of 82.71 ± 2.85 % for simple food holding, whereas the greatest mean strength of preference they displayed for locomotory behaviours was 61.35 ± 1.65 % and this was for hand use in landing. The preferences found for hand use in the initiation of locomotory activities were also significantly weaker than those found on each of the tests of visuospatial reaching (Wilcoxon tests, $p < 0.01$ in all comparisons).

5.4   DISCUSSION

Most studies on the lateralization of locomotory behaviour of nonhuman primates have examined hand and foot preferences for the initiation of walking. Walking in primates is characterized by the movement of one hand before the other hand and before both of the feet, and thus there is potential for lateralization of this behaviour. It was shown in the present study that, like other primate species (Napier, 1976; Hunt et al. 1996), marmosets display a crossed diagonal gait when walking (p. 174). For initiating walking, hand preference was correlated negatively with foot preference. Thus, in most cases, movement of one hand was followed by movement of the contralateral foot, and lateral biases could be recorded easily. However, leaping and landing might be better measures of the lateralization of locomotory behaviours in arboreal species, as they represent more commonly used patterns of locomotion (Garber, 1993).

During leaping, all of the marmosets preferred to push off with one hand, so that one hand left the surface at least 2.5 milliseconds before the other hand, rather than pushing off with both hands simultaneously. The feet left the platform after the hands (Figure 5.9b, p. 178) and 16 of the 17 subjects preferred to push off with one foot leaving the platform before the other, instead of pushing off with both together. The hand and the foot that left the platform first in leaping tended to be on the same side of the body. Although the correlation between percentage left-hand use and percentage left-foot use for initiating leaping was not quite significant, this result may have been caused by the absence of data on hand movements in some of the sequences.

The marmosets tended to land with one hand contacting the surface first, rather than with both hands (and feet) together. In most sequences of landing, one hand contacted the surface followed by the other hand and then one foot followed by the other foot (Figure 5.11b, p. 180). There was a significant positive correlation between hand preferences and foot preferences in landing. Thus, the hand and foot that landed first tended to be on the same side of the body. In some sequences, however, both hands or both feet touched the surface simultaneously. The marmosets landed with both hands contacting the substrate simultaneously on 29.8± 1.7% of occasions and this was significantly more often than they leapt with both hands leaving the surface together (12.0±1.4%). Landing with the two hands simultaneously contacting the surface would aid in deceleration of the body by distributing the impact of contact with a surface between the limbs. Even though there is a possible advantage for bimanual hand use in landing, however, it occurred in less than one third of the sequences analyzed.

Despite the more frequent occurrence of unimanual hand use and unipedal foot use, most subjects did not display significant hand or foot preferences for walking, landing or leaping. Ambipreference was characteristic of the group for walking, which confirms the result of Box (1977a). Only two of the 17 subjects displayed significant hand and foot preferences for initiating walking. The absence of leading-hand preferences in marmosets for initiating walking is disparate with reports of significant

leading-hand preferences in all of the other primate species that have been studied (Heestand, 1986, cited in Hopkins et al. 1993; Forsythe and Ward, 1987; Cunningham et al. 1989; Hopkins et al. 1993; Hopkins and deWaal, 1995; Marchant and McGrew, 1996; Hopkins et al. 1997). It is possible that any hemispheric specialization for control of the limbs in walking, present in other primate species, might not have been retained in the arboreal callitrichids, as walking is not a form of locomotion commonly used by these species (Garber, 1993).

Callitrichid locomotion is largely comprised of leaping and landing (Garber, 1993). It was hypothesized that the marmosets would display left leading-limb preferences during leaping and landing, reflecting specialization of the right hemisphere for visuospatial processing, as found in other species (Chapter 4, p. 141). Although more subjects displayed significant hand and foot preferences in leaping and landing, compared to walking, over 50% of the subjects were still ambipreferent. Furthermore, even though landing should demand very high levels of visuospatial processing for the accurate assessment of the position of the substrate, and use of the right hemisphere might have been an advantage, there was a tendency for more subjects to land with the right hand and foot contacting the substrate first. It was noted that 11 of the 17 subjects landed with the right hand and foot contacting the platform first in more than 50% of sequences (p. 180). Only 3 subjects landed with the left hand and foot contacting the substrate first in more than 50% of sequences analyzed (p. 180). Thus, rather than left-limb preferences there was a tendency for increased right-limb use. It should be emphasized that although a significant group bias was not present, these results indicate that right handedness might occur in a larger sample or on more motorically complex tests. The suggestion of a right-hand bias in landing may indicate that this arm is stronger, as the stronger arm would be used to decelerate the body. During quadrupedal landing both the forelimbs and hindlimbs decelerate the body, however the hands contact the landing substrate before the feet and absorb most of the impact of contact with the substrate (Hunt et al. 1996). Therefore, the hand that contacted the substrate first should be indicative of the stronger forelimb. Increased right-foot use in landing

does not indicate that this foot is significantly stronger, however, as most of the impact of landing would have been absorbed by the right and then the left hand. It may be that increased use of the right hand led to increased use of the right foot, as subjects tended to land with the hand and foot on the same side of the body contacting the surface first. It is possible that in the present experiments use of the strong forelimb in landing masked asymmetries for visuospatial processing.

Alternatively, the leaping and landing required in this study may not have been visuospatially complex enough to demand use of underlying hemispheric specializations for visuospatial processing. The perspex platform used in the present study was reasonably large (44cm x 44cm) and the subjects did not have to leap a great distance to land on the platform (20cm). Therefore, this task may not have required high levels of visuospatial processing for assessment of the position of the substrate on which to land. Left leading-limb preferences may, possibly, be expressed on more visuospatially demanding tasks, for example if subjects were required to leap onto a very narrow substrate or through a narrow opening.

The tendency for increased use of the right hand in landing, possibly indicative of a stronger right arm in marmosets, does concur in part with the hypothesis of MacNeilage et al. (1987), who proposed that the right arm would be used for postural control in arboreal New World primates. leaving the left hand free for visually guided reaching tasks. However, despite the possibility of a stronger right arm, there is no evidence that asymmetries of postural control led to handedness in marmosets. As shown in Chapters 3 and 4, marmosets do not display left handedness for simple food holding or for visuospatial reaching. Even at the individual level, there was no evidence to suggest that asymmetries of postural control influence hand preferences for simple food holding or visuospatial reaching. Of the 9 marmosets that displayed a significant preference for using the right hand or foot in landing, 6 displayed left-hand preferences for simple food holding and 3 displayed right-hand preferences. Of the 2 subjects displaying a significant preference for the left hand or foot, one was left-hand preferent and the other was right-hand preferent for simple food holding. There was

also no correlation between leading-hand preferences in landing and the hand preferences displayed by the same subjects for simple food holding and visuospatial reaching. Thus, postural asymmetries may not be the determinant of hand preferences for feeding as was suggested in the 'postural origins theory' (MacNeilage et al. 1987).

Moreover, MacNeilage et al. (1987) do not distinguish between the roles of the forelimbs and the hindlimbs in postural control. MacNeilage (1991) suggests that the right side of the body (hand and foot) is used for postural control and is stronger in nonhuman primates. In fact, he implies that the greater strength of the right arm and foot in nonhuman primates led to right handedness and right footedness in humans, with both the right hand and foot becoming 'favored for the application of force on environmental objects' (MacNeilage, 1991). However, the present experiments have shown that there is a tendency for the left leg to be stronger in marmosets. Eight of the 17 subjects leapt with the right hand and foot pushing off before the left hand and left foot in more than 50% of sequences analyzed (p. 178). Only 3 subjects used the left hand and left foot to initiate leaping in more than 50% of sequences. As Hunt et al. (1996) define leaping as a 'gap crossing movement in which the hindlimbs are primarily used as propulsors', the foot providing most of the propulsive force would be the one that was second to leave the perspex substrate. The tendency to initiate leaping with the right foot leaving the platform before the left foot, indicates that the left foot was used more often to provide the propulsive force for this motor action. Thus, it would appear that there is a tendency for right arm and the left leg to be stronger in marmosets, rather than the right arm and right leg as MacNeilage et al. (1987) proposed. The direction of the asymmetry in strength between the two hindlimbs in marmosets would be, in fact, congruent with asymmetries found for humans. Human studies suggest in most individuals, the right leg is used for mobilizing-flexion actions, while the left leg is used for providing postural support (Nachson and Denno, 1986; Seltzer et al. 1990; Dargent-Paré et al. 1992; Gabbard and Iteya, 1996). Similarly in marmosets the right hand and foot tend to mobilize the body, while the left leg (foot) appears to provide the propulsive force for leaping.

There was a significant positive relationship between percentage left-foot use

for walking and percentage left-foot use for landing. Therefore, the same foot is used

more often to lead in both walking and landing. Also, hand preferences for walking

and hand preferences for landing tended to be negatively correlated (Figure 5.19).

Thus, as shown in Figure 5.19 the marmosets tended to step out with their weaker arm,

opposite to the stronger arm used to contact the substrate first in landing. Moreover,

they used their weaker leg to step first (Figure 5.19). As there was a tendency for the

left leg to provide the propulsive force in leaping, the right leg which is used more often

to land first would be the weaker leg. Thus, the weaker arm and leg are used more

often to mobilize the body during walking, possibly with the stronger limbs providing

postural support. It should be noted, however, that only two subjects displayed

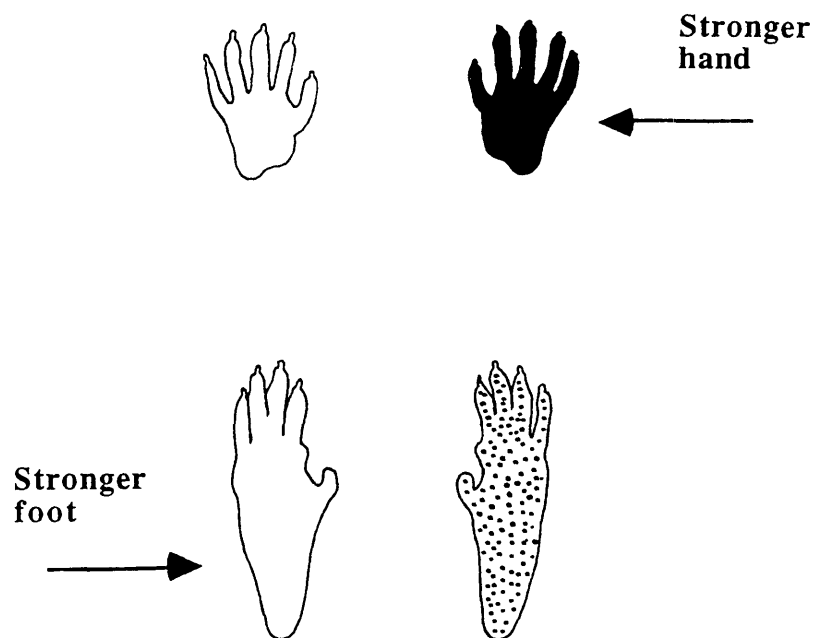significant leading-hand and leading-foot preferences in walking. However, as the

Figure 5.19 The relationship between leading-hand and leading-foot preferences in walking and landing. The white hand is used to represent the leading-hand in walking, whereas the black hand represents the leading-hand in landing. The dotted foot is used to demonstrate that the same foot tends to be used for both walking and landing. The tendency for most subjects to use the right hand to contact the substrate first in landing suggests that the right arm may be stronger in marmosets. Note that the right arm, used in landing, would not be used to initiate walking. Also, there was a tendency for most subjects to leap with the left foot leaving the platform last and providing most of the force for propulsion. Thus, the left leg may be stronger in marmosets. It should also be noted then that the weaker leg would move first during walking.

marmosets were walking on a flat perspex surface in the experiments reported in this chapter there would not have been any need for increased postural control during walking. It is possible that in more unstable conditions, marmosets may display stronger hand and foot preferences, even for walking.

