CHAPTER 3

THE DEVELOPMENT OF HAND PREFERENCES FOR SIMPLE FOOD HOLDING

3.1 INTRODUCTION

The experiments reported in this chapter examined the development and distribution of hand preferences for simple food holding in marmosets of the colony at the University of New England. Previous studies suggest that at a group level marmosets display a symmetrical distribution of hand preferences for taking and holding food (Box, 1977a; Matoba et al. 1991; Guerra and DaSilva, 1996). There were a total of 86 marmosets in these three studies. It is noted that Box (1977a) and Matoba et al. (1991) reported a tendency toward increased left-hand preferences for taking and holding food in marmosets, but no significant group bias was found in either study. Should these results be confirmed with the addition of 21 more subjects in this study, the absence of handedness during feeding in *Callithrix jacchus* would contrast with the evidence for left handedness in several prosimian species (Ward et al. 1990) and with right handedness in *Saguinus oedipus*, a closely related tamarin species (Diamond and McGrew, 1994; King, 1995).

The present study also investigated the effects of age, posture, gender and experience on hand preferences. The effects of age and posture on hand preferences have not been investigated previously in marmosets, although both variables have been shown to influence the distribution of hand preferences in other nonhuman primates (MacNeilage et al. 1987; Fagot and Vauclair, 1991). For example, in various species of lemur it has been shown that the proportion of right-hand preferent subjects increases with age (Ward et al. 1990). It has also been found that capuchins display handedness when reaching from bipedal postures but not when reaching for food from tripedal postures (Westergaard et al. 1997). Although these variables have been demonstrated to affect hand preferences in some primate species, the effects are not always replicated across studies and certainly cannot be generalised across species (see Chapter 1). Thus, it was considered necessary to examine the effects of both age and posture on hand preferences for simple food holding in marmosets.

Matoba et al. (1991) have presented evidence of a maternal effect on the hand preferences of juvenile marmosets. They found a significant positive correlation between hand preferences displayed by juvenile marmosets for taking food and the hand preferences of their mothers, but not their fathers (Matoba et al. 1991). Reanalysis of the data presented by Matoba et al. (1991) indicated that gender does not affect hand preferences in this species (see Chapter 1, p. 5). Therefore, it would appear that the maternal effect on hand preference affects male and female subjects similarly. Whether maternal effects on hand preference are genetic or represent learning in the infant marmosets is unknown. In the present study, the influences that parental care and the family group environment had on the development of hand preferences in marmosets were considered.

Most studies that have investigated the development of hand preferences in nonhuman primates have used cross-sectional techniques to elucidate the effects of age. Cross-sectional data are collected from different individuals at different ages (Martin and Bateson, 1993). A criticism of the cross-sectional approach is that it does not take into account individual differences and the influence of experience on the development of hand preferences. Thus, it is preferable to investigate the influence of age and the effects of other variables on the development of hand preferences using a longitudinal design. The latter involves scoring the same individuals at various ages. In addition, several variables may be measured to elucidate their effects on the development of hand preferences using each individual as its own control (Martin and Bateson, 1993).

Only a few studies have examined the ontogeny of lateralization in nonhuman primates using longitudinal techniques. Thus, another of the aims of the experiments reported in this chapter was to determine the development of hand preferences for simple food holding and the development of preferred feeding postures in marmosets using longitudinal sampling. The hand preferences of 15 of the subjects were scored at all ages and their data were analyzed longitudinally. Data were also collected for the 6 founding members of the colony but their hand preferences could not be scored at all ages and could not be analyzed longitudinally (Chapter 2, pp. 46-48).

3.2 METHODS

3.2.1 Development of Unimanual Hand Use and Hand Preferences for Simple Food Holding

The hand preferences during feeding of 15 marmosets were assessed from 0-2 to 22 months of age. The data were collected when the individuals were infants (0-2 months), juveniles (5-8 months), subadults (10-12 months, 14 months, 15-18 months) and adults (22 months). Three stages of subadulthood were selected for testing as they represent significant periods in the development of sexual and social maturity in the marmoset (Clarke, 1994; see Chapter 2, p. 51).