For the shifter subgroup (Chapter 4, p. 133), there was also a negative relationship between leading-hand preferences in walking and hand preferences displayed for successful reaches into the bowl. Therefore, the shifters tended to use one hand to reach into the bowl and the other hand slightly more often to initiate walking. However, the significance of this relationship is unclear. The correlation between these two types of hand preference is very strong, but it cannot be clearly explained as the subjects displayed very weak preferences for initiating walking with one hand. The mean strength of leading-hand preferences in walking for subjects in the shifter subgroup was only equal to 55.42±1.43%. It is possible that hand preferences for initiating walking and hand preferences for visuospatial reaching are both related to a third variable (Martin and Bateson, 1993) such as hand preferences for simple food holding. Correlation between hand preferences for initiating walking and hand preferences for simple food holding could not be calculated in the present study as the data were clustered. However, a significant positive relationship between hand preferences for initiating walking and hand preferences for reaching for food has been found with bonobos (Hopkins et al. 1993). The relationship between hand preferences for initiating walking and hand preferences for simple food holding deserves further examination with a larger group of subjects.

The lack of significant leading-hand and leading-foot preferences in walking, leaping and landing also needs to be addressed. Even when the subjects displayed hand preferences for initiating and terminating locomotion they were significantly weaker than hand preferences found for simple food holding and visuospatial reaching (Chapters 3 and 4). Although there was a tendency for subjects to use the right hand more often to contact the substrate first in landing, and for subjects to push off with the left leg more often in leaping, most subjects did not display significant hand or foot

preferences for either locomotory activity. It is possible that there is not a large difference in the strength of the two forelimbs and of the two hindlimbs. Alternatively, asymmetries of strength between the two sides of the body may decrease with experience. It is possible that stronger hand and foot preferences for initiating and terminating locomotion may be found in juvenile or infant marmosets.

Both hemispheres may become competent at controlling leaping and landing with practice. During leaping and landing both sides of the body are performing the same movements, even though one hand is subjected to greater impact in landing and one foot provides more propulsive force in leaping. As both limbs are used and perform the same action it is possible that a weaker side would be masked with experience. With increased use, each of the forelimbs would have sufficient strength to decelerate the body in landing, and each of the hindlimbs would be very capable of propelling the body in leaping. This differs from unimanual tasks such as simple food holding. The strength of unimanual hand preferences for simple food holding might increase with practice because the subjects might form motor habits or set movement patterns in the hemisphere contralateral to the preferred hand, as discussed previously (Fagot and Vauclair, 1991; Nudo et al. 1992; Preilowski, 1993; Chapter 4, p. 139). While practice might not affect the strength of hand preferences on novel tasks (100 scores) significantly (e.g. those presented in Chapter 4), it is likely that the strength of unimanual hand preferences would increase with experience over much longer periods of time (22+ months). It should also be noted that the results of this thesis indicate that early experience may affect lateralization for locomotory behaviours. Subjects in Experience Group 1 displayed stronger foot preferences in leaping than those found for subjects in Experience Group 2. Subjects in Experience Group 1 were born and raised, for their first 6 months of life, in very much smaller cages than those at the University of New England (Chapter 2, p. 48). It is possible that their lack of locomotory experience in this period delayed the masking effect of practice on leading-limb preferences. Gender and family group membership did not significantly affect the strength of preferences displayed by the subjects.

There may be no advantage in having leading-limb preferences in the arboreal environment. In fact, leading-limb preferences might be disadvantageous in situations that do not demand high levels of visuospatial processing. When locomoting in the arboreal environment, it might be necessary for both sides of the body to be able to control visuomotor movements and to have sufficient strength for initiating leaping or decelerating the body in landing. When moving to evade a predator it would be essential for an individual to be able to leap rapidly in either the left or right direction and to accurately assess the spatial position and distance of the landing substrate. It is noted that the use of one side of the body to push off from a surface propels the body in the opposite direction, and in the direction of the guiding limb. Thus, both sides of the body must be capable of propelling and guiding the body in locomotion to ensure that direction of movements or speed of responses is not limited. Marchant and McGrew (1996) also suggested that the absence of a group bias in the wild chimpanzees (*Pan troglodytes schweinfurthii*) compared to captive chimpanzees that have been studied may be due to the increased opportunity for arboreal locomotion in the natural environment. In the natural habitat they suggested that it would be a disadvantage to have hemispheric specializations for the control of limb use, as in most cases it would be a limitation. For example, they suggested that if the next highest branch on which a chimpanzee wanted to climb projected to their right it would be convenient to be able to grasp it with the right hand, and not to have to reposition so as to take the branch with the left hand (Marchant and McGrew, 1996).

5.5   SUMMARY

Most of the subjects did not display significant hand or foot preferences for walking, leaping or landing, even though they displayed strong and significant hand preferences for simple food holding and visuospatial reaching. There was some evidence to suggest, however, that the right arm may be stronger in marmosets, because most of the marmosets used the right hand more often to contact the perspex substrate first in landing. Therefore, the right arm is used to initially decelerate the body and absorb the impact of contact with the landing substrate. However, despite the finding

of a strong arm there was no evidence that this asymmetry was the determinant of individuals' hand preferences for simple food holding or visuospatial reaching. Thus, there was no evidence that supported the hypothesis of MacNeilage et al. (1987) that one hand is used for postural control and the other for simple food holding or visuospatial reaching. Moreover, there is no evidence to suggest that one side of the body only would be used for postural control in marmosets. Although there is a tendency for the right arm to be stronger in most marmosets, this is balanced by a tendency for the left leg to be stronger, providing most of the force needed for propulsion in leaping. The absence of strong leading-limb preferences in most marmosets suggests that it might be disadvantageous to have an absolute preference for one limb only during the performance of locomotory activities in an arboreal environment.

CHAPTER 6

EYE PREFERENCES

6.1   INTRODUCTION

The experiments reported in previous chapters have examined different forms of motor lateralization in the marmosets. The aim of the experiments reported in this chapter was to examine eye preferences. Despite increasing interest in the study of functional asymmetries in nonhuman primates, information on perceptual asymmetries is sparse. Monocular viewing tests may provide a noninvasive means of examining a lateralization of perceptual processing, although it is recognised that they may be influenced by motor lateralizations. For example, asymmetries of postural control could influence the way in which subjects perform a task, causing a subject to lean in one direction while looking through a monocular hole and biasing the response (Ward and Cantalupo, 1997).

In primates the eyes are placed frontally and, therefore, it is not possible to determine eye preferences from the postural orientation of the head, a technique employed with other nonprimate species that have laterally placed eyes (Dharmaretnam and Andrew, 1994; Deckel, 1995). Eye preferences in primates have been determined in tasks requiring the subjects to look with one eye through a peephole or down a tube (see Chapter 1). The term *eye preference* refers to the consistent choice of one eye over the other in such a monocular viewing situation.

In primates each eye provides sensory input to both of the cerebral hemispheres. Thus, use of one eye does not restrict primary visual input to the hemisphere contralateral to the eye being used as it does in birds. Nevertheless, the crossed fibres

of the optic nerve have larger diameters, are better myelinated and transmit sensory information faster than the uncrossed fibres (Bishop et al. 1953; Maddess, 1975). In diurnal primates, there are higher densities of photoreceptors in the nasal hemiretina compared to the temporal hemiretina (Curcio et al. 1987; Packer et al. 1989). Ganglion cell density decreases with distance from the fovea and in diurnal primates, including the marmoset, a steeper gradient of decline is found in the temporal hemiretina compared to the nasal hemiretina (Wässle et al. 1990; Wilder et al. 1996). There is evidence for a strong positive correlation between ganglion cell density and cortical magnification in primates (Wässle et al. 1990). Thus, in a monocular viewing situation the contralateral hemisphere would receive qualitatively different sensory information than the ipsilateral hemisphere. It has been suggested that these morphological differences between the nasal and temporal hemiretinas may result in a stronger cortical representation in the hemisphere contralateral to a viewing eye (Rowe, 1991; Weisz et al. 1994), because this hemisphere receives sensory information via the crossed optic nerves originating in the nasal hemiretina. Indeed, it has been demonstrated in humans that the region of highest image quality is located approximately 5° nasal to the fovea (Jennings and Charman, 1981), and that the decline in image quality with eccentricity is slower in the nasal hemiretina compared to the temporal hemiretina in macaques (Merigan and Katz, 1990). Thus, fibres originating in the nasal hemiretina would transmit a higher quality image to the contralateral hemisphere in humans and macaques. To the author's knowledge, the image quality transmitted via the contralateral and ipsilateral fibres originating in the nasal and temporal hemiretinas, respectively, has not been investigated in marmosets. Nevertheless, the similar distributions of ganglion cells in the nasal and temporal hemiretinas of marmosets and macaques would suggest that images of higher quality would be transmitted via the contralateral projections in marmosets. Monocular eye preference may, therefore, be indicative of lateralization of the hemispheres for perceptual processing (Rogers et al. 1994), as more detailed images of visual stimuli may be transmitted to the hemisphere contralateral to the viewing eye.