The percentage of bimanual food holding was calculated from the total simple food holding scores (bimanual and unimanual) collected for each subject at each age. The procedure for scoring unimanual and bimanual food holding acts are described below. The percentage of bimanual food holding at the various ages was compared. Individual hand preferences for use of the left or right hand and the strength of these preferences for simple food holding were calculated using the scores for unimanual hand use only. Percentage left-hand use and the strength of unimanual hand preferences displayed at each age were then compared. The distribution of hand preferences displayed by the 15 subjects was analyzed at each age. The nonparametric statistical procedures used to analyze the data are detailed in Chapter 2 (pp. 62-64).

Bimanual versus unimanual hand use

The hand use of the subjects during feeding was scored as unimanual (left or right) or bimanual. Bimanual hand use was scored when both hands were used together to take food to the mouth, whereas unimanual hand use was scored when only one hand was used to hold the food and take it to the mouth (Figure 3.1). Repeated taking of the same piece of food to the mouth while maintaining a stationary posture and without dropping the food was scored as only one act. When a subject moved carrying food in the mouth (without using a hand) and then stopped, took the food with one or both hands and resumed eating, hand use was scored. During incidences of unimanual hand use in which a subject switched hands while eating, a score was taken for both the left and right hand. One hundred to 130 incidences of unimanual hand use were recorded for each individual over a minimum period of 8 and a maximum of 20 days. The minimum of 100 scores of unimanual hand use applied to all ages except 0-2 months as discussed below. All incidences of bimanual hand use observed during the testing sessions were recorded.

Data on the hand use of the infants (0-2 months) for simple food holding were collected as part of a larger study involving 8 different observers, including the author of the thesis. The behaviour of the infants was recorded in four sessions of 30 minutes duration per day for the first month after birth, and two half hourly sessions per day in the second month after birth. In the first month, two of the sessions followed presentation of food and in the second month both sessions followed presentation of food. Observers were instructed to note whether food was held in the hand and taken to the mouth and to score the preferred hand for simple food holding using the procedure described above. The number of incidences of unimanual hand use observed varied between infant marmosets, ranging from a minimum of 12 to a maximum of 67 scores. However, the significance of preference scores was only assessed for infants that displayed 15 or more unimanual hand use acts. Two infants displayed 10-15 incidences of unimanual hand use for simple food holding, 10 infants displayed 15-50 incidences of unimanual hand use and 3 infants displayed more than 50 incidences of unimanual

a. Tripedal

b. Seated

c. Suspended

d. Bimanual

Figure 3.1 Simple food holding The photographs illustrate the methods used to categorize simple food holding scores. Figure 3.1a, b and c show unimanual food holding acts in a tripedal, seated and suspended posture respectively. In Figure 3.1d, Maylin is holding a peanut bimanually and taking it to the mouth. All incidences of bimanual food holding were recorded when the marmosets adopted a seated posture.

hand use from 0-2 months. The limited number of unimanual scores during this period was partly due to the predominance of bimanual hand use. Hand use for simple food holding begins to develop in marmosets at only 4 weeks of age (Box, 1975; Missler et al. 1992; Yamamoto, 1993), and in the colony at the University of New England no cases of simple food holding by the infant marmosets were observed in the first 3 weeks of life. The infants began to hold food at 4 weeks of age.

3.2.2 Development of Feeding Postures and their Relation to Hand Use

The posture adopted during each incidence of bimanual and unimanual hand use in feeding was recorded for 11 individuals (7 females, 4 males) in the tests from 5-8 to 22 months of age. These subjects were also part of the longitudinal assessment of the development of hand preferences. Three postures were adopted most frequently during feeding; 1) tripedal, one hand and the two hindlimbs on the ground, 2) seated, two hindlimbs and lower body on ground with forelimbs free and body vertical and 3) suspended on wire mesh holding on with one hand and two feet (Figure 3.1). The marmosets were observed feeding in a rampant posture (Stevenson and Poole, 1976), on two occasions only and so these scores were eliminated from the data set. The percentage occurrence of the tripedal, seated and suspended postures adopted during feeding was determined for each individual at each age. The Friedman statistic was used to determine whether the percentage occurrence of any of the postures adopted during feeding changed with development.

3.2.3 The Relationship between Unimanual Hand Preferences and Posture

The percentage left-hand use displayed for simple food holding and the percentage occurrence of each posture were correlated at each age. Clustering occurred with some correlations and it was necessary to test the left and right-hand preferent subgroups separately. As the 11 subjects did not constitute a very large sample, the remaining 4 subjects that had been part of the longitudinal assessment of hand preferences were added to the sample when the postures they adopted during feeding were recorded. The postures adopted during feeding were known for 2 of these subjects at 10-12 and 14 months and for the extra 4 subjects at 15-18 and 22 months.

It was not possible to investigate the effect of posture on the strength of hand preferences using the longitudinal design as most subjects displayed less than 10 incidences of unimanual hand use for at least one of the postures, usually the suspended posture. When the total 21 marmosets were considered, however, there were 12 subjects that had assumed each posture on at least 10% of feeding incidences. Using these subjects, it was possible to compare the strength of hand preferences displayed in each posture. The ages of the subjects used in these analyses ranged from 10 months to 42 months.

3.2.4 The Influence of Gender, Parental Group and Early Experience on Hand Use

The influence of gender on the distribution of hand preferences was investigated using Fishers exact tests (2x2 contingency table). The distributions of left and right-hand preferences in the female and male subgroups were compared at each age. The total 21 marmosets were used in these analyses. Ambipreferent subjects were not included in the Fishers analyses. The percentage left-hand use and strength of preferences displayed by the female and male subjects were also compared at each age.

It was also possible to examine the influences of family group membership and early experiences, including stressful rearing conditions in the first 6 months of life, on the development of hand preferences in later life. The percentage left-hand use and strength of preferences displayed by subjects in each of the Family Groups (Chapter 2, p. 47) were compared at each age. The percentage left-hand use and strength of preferences displayed by subjects in the two Experience Groups were also compared (Chapter 2, p. 48).

3.3 RESULTS

3.3.1 Development of Unimanual Hand Use and Hand Preferences for Simple Food Holding

Bimanual versus unimanual hand use

The data for bimanual hand use are presented as a percentage of unimanual and bimanual hand use in Figure 3.2a. A significant effect of age on the relative percentage of bimanual hand use was found (Friedman statistic, using age as repeated measure, F_r= 38.28, p<0.0001). Subsequent paired comparisons revealed significant decreases in the incidence of bimanual hand use between 0-2 and 5-8 months (Wilcoxon, T^+= 15, p= 0.0007) and between 5-8 and 10-12 months of age (Wilcoxon, T^+= 9, p=0.01). As can be seen in Figure 3.2a the largest decrease in percentage bimanual hand use was between 0-2 and 5-8 months (approximately 43%). The decrease between 5-8 and 10-12 months, was comparatively minor (approximately 4%). No differences were found from 10-12 to 22 months (Wilcoxon tests, p≥0.13 in all comparisons).

Development of hand preferences

Age had no significant effect on percentage left-hand use for simple food holding (Friedman statistic, using age as repeated measure, F_r= 4.12, p= 0.53; Figure 3.3), but there was a significant effect of age on the strength of hand preferences (Friedman statistic, F_r= 41.93, p<0.0001; Figure 3.2b). The strength of preference refers to the absolute preference score for one hand regardless of the direction of the bias. *Post hoc* analyses revealed a significant increase in the strength of preferences between 0-2 and 5-8 months (Wilcoxon, T^+= 1, p= 0.001). There was another significant increase in the strength of preferences between 5-8 and 10-12 months (Wilcoxon, T^+= 2, p= 0.008). As can be seen in Figure 3.2b, the strength of hand preferences increased by approximately 18% between 0-2 and 5-8 months, whereas a much smaller increase in preferences, of approximately 7%, was displayed between 5-8 and 10-12 months. The increase in the strength of unimanual hand preferences with age is almost the inverse of the decreasing pattern found for the development of bimanual,