Studies of simple reaction time in humans have shown that information from the dominant or preferent eye is responded to more rapidly than information from the nonpreferred eye (Minucci and Connors, 1964). Coren and Porac (1976) reported, for human subjects, that there is size enhancement of a stimulus presented to the dominant eye, but not of a stimulus presented to the nonpreferred eye. The image from the dominant eye has also been described as clearer than the image seen by the nonpreferred eye. It is more satiated in colour (Porac and Coren, 1981) and produces a more stable retinal image that takes longer to fade than the image of the nonpreferred eye (Wade, 1975; Porac and Coren, 1982). These observations indicate that there are asymmetries in the efficiency of processing and perception between the preferred and nonpreferred eyes and these may be a consequence of differential processing in the hemispheres.

Very few studies of functional lateralization in nonhuman primates have examined eye preference. There have been only four studies of eye preference in the platyrrhine species and each of these has produced different results (Chapter 1, pp. 32-33). Capuchins have right-eye preferences (Kounin, 1938) or a symmetrical distribution of eye preferences (Westergaard and Suomi, 1996b) and tamarins do not display an eye preference (McFerran, 1992). It was suggested that the different results may indicate inconsistency in the presence and direction of lateral bias for eye preference among New World primates or that they may reflect the methodological differences between experiments. Arousal and/or conditioning of subjects' responses may have led to differences between eye preferences in capuchins (Kounin, 1938), and tamarins (McFerran, 1992). Unfortunately, Westergaard and Suomi (1996b) do not provide details on their procedures for measuring eye preferences in capuchins, and it is not possible to speculate whether their methods might have influenced the eye preferences of the subjects. For example, it is not stated whether subjects were tested individually or in groups.

The experiments reported in this chapter also investigated whether variables including age, arousal, the hand used by the experimenter to present the reward and the

subjects' hand preferences influenced the eye preferences of the marmosets. As hand preferences may be dependent on the components of the task (Chapter 4), the relationships between eye preference and hand preferences displayed on a variety of tasks were examined.

6.2 METHODS

Twenty-one marmosets (8 males, 13 females) were tested. The method was based on that described previously by Rogers et al. (1994). The testing apparatus was modified for the smaller size of the marmosets. The testing apparatus was designed so that it could be hooked onto the wire wall of the home cage. Subjects were tested individually in one half of the home cage. The testing apparatus consisted of a sheet of galvanised steel (56 x 56cm) with a steel box (15cm deep x 17cm x 17cm) secured on the centre back, facing the experimenter (Figure 6.1). There was a horizontal slit (1cm x 0.5cm) in both the front and back of the box, allowing the subjects to look into the box through a slit to view a stimulus. The experimenter looked through the other slit, located directly opposite to the slit through which the marmosets could look. The experimenter monitored the eye used by the subject. The subjects were trained to look through the horizontal slit to view a piece of banana with both eyes. After binocular gaze was held for approximately two seconds, the subject was rewarded with the piece of banana. A hinged door, in the left side of the box, allowed the experimenter to hold the reward directly in front of the horizontal slit using her left hand. The experimenter's hand was used to present stimuli as it was familiar to the marmosets and because it facilitated transfer of the reward through the slit. It should be noted that these marmosets are very relaxed in the presence of humans and are very familiar with the experimenter. The subjects were trained in a minimum of 200 trials over 5-10 days.

In the testing trials the slit was replaced by a centrally located hole (0.5 cm diameter) by sliding across a panel (Figure 6.1). This allowed only monocular viewing of the stimulus and the eye used to view was scored. The inner canthi of the left or right eye was visible when a subject looked through the monocular viewing hole and
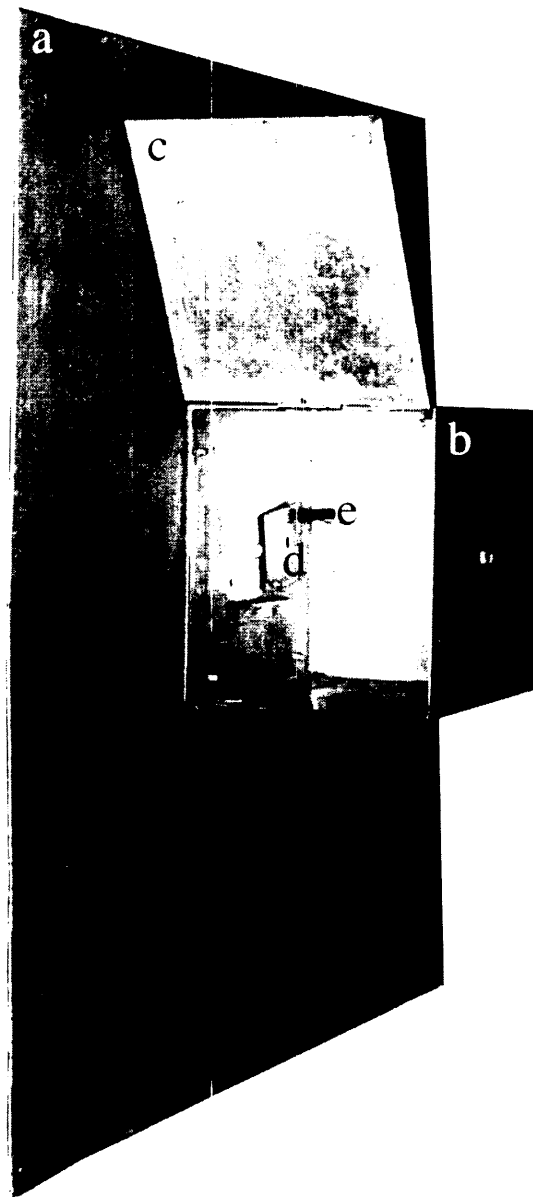
Figure 6.1 Apparatus used to test eye preferences. a. sheet of galvanized steel, b. steel box secured on centre back of sheet, c. hinged door allowing the experimenter to place her hand in the box, d. panel with a centrally located hole which was slid in front of the horizontal slit to allow determination of monocular viewing preferences in testing, e. handle used to slide the panel in front of the horizontal slit. A second slit was located opposite in the front side of the box allowing the experimenter to monitor the eye used by the subjects.

this allowed the experimenter to determine which eye was used to view a stimulus. Monocular eye use was not rewarded. Rewarded trials of binocular eye use were randomly distributed between monocular eye use trials to maintain the marmoset's interest in the task. Subjects were required to display a minimum of two incidences of monocular eye use before a binocular eye use trial was presented. On average four incidences of nonrewarded monocular viewing events were recorded before a rewarded binocular trial was presented. Only one or two rewarded trials occurred between the monocular trials. Rewarding subjects for binocular eye use only aimed to ensure that eye preferences were not conditioned. The scoring criterion for the eye preference tests is detailed in Chapter 2 (p. 61). The data were analyzed using the nonparametric statistical procedures outlined in Chapter 2 (pp. 62-64).

6.2.1 Eye Preference for Viewing Familiar Food at Various Ages

The eye preferences of the marmosets were scored at 3-8 months (15 subjects), 12 months (15 subjects), 15-18 months (15 subjects) and 22 months (21 subjects). At each age subjects were required to view a piece of familiar food (banana). Fifteen subjects were tested at all four ages.

6.2.2 Eye Preferences Tested by Presenting Various Stimuli

On completion of the eye preference tests at the various ages, additional monocular viewing tests were conducted to determine whether the stimulus viewed influenced the eye preferences of the marmosets. Fourteen adult subjects (older than 22 months), 4 males and 10 females, were tested in two test series. In the first test series 4 stimuli were presented, a gold watch, a small mirror held so that the marmoset could see their own eye (6cm x 3cm), a small wooden beetle with moving appendages and a piece of familiar food (banana), the latter being used as a control. For the second test series, 3 stimuli were presented, the experimenter's left hand, a model resembling two rearing snakes ('snake model') and, again, a piece of banana as a control. For both test series the order of presentation of the stimuli was randomized with respect to the testing session (test per day) and for each individual. All stimuli were held in the

experimenter's left hand, positioned centrally in the box, directly in front of the peephole. The time taken to conduct the eye preference tests varied between subjects, stimuli and across days. Five to fifteen scores were collected per day irrespective of the time taken.

For each stimulus the mean duration between incidences of monocular eye use, calculated by dividing the total time taken to conduct the test by the number of monocular eye use scores, was used as an indicator of arousal. Vocalizations indicative of arousal ('tsik', 'egg' and 'ock': Epple, 1968) were also recorded for each testing session. The tsik, egg and ock vocalizations of the common marmoset evoke increased alertness in the group and are emitted when mobbing a potential predator and during hostile encounters between marmosets (Epple, 1968). All of the vocalizations heard in the testing room during a session were recorded. The number of vocalizations calculated for each testing session was divided by the number of individuals in the room and then by the total time taken to conduct the test to produce a standardised vocalization rate (vocalizations/second). Both durations between the events of monocular eye use and the vocalizations made in each testing session were determined from *post hoc* video analyses. Each testing session was recorded using a Sony Hi8 video camera positioned directly behind the experimenter.

6.2.3   Testing for any Effect of the Hand Used by the Experimenter

In the tests outlined above, the experimenter's left hand was placed into the box to hold the stimulus. As it was recognised that this might bias the eye preferences of the marmosets, a new apparatus was constructed with the hinged door on the right, rather than the left. This allowed the experimenter to use the right hand to present the stimulus. For each individual, 50 scores of monocular eye use were collected when the experimenter presented familiar food with the left hand using the original apparatus. Another 50 scores were taken using the new apparatus which allowed right-hand presentation. Twenty subjects were tested (one subject had died, see Chapter 2). Presentation of familiar food with the experimenter's left or right hand was randomized

between testing sessions, using the different apparatus on different days, and for each subject. The percentage left-eye use of the subjects was calculated separately according to whether the experimenter presented food with the left or right hand. The percentage left-eye use and the strength of preferences displayed in each condition were then compared using Wilcoxon signed rank tests.

A period of 6-14 months separated the tests in which the stimulus was held in the experimenter's left hand only and those in which it was presented randomly with the left and right hands. However, it remained possible that the marmosets' eye preferences were conditioned in the first tests, in which the experimenter used the left hand only. To investigate this possibility, the first and second 50 incidences of monocular eye use were compared for all testing sessions.

6.2.4 Relationships between Eye and Hand Preferences

Eye preferences for viewing the various stimuli were correlated (for both direction and strength) with the hand and foot preferences displayed by the marmosets during simple food holding (Chapter 3), during visually guided reaching (Chapter 4) and when leading movement in leaping and landing (Chapter 7). Most correlations compared eye and hand preferences that had been measured at the same age on tests conducted within 4 weeks of one another. However, the eye preference tests and the tests of locomotory behaviours were conducted up to 12 months apart.

6.3   RESULTS

6.3.1 Eye Preference for Viewing Familiar Food at Various Ages

The percentage left-eye use displayed by each individual on each of the preference tests is shown in Figure 6.2. The Friedman statistic, using age as the repeated measure, showed that there was no significant change with age in either percentage left-eye use or the strength of eye preference in the 15 subjects tested at each
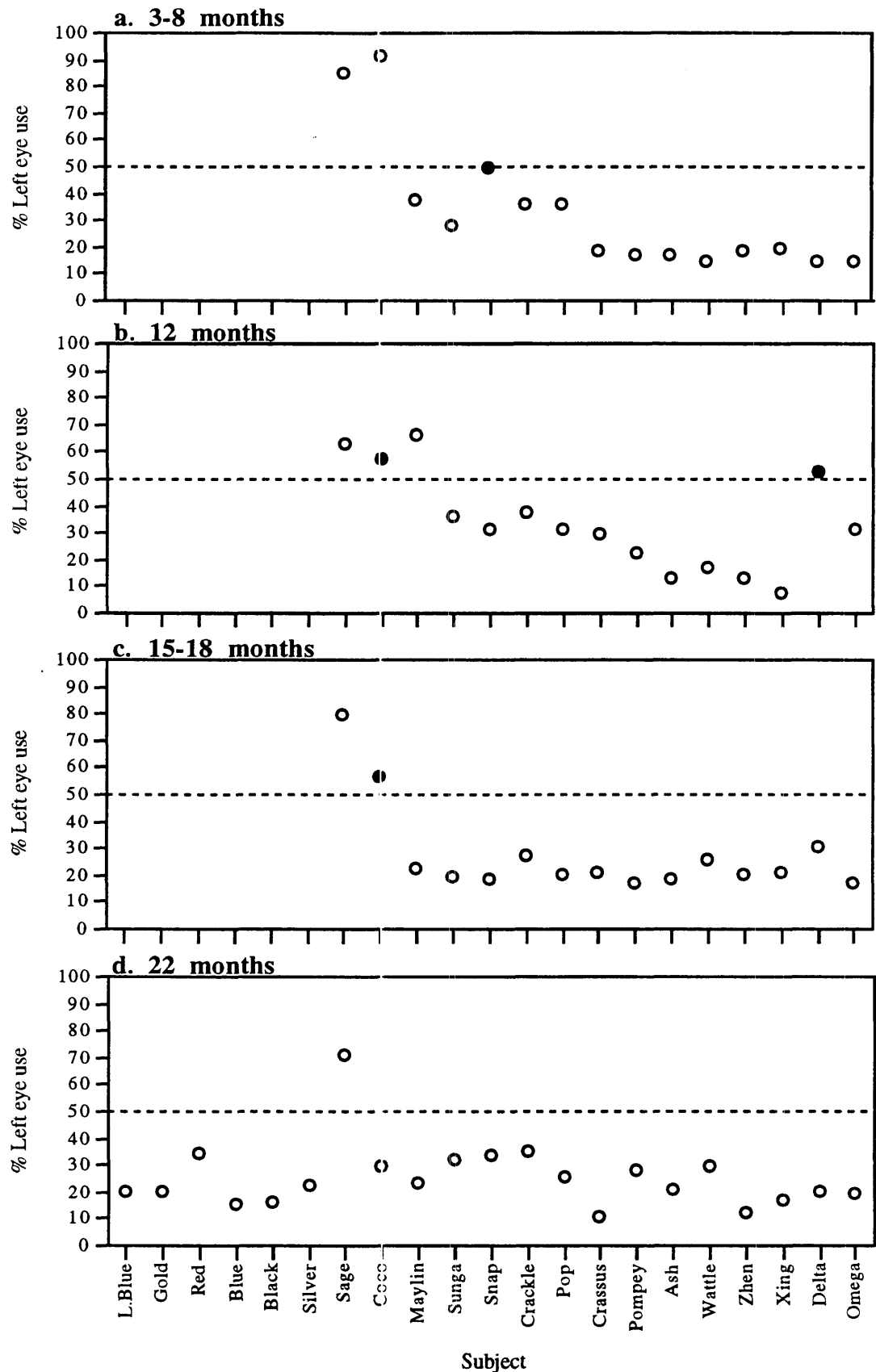
Figure 6.2 Individuals' eye preferences for viewing banana at each age. The percentage left-eye use for each individual when viewing banana is plotted for the four ages at which testing occurred. Subjects are presented on the x axis and percentage left-eye use is shown on the y axis. The white circles (O) indicate a significant eye preference, and the black circles (●) indicate ambipreference. Significance was tested using the z score test. This data is summarized for the group in Figure 6.3.

of the four ages (Friedman statistic; percent left, $F_r = 1.70$, p= 0.64 and strength, $F_r = 1.05$, p=0.79).

As can be seen in Figure 6.3, the marmosets displayed a group bias toward right eyedness for viewing the familiar food at all of the four ages examined. Figure 6.3 summarizes the eye preference data collected for the group and shows the distribution of eye preferences at each age. At 3-8 months of age, 12 of the 15 marmosets tested displayed significant right-eye preferences, two preferred the left eye and one did not display a preference (z score test). Thus, there was a group bias toward right eyedness $(\chi^2$ (2)= 14.8, p≤0.001; Figure 6.3). Most of these subjects maintained these eye preferences at 12 months of age: there was significant right eyedness in the group also at this age $(\chi^2$ (2)= 10.8, p<0.01; Figure 6.3). A significant right-eye bias at the group level was found also at 15-18 months $(\chi^2$ (2)= 19.2, p≤0.001; Figure 6.3), and at 22 months $(\chi^2$ (2)= 15.21 p≤0.001; Figure 6.3). One individual (Coco), displaying a left-eye preference at 3-8 months, had no preference at 12 and 15-18 months and a right-eye preference at 22 months (Figure 6.2). Only one subject (Sage) displayed a consistent left-eye preference across the four age tests (Figure 6.2). Thus, 20 of the 21 subjects tested displayed significant right-eye preferences and only one subject was left-eye preferent at 22 months.

6.3.2 Eye Preferences Tested by Presenting Various Stimuli

Before analyzing the distribution of eye preferences when viewing the various different stimuli, each stimulus was assessed in terms of the degree of arousal it elicited. The data of the two test series were analyzed separately (Figure 6.4). The mean duration between monocular viewing events and the number of aroused vocalizations per second were compared across stimuli within each test series (Figure 6.4).

In the first test series, there were slight but significant differences in the mean interval between monocular viewing events scored for the various visual stimuli (Friedman statistic, $F_r = 11.57$, p=0.009). The marmosets displayed longer intervals between viewing events when the mirror and beetle were presented in comparison to
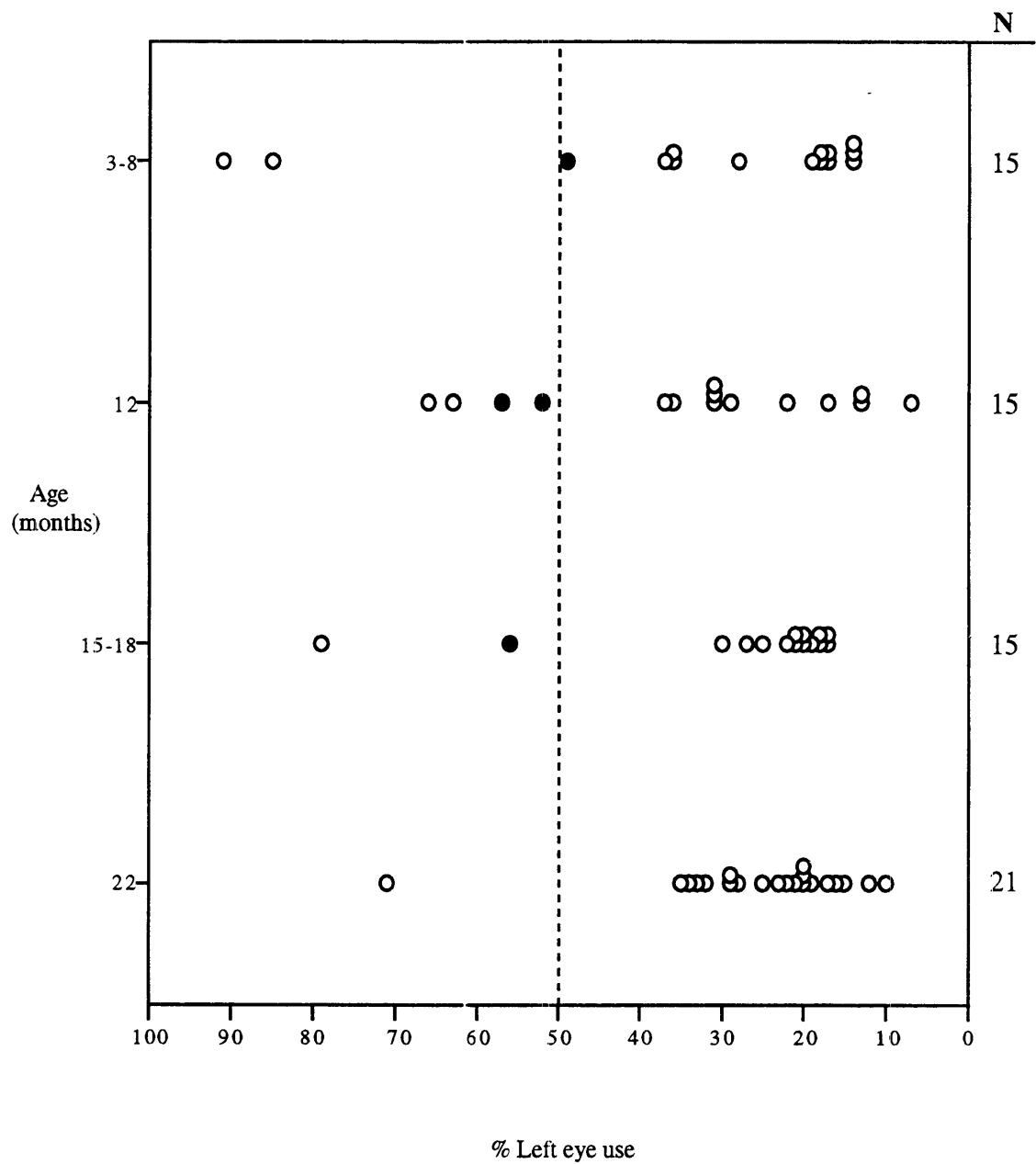
Figure 6.3 The distribution of eye preferences for viewing banana. The percentage left-eye use for each individual when viewing banana is plotted for the four ages at which testing occurred. Ages are depicted on the x axis. The white circles (O) indicate that scores were significant at $p \leq 0.05$, and the black circles (●) represent nonsignificant scores. Significance was tested using the z score test. Note that the x axis has been reversed so that subjects with a left-eye bias are on the left of the reader and those subjects with a right-eye bias are on the right side of the graph.

a. Duration between monocular viewing events

Test Series 1   Test Series 2
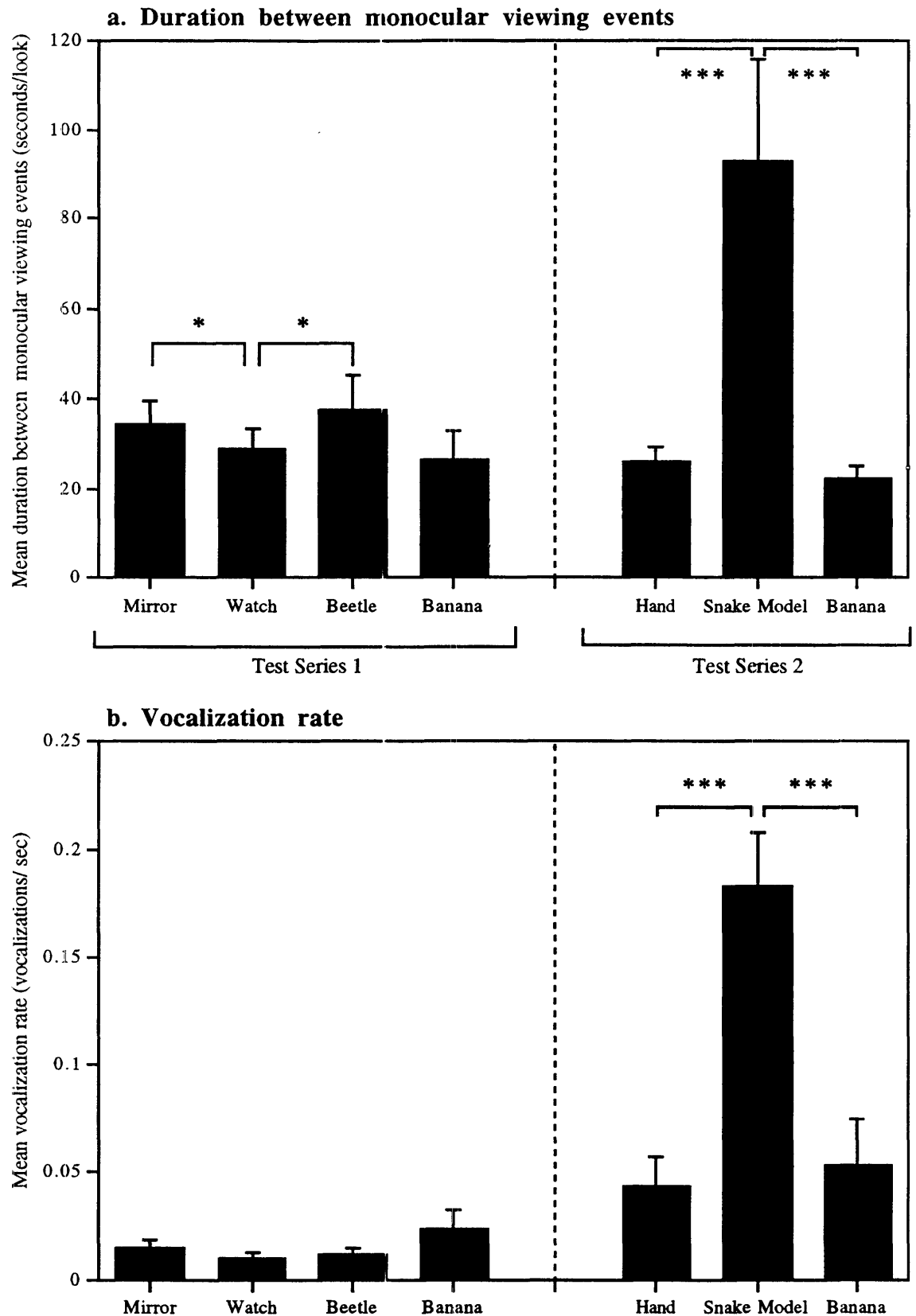
b. Vocalization rate

Figure 6.4 Measurements of arousal when viewing different stimuli. In Figure 6.4a the mean duration between monocular viewing events determined at the group level is plotted. The mean duration of the interval between monocular viewing events was determined for each individual and each stimulus. Individual mean durations between monocular viewing events were used to calculate the group means (±SEM) depicted. The rates of producing tsik, egg and ock vocalizations were determined for each stimulus, and for each individual, and total scores for these vocalizations are presented as group means (±SEM) in Figure 6.4b. * $p \leq 0.05$, *** $p \leq 0.005$.

presentation of the watch (Wilcoxon tests; mirror versus watch, $T^+= 11$, p= 0.04; beetle versus watch, $T^+= 11$, p= 0.02). However, there were no differences in the mean duration between monocular viewing events for the banana compared to the other three stimuli (Wilcoxon tests; banana versus mirror, $T^+= 4$, p= 0.10; banana versus watch, $T^+= 5$, p= 0.18; banana versus beetle, $\Gamma^+= 3$, p= 0.06). There was no effect of stimulus on the vocalization rates found in the first test series (Friedman statistic, $F_r= 1.21$, p= 0.75). Thus, although there might have been slight differences in motivation for viewing the stimuli presented in this series, there were no marked differences in arousal expressed in vocalization rates.

In the second test series, the snake model proved to be greatly arousing (Figures 6.4a and b). Comparison between the stimuli presented in the second test series (experimenter's hand, banana and snake model) revealed significant effects of stimulus on both the mean interval between monocular viewing events and vocalization rate (Friedman statistic, $F_r= 16.71$, p= 0.0002 and $F_r= 11.11$, p= 0.004 respectively). Presentation of the snake model resulted in significantly longer durations between monocular viewing events compared to the banana and hand (Wilcoxon, $T^+= 13, 13$, respectively, p<0.002; Figure 6.4a) and a higher rate of producing aroused vocalizations (Wilcoxon, $T^+= 10, 12$, respectively, p<0.005; Figure 6.4b). No differences were found for either measure of arousal when the hand and banana were presented (Wilcoxon tests, mean duration between monocular viewing events, $T^+= 10$, p= 0.22 and vocalization rate, $T^+= 5$, p= 0.73). It is noted, in Figure 6.4b, that a higher vocalization rate to banana was found in the second test series compared with the first, although it was not significantly higher (Wilcoxon, $T^+= 9$, p= 0.25). It is likely, however, that the rate of producing aroused vocalizations in the second series was influenced by the random presentation of the hand, snake model and banana: arousal induced by viewing of the snake model may have produced carry-over affects that increased the production of aroused vocalizations to the other stimuli, at least at the beginning of each testing session with the hand and banana.

Analysis of the distribution of eye preferences, for viewing the stimuli that did not elicit aroused behaviour (the watch, mirror, wooden beetle, experimenter's hand and the piece of familiar food) demonstrated no differences between the eye preference scores determined for each stimulus (Friedman statistic, $F_r = 8.86$, p= 0.11). There was also no effect of stimulus on the strength of preference displayed by the subjects (Friedman statistic, $F_r = 3.77$, p= 0.58). Of the 14 subjects tested, 12 to 13 displayed significant right-eye preferences for viewing each of these stimuli (see Figure 6.5). For each stimulus there was a significant group bias for right eyedness (binomial: p<0.002, 0.004, 0.006).

When the marmosets were presented with the snake model, 3 subjects displayed significant left-eye preferences, 8 did not display a preference for either eye and 3 had a right-eye preference (Figure 6.5). Thus, no group bias toward left or right eyedness was found when the snake model was viewed (binomial test: p= 0.69). An overall comparison of the eye preferences displayed when viewing the various stimuli showed that significant differences occurred between stimuli (Friedman statistic, $F_r = 31.99$, p<0.0001). Subsequent paired comparisons, using Wilcoxon signed rank tests, between the eye preferences displayed when viewing the snake model and the other stimuli revealed significant differences in all cases (Wilcoxon tests, $T^+ = 14$, 13, 13, 12,14, respectively, p<0.0005 in all cases). This means that when the snake model was presented there was a significant change from right eyedness to no significant eye bias in the group.

6.3.3 Testing for any Effect of the Hand Used by the Experimenter

The hand used by the experimenter to present the reward did not affect the eye preferences of the marmosets. There was no difference between percentage left-eye use or the strength of preference displayed by the subjects when the experimenter used the left versus the right hand (Wilcoxon tests, percent left, $T^+ = 9$, p= 0.79 and strength, $T^+ = 10$, p= 0.98). As can be seen in Figure 6.6, there was a strong correlation between the preferences displayed when the left hand versus the right hand was used (Spearman
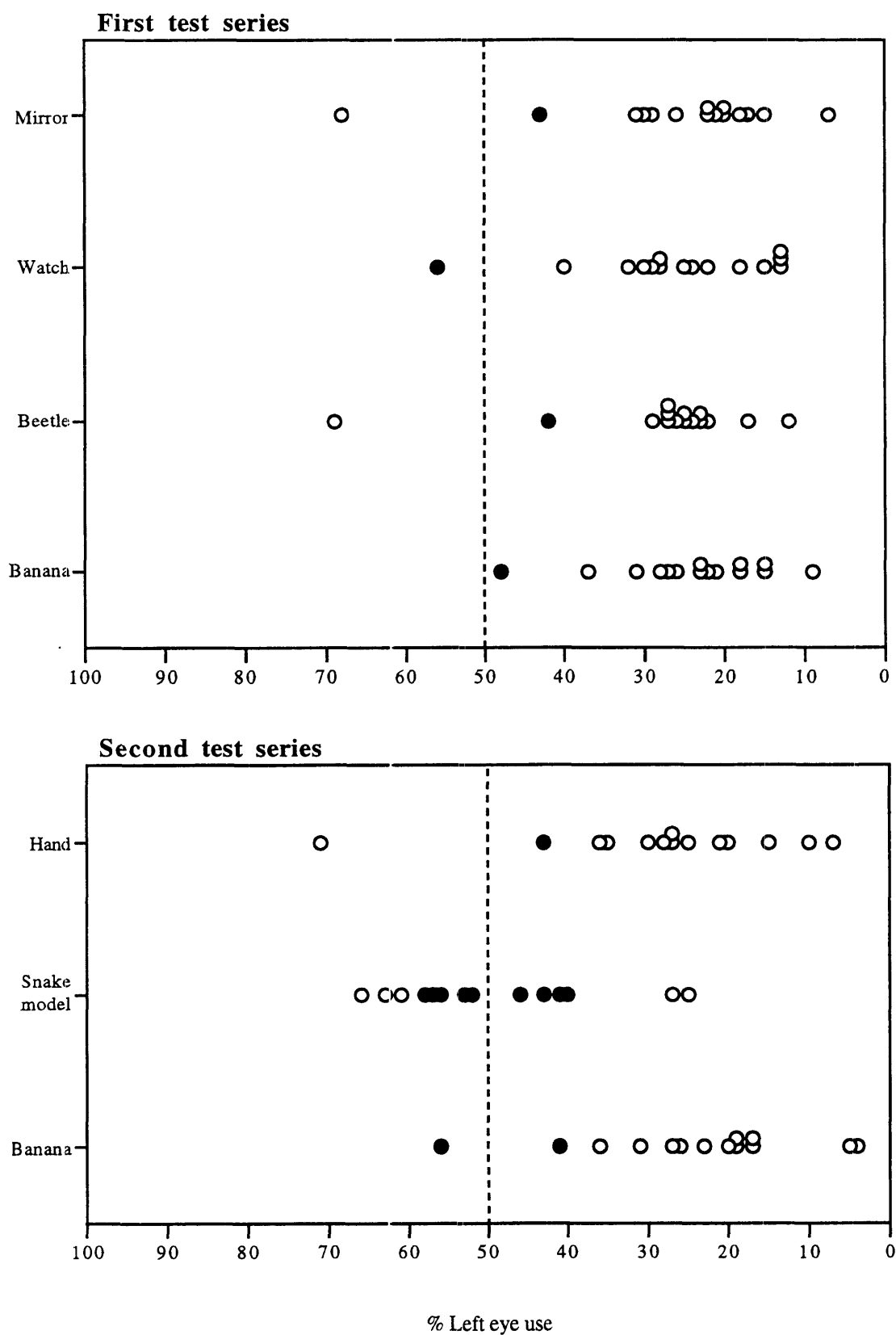
Figure 6.5 **Distribution of eye preferences when viewing different stimuli.** The percentage of left-eye use for viewing a variety of stimuli is plotted on the x axis for each individual (O). Stimuli are plotted on the y axis. The white circles (O) indicate significant scores at p≤0.05, and the black circles (●) represent nonsignificant scores. Note the right eyedness for all stimuli except the snake model.
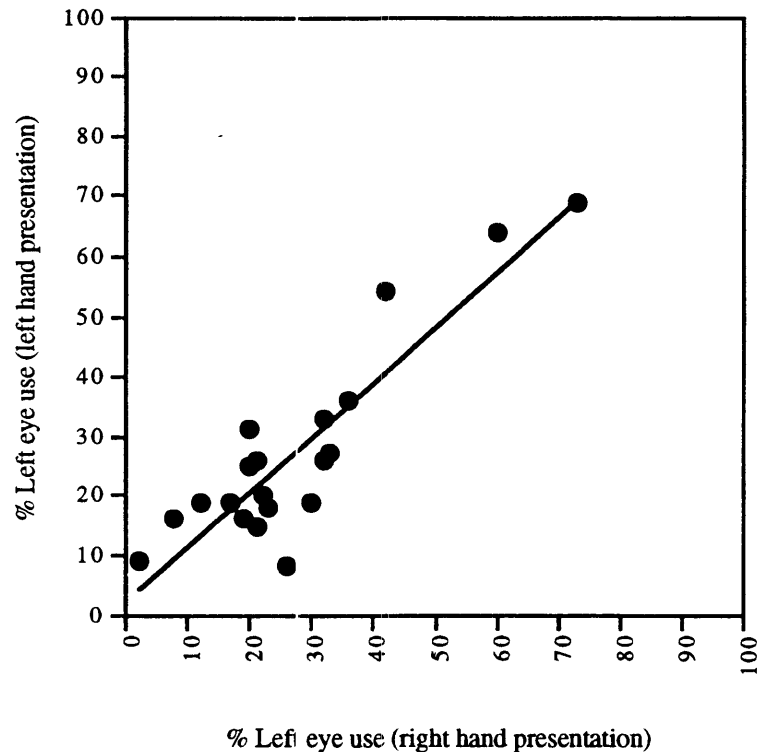
Figure 6.6 Eye preferences and the hand use of the experimenter. The percentage left-eye use displayed by the subjects when the experimenter presented the familiar food with the left (y axis) or right (x axis) hand were correlated. There was a strong positive correlation between the eye preferences displayed in the two conditions.

rank, r_s= 0.72, p=0.002). Therefore, the lateral bias of the experimenter and testing apparatus did not affect the eye preferences to any great extent.

The data were further investigated for possible effects of learning on eye preferences. Comparison was made between the percent left-eye use displayed when viewing the banana in the first 50 and the last 50 scores of each test (Figure 6.7a). Individual Wilcoxon signed ranks tests revealed no significant differences between percent left-eye use in the first and last 50 scores at 3-8, 12 and 15-18 (Wilcoxon tests, T^+= 7, 6, 4, respectively, p= 0.58, 0.78, 0.82), but there was a tendency for a decrease in percent left-eye use in the first 50 scores at 22 months (Wilcoxon, T^+= 5, p= 0.06). If this represents within test learning, it is a minor effect as the mean percent left-eye
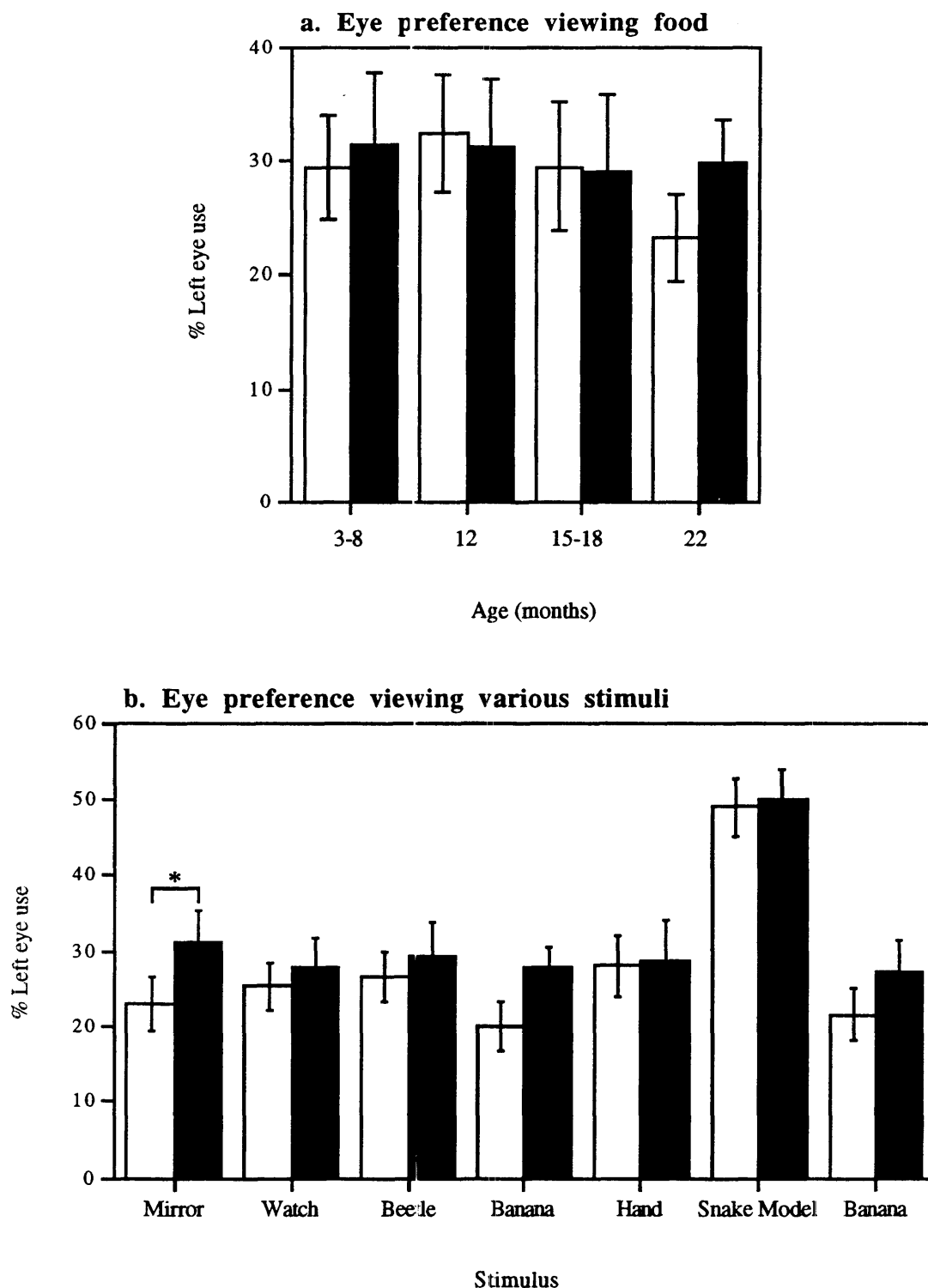
a. Eye preference viewing food

b. Eye preference viewing various stimuli

Figure 6.7 Comparison between the percent left-eye use in the first and last 50 incidences of monocular eye use. The white columns (□) represent the mean percent left-eye use (±SEM) for the first 50 incidences of monocular eye use in each test and the black columns (■) the mean percent of left-eye use (±SEM) in the last 50 scores of each test. In Figure 6.7a, the ages at which the eye preference tests for viewing banana were conducted are presented on the x axis and the percentage left-eye use is on the y axis. Figure 6.7b compares between percent left-eye use in the first and last 50 incidences of monocular eye use when the marmosets viewed the various stimuli. * indicates that p=0.02.

use changed by only 5% (Figure 6.7a). The first and last 50 scores were compared for all of the other stimuli and for the control tests with banana (Figure 6.7b). There were no significant differences between percentage left-eye use in the first and last 50 scores for the watch, beetle, hand or statue (Wilcoxon, p>0.22 in all cases). There was a significant difference between the first and second 50 scores when subjects viewed the mirror (Wilcoxon, $T^+= 2$, p= 0.02) but, again, this is a minor change of approximately 5%. There was also a tendency, although not significant, for subjects to display a slight increase in left-eye use in the last 50 scores when viewing banana in both test series (Wilcoxon, $T^+= 4$, 4, respectively, p= 0.06, 0.08).

6.3.4   Relationship Between Eye and Hand Preferences

Eye preferences and hand preferences for simple food holding

All comparisons between eye preferences when viewing banana and hand preferences for simple food holding were made using tests conducted at approximately the same age. There was no relationship between hand and eye preferences at 5-8 months (Spearman rank, $r_s= 0.60$, p= 0.14).

As the data were clustered bimodally after 10-12 months of age, correlations between percentage left-eye preference and percentage left-hand use for simple food holding were determined separately for left and right-handed subjects at the latter ages. The data for the right-handed subgroup at 10-12 months was clustered with respect to eye preferences, with three individuals displaying strong right-eye preferences and 3 displaying 50-70% left-eye use. Thus, these data could not be correlated. There was a tendency for a correlation between eye and hand preferences in the left-handed subgroup, but it was not significant at the stringent level of p≤0.01 set prior to commencing these tests (Spearman rank, $r_s= 0.70$, p= 0.05; Figure 6.8). At 15-18 and 22 months of age there was no evidence of a relationship between hand and eye preferences in either the left or right-handed subgroup (Spearman rank, p≥0.20 in all cases).

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60

50

40

30

20

10

0

% Left eye use (10-12 mths)

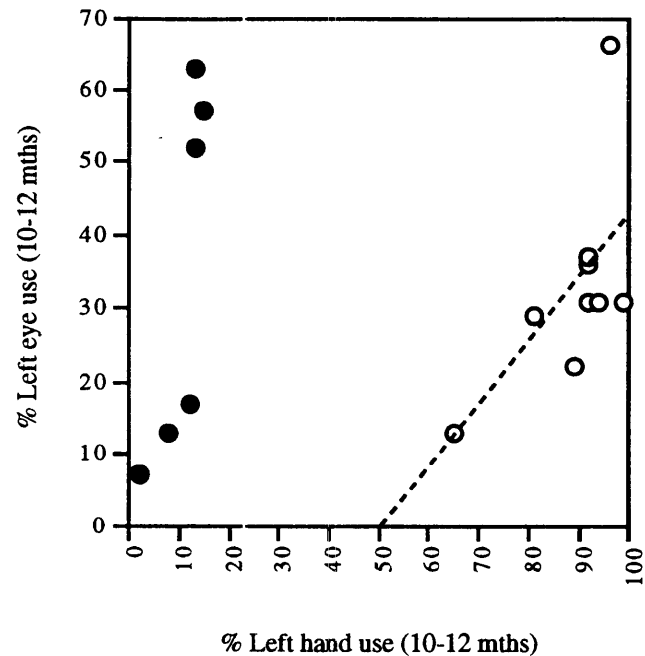0 10 20 30 40 50 60 70 80 90 100

% Left hand use (10-12 mths)

Figure 6.8 Relationship between hand and eye preferences at 10-12 months. As the data were clustered, separate correlations were calculated for the left and right-hand preferent subgroups. There was a tendency for a positive correlation in the left-hand preferent subgroup (O), although it was not significant. Note that there was further clustering of data in the right-hand preferent subgroup (●) and hand and eye preferences were not correlated.

There was also no significant relationship between percentage left-eye use when viewing the mirror, watch, beetle, experimenter's hand or the snake model and percentage left-hand use for simple food holding at 22 months (Spearman rank, p>0.30 in all cases).

There was an indication of a negative correlation between the strength of eye preferences when viewing banana and hand preferences for simple food holding at 5-8 months of age, but it was not quite significant (Spearman rank, r_s= -0.62, p= 0.02; Figure 6.9). No evidence of any relationship was found between the strength of eye preferences for viewing banana and hand preferences for simple food holding at the other ages (Spearman rank, p>0.05 in all cases). Nor were the strength of eye and hand preferences related when the subjects viewed stimuli other than familiar food (Spearman rank, p>0.05 in all cases).
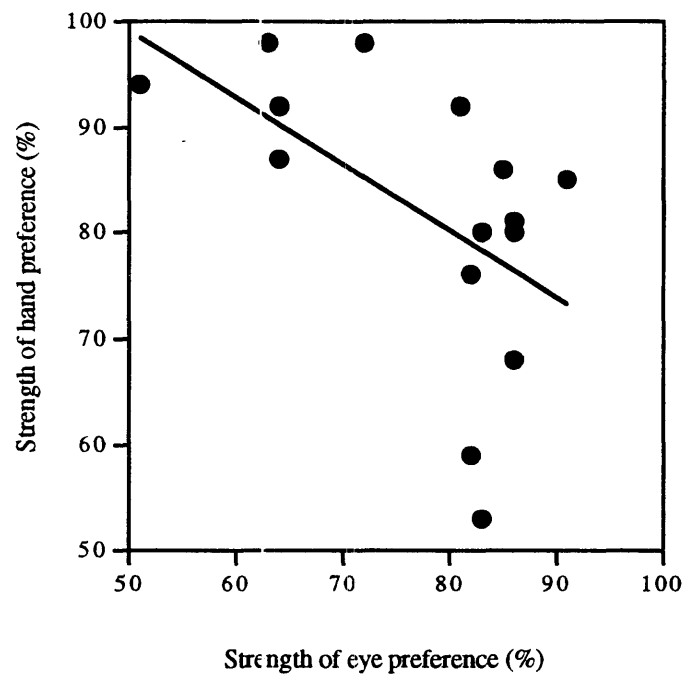
Strength of eye preference (%)

Figure 6.9 Relationship between the strength of hand and eye preferences at 5-8 months. The strength of eye preferences displayed by the subjects at 5-8 months is shown on the y axis, and the strength of hand preferences for simple food holding at the same age is represented on the x axis. Although there was a tendency for a negative relationship between these the strength of preferences displayed for eye and hand use, it was not quite significant.

Eye preferences and hand preferences for visually guided reaching

It was possible that eye preferences may have been related to hand preferences on tasks that demanded visual guidance while reaching. However, there was no evidence of a relationship between eye preference at 10-12 months and visuospatial reaching preferences displayed by the subjects when reaching from a tripedal posture for food in the bowl (Spearman rank, $r_s = 0.40$, p= 0.17). Similarly, the preferences displayed on the rotating disc tasks were not correlated with eye preferences for viewing banana at 15-18 months (Spearman rank, 3.5 rev./min., $r_s = 0.20$, p= 0.49 and 7 rev./min., $r_s = -0.20$, p= 0.64).

As there was clustering of data, when eye preferences were plotted against hand preferences for taking food from a place and grasping a string, the subjects were divided into left and right-handed subgroups. Separate Spearman rank correlations were

computed for each group. The preferences displayed when reaching for food on the plate were not significantly correlated with eye preferences in either the left or right-handed group (Spearman rank; left, $r_s = 0.00$, p= 0.95; right, $r_s = -0.40$, p= 0.39). There was also no relationship between eye preferences and hand preferences when the marmosets were required to grasp the swinging string while maintaining a suspended posture (Spearman rank; left, $r_s = 0.20$, p= 0.64; right, $r_s = 0.50$, p= 0.32). Percentage left-eye use for viewing the nonfood stimuli was also not significantly related to percentage left-hand use displayed on any of the visuospatial reaching tasks (Spearman rank, p>0.05 in all cases).

There were no significant relationships between the strength of eye preferences for viewing familiar food, or the nonfood stimuli, and the strength of hand preferences expressed on any of the visuospatial reaching tasks (Spearman rank, p>0.05 in all cases).

Eye preferences and leading-limb preferences in leaping and landing

It was considered possible that eye preferences may be influenced by strength asymmetries between the two sides of the body, causing subjects to lean while looking through the viewing hole and thus biasing responses. To investigate this possibility, eye preferences were correlated with the leading-hand and leading-foot preferences found in leaping and landing. There was no significant correlation between percentage left-hand use or percentage left-foot use in the initiation of leaping and percentage left-eye use when viewing familiar food at 22 months (Spearman rank; hand, $r_s = -0.20$, p= 0.42; foot, $r_s = -0.40$, p= 0.13). Percentage left-hand and percentage left-foot preferences in leaping were also not related to eye preferences displayed for viewing the nonfood stimuli (Spearman rank, r_s between -0.40 and 0.00, p>0.11 in all cases).

There was no correlation between percentage left-hand use or percentage left-foot use in landing and percentage left-eye use when viewing familiar food at 22 months (Spearman rank; hand, $r_s = -0.20$, p= 0.50; foot, $r_s = -0.20$, p= 0.45). Percentage left-hand and percentage left-foot preferences in landing were also not correlated with

eye preferences displayed for viewing the nonfood stimuli (Spearman rank, r_s between -0.45 and 0.08, $p \geq 0.11$ in all cases).

The strength of hand and foot preferences displayed for leaping and landing were not related to the strength of eye preferences for viewing banana (22 months) or for viewing other nonfood stimuli (Spearman rank, r_s between -0.50 and 0.50, $p > 0.05$ in all cases).

6.4   DISCUSSION

Twenty of the 21 marmosets tested displayed significant right-eye preferences for viewing a piece of familiar food (banana) held in the experimenter's hand. The remaining subject displayed a significant left-eye preference. The finding of a right-eye bias within the marmoset group concurs with the findings of Kounin (1938) for capuchins, but contrasts with those of Westergaard and Suomi (1996b), who reported a symmetrical distribution of eye preferences for capuchins. The results are also inconsistent with the results of McFerran (1992), who reported no eye preferences for most tamarins, and of the seven subjects with an eye preference, six preferred the left eye.

As McFerran (1992) tested the tamarins in a group situation, competition between subjects as they tried to look through the monocular viewing hole may have increased arousal. The experiments reported in this chapter suggest that increased arousal levels may explain the different result in McFerran's study, as it was found that viewing an arousing stimulus caused the marmosets to change their right-eye preference for no preference or ambipreference. This occurred when they were presented with the model resembling two rearing snakes. The ambipreference at the group level when viewing the fear inducing stimulus may reflect a conflict between use of the preferred eye and use of left eye with better quality input to the right hemisphere. This may occur because the right hemisphere is dominant for the production of emotional responses. There is evidence of right hemisphere dominance for the mediation of emotional responses in many species. For example, Deckel (1995) has found a left-eye bias for

the mediation of aggressive behaviours in the lizard (*Anolis*) and right hemisphere control for negative emotional responses has been shown in chicks (Andrew and Brennan, 1983; Phillips and Youngren, 1986), rats (Garbonati et al. 1983), rhesus macaques (Hauser, 1993), gelada baboons (Casperd and Dunbar, 1996) and humans (Sackeim et al. 1978). Activation of the right hemisphere in situations that increase arousal may mask or even reverse eye preference.

Overall, the results of the present study demonstrate that, as for *Otolemur garnettii* (Rogers et al. 1994; Ward and Cantalupo, 1997), the eye preference of marmosets depends on the stimulus being viewed and/or the state of arousal. The demonstrated effect of arousal on this form of lateralization, emphasizes that caution is required when designing experimental studies of lateralization, and it also shows the importance of maintaining a stable environment in the daily care and maintenance of experimental subjects. These results also suggest that studies of eye preference should include measures of arousal (e.g. vocalizations).

The eye preferences reported for the marmosets are opposite to those found for *Otolemur garnettii* (Rogers et al. 1994; Ward and Cantalupo, 1997). Whereas marmosets displayed right-eye preferences for viewing nonarousing stimuli and ambipreference with increasing arousal, the bushbabies displayed left-eye preferences for viewing neutral stimuli, and ambipreference when aroused. The opposite eye preferences of the marmosets, compared with the prosimian species, may relate to evolutionary adaptations for their respective diurnal and nocturnal environments. As Rogers et al. (1994) suggest, eye preferences may have shifted throughout the course of primate evolution. There is some evidence that the asymmetrical distribution of ganglion cells, with densities higher in the nasal than the temporal hemiretina, reported for marmosets and other diurnal primates may not be present in prosimians (DeBruyn et al. 1980). In *Galago sengalensis*, a prosimian species closely related to *Otolemur garnettii*, the ganglion cell distribution appears to be marginally biased towards a slower decline in density in the temporal, compared to the nasal, hemiretina (DeBruyn et al. 1980). In the nocturnal prosimian species, there may be a slightly better cortical

representation in the ipsilateral hemisphere, whereas in marmosets there would be a stronger cortical representation in the hemisphere contralateral to the viewing eye (Rowe, 1991; Weisz et al. 1994). Thus, the highest image quality would be transmitted to the left hemisphere by viewing with the left eye by *Otolemur garnettii* and with the right eye by *Callithrix jacchus*. This retinal organization may cause opposite eye preferences in diurnal and nocturnal species. This hypothesis could be tested by determining eye preferences in more nocturnal and diurnal species.

The specialization of the right hemisphere for processing arousing stimuli appears to have evolved very early, in fact there is evidence that fish have a right hemisphere specialization for the control of negative emotional responses. Cantalupo et al. (1995) suggested that the teleost fish (*Girardinus falcatus*) may display complementary hemispheric specializations when categorising threatening and nonthreatening stimuli. They found a population bias for turning right to escape when a simulated predator was first presented. The fish viewed the predator with the left eye while turning right to escape. However, on subsequent presentations there was a shift to leftward turning, viewing the predator with the right eye. They suggested that these asymmetries may reflect an inborn right hemisphere bias for responding to frightening stimuli and a left hemisphere bias for categorization of neutral stimuli (Cantalupo et al. 1995). Left hemisphere specialization for categorization has been found in chicks (Andrew, 1991) and in humans (Gross, 1972; Bradshaw et al. 1977; Jones, 1979; Sergent et al. 1992). The differential eye preferences displayed by the marmosets appear to indicate that they have the same directional specializations as present in teleost fish and chicks. Categorization of stimuli may be performed by the left hemisphere, producing right-eye dominance so that the more detailed cortical representation is transmitted to the left hemisphere. Use of the left eye for monocular viewing would, therefore, produce the more detailed cortical representation in the right hemisphere which is specialized for emotional response. Equal use of both eyes when viewing an arousing stimulus could allow both hemispheres to receive direct and rapid input of information (i.e. not via the corpus callosum), and thus the separate

specializations would be able to contribute to assessing a threatening situation.

In addition to the influence of arousal on eye preference, the influences (on lateralized eye use) of age of the subjects and manual bias of the experimenter were examined. Age did not affect eye preferences. In addition, the eye preferences of the subjects were not affected by which hand the experimenter used: the marmosets displayed the same eye preferences when the experimenter used the left or right hand. It is unlikely that the right-eye preferences of the marmosets were experimentally induced early in the testing sessions in which the experimenter presented the stimulus using her left hand, as there was no indication of a change in eye preference for viewing the banana with age (i.e. successive testing) and no evidence of within-session learning effects on eye preference. Out of eleven cases analyzed, in only two cases was there a significant, or near significant, but small (5%) increase in percentage left-eye use from first to last 50 scores in a test. Any minor changes in eye preference, when they do occur, might be a result of changed arousal rather than learning.

The eye preferences of the marmosets did not correlate with hand preferences at any age. These results concur with most findings for other nonhuman primate species, including bushbabies (Rogers et al. 1994), pig-tailed macaques (Cole, 1957), rhesus macaques (Kruper et al. 1966) and capuchins (Westergaard and Suomi, 1996b), but do not concur with evidence that suggests that there is a relationship between eye preference and hand preference in humans (Harris and Lovegrove, 1984; Metalis and Niemic, 1984; Brown and Taylor, 1988). Only one study with a nonhuman primate species, *Otolemur garnettii*, has found a relationship between eye and hand preferences (Ward and Cantalupo, 1997). Ward and Cantalupo (1997) found a significant positive correlation between eye preference and hand preference when bushbabies reached from a tripedal posture. On this task, the prosimians had to take a piece of food from inside a jar with one hand. However, the presence of a relationship between these functions in bushbabies depended on the consistency of hand preferences displayed when reaching from quadrupedal and bipedal postures. Significant correlation was present only for subjects that displayed a shift in hand preferences between the two postural conditions

('shifters'). Moreover, Ward and Cantalupo (1997) suggested that this relationship may have been due to task requirements when measuring hand preferences in this study. They observed that the bushbabies looked into the jar before reaching into it to take a mealworm and postulated that this viewing behaviour may have caused postural tilt in the subjects before reaching and subsequently influenced the hand used to reach. They argued that sensory/perceptual lateralization is secondary to motoric lateralization and it is possible that posture influenced eye use for looking into the jar and also the eye preferred in the monocular viewing tests (Ward and Cantalupo, 1997). The finding of this correlation in the bushbabies does raise the question as to whether eye preferences reflect motoric or perceptual lateralizations.

Ward and Cantalupo (1997) also found a relationship between the strength of eye preferences and strength of rotational behaviour in bushbabies *(Otolemur garnettii)*, but no evidence of a relationship between the direction of the preferences displayed for the two functions. Significant correlation between the strength of eye preferences and the strength of rotational behaviour, however, was found only in subjects that displayed consistent hand preferences when reaching from tripedal compared to bipedal postures ('nonshifters'; Ward and Cantalupo, 1997). Westergaard and Suomi (1996b) reported that rotational behaviour and eye preference may be related in capuchins *(Cebus apella)* also. Rather than finding a correlation between the strength of preferences displayed for the two functions, as found for the bushbabies, they found a significant positive correlation between percentage right-eye use when looking at food and the strength of biases for rotational behaviour (Westergaard and Suomi, 1996b). In the capuchins it appears that subjects displaying greater left-eye use are more likely to lack a directional bias for rotational behaviour. As the underlying significance of rotational behaviour has not yet been established it cannot be proposed that its relationship with eye preference reflects interdependence of a motor and a perceptual function in nonhuman primates. Some authors have postulated that rotational behaviour is related to other perceptual processes, such as spatial processing in rats (Glick and Ross, 1981). Others have suggested that it may be caused by eye dominance (Ridgeway, 1986; Rogers and

Bradshaw, 1996), and yet others have proposed a motoric explanation for this behaviour (Ward and Cantalupo, 1997). The mechanism underlying rotational behaviour needs to be investigated further in order to clarify the nature of its relationship with eye preference.

Although eye preferences were not correlated with hand preferences for simple food holding, it remained possible that hand preferences measured for visuospatial reaching or for the initiation of leaping and landing might correlate with eye preferences. However, there was no evidence of a relationship between eye preferences and hand preferences measured in the various visuospatial reaching tasks, requiring different amounts of postural control (Chapter 4), or during locomotory activities (Chapter 5). In Chapter 5 it was proposed that the hand that contacts the platform first in landing would be stronger, and there was evidence of a tendency for more subjects to display right leading-hand preferences in landing. Also, more subjects displayed a tendency to leap with the left foot leaving the platform last, providing most of the force for propulsion. Thus, the left leg tended to be stronger in the marmosets. However, no relationship was found between eye preferences and hand or foot preferences in leaping or landing. In addition, the eye preferences found on the monocular viewing tests were significantly stronger than the leading-hand and leading-foot preferences displayed by the same subjects during leaping and landing. The posture assumed by the marmosets in the tests of monocular viewing would have distributed their weight evenly across the forelimbs and the hindlimbs also. As the marmosets assumed a seated posture and pressed against the wire mesh with the two hands, a stronger left leg would have been balanced by the stronger right arm in this posture. On the basis of these results, it is unlikely that the posture adopted during viewing through the peephole determined eye preference.

The absence of correlation between eye preferences and hand and foot preferences, measured on a variety of tasks, in the marmoset suggests that these forms of lateralization depend on different mechanisms and that eye preferences are not likely to be caused by lateralized motor control or vice versa. The lack of a group bias on any

of the hand use tasks contrasts with the strong right eyedness found for the marmoset group. Thus, it is likely that eye preferences in marmosets primarily reflect perceptual asymmetries rather than motor biases. It is possible, however, that the degree to which perceptual and motor asymmetries are related may depend on the task constraints (e.g. Ward and Cantalupo, 1997), and on the processing strategies that are used by a species, for example in foraging, as proposed in Chapter 3.

6.5   SUMMARY

The strong group bias for right eyedness when viewing nonarousing stimuli indicates that marmosets have hemispheric specialization. The hemispheric specialization that is manifest in eyedness does not appear to be related to asymmetries of limb control or to asymmetries of strength between the two sides of the body. Thus, eye preferences in marmosets may represent an independent form of hemispheric specialization that needs to be explained in its own right, not as a consequence of postural demands or hand preferences. Also, the strong group bias for eyedness was not affected by variables such as age, practice and the lateral bias of the experimenter.

It is proposed that right eyedness in marmosets when viewing nonarousing stimuli might be indicative of underlying perceptual specializations, with a detailed cortical image being sent to the left hemisphere. The change from right-eye preferences to no eye preference with arousal might be due to increased use of the right hemisphere, which is specialized for the control of emotional responses in other species. Although marmosets do not display hemispheric specialization for the control of motor functions, they do appear to have hemispheric specializations for perceptual processing.