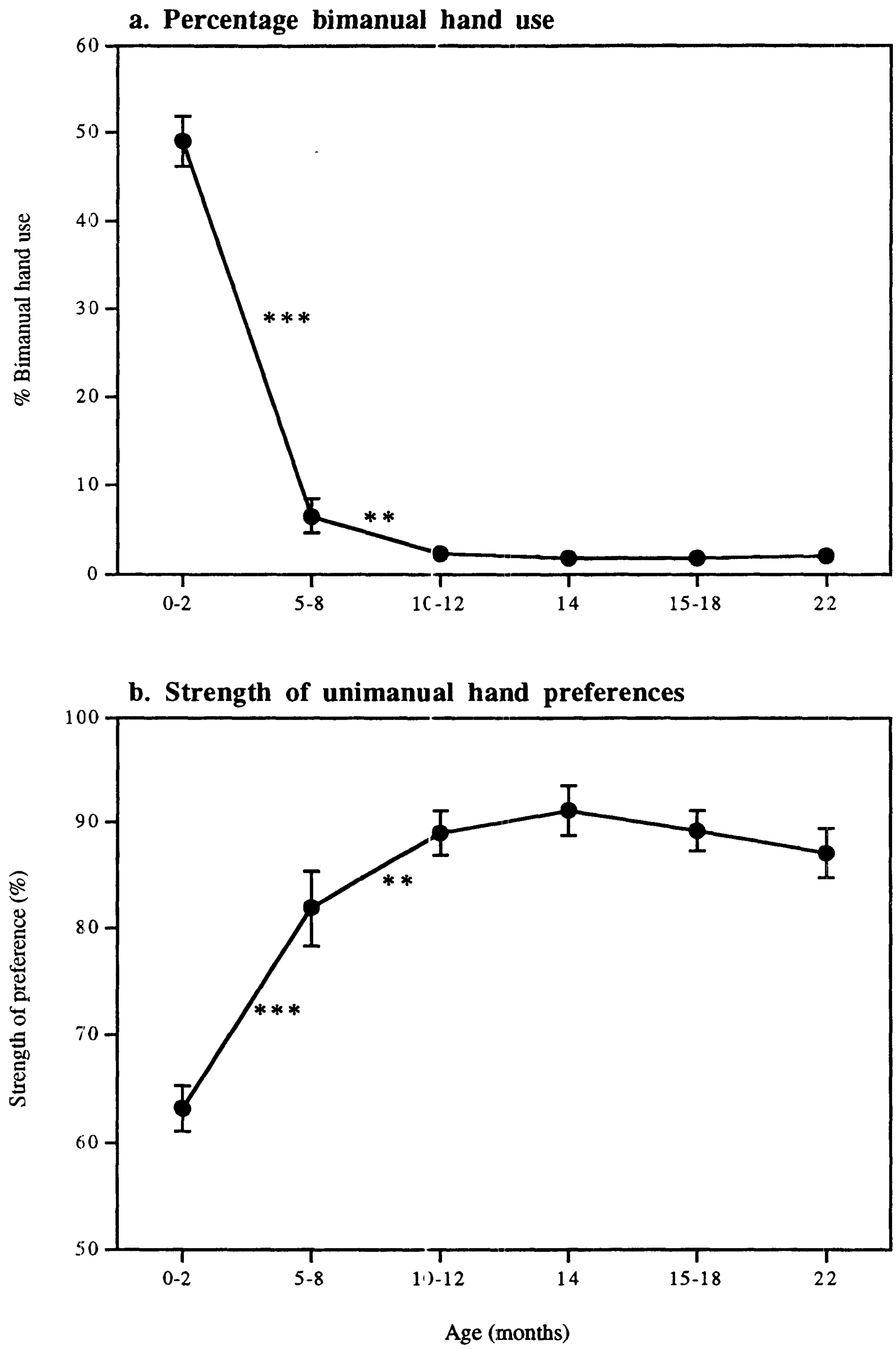

Figure 3.2 The development of unimanual, compared to bimanual, hand use and strength of unimanual hand preferences for simple food holding. Figure 3.2a shows the mean percentage of bimanual hand use (± SEM) at various ages (x axis). This graph illustrates the decrease in bimanual, versus the increase in unimanual, hand use for simple food holding with increasing age. In Figure 3.2b the development of unimanual hand preferences is depicted as the mean strength of preference (±SEM) at the ages tested. 15 subjects were used to calculate the means in both graphs. *** indicates that $p \leq 0.001$, ** $p \leq 0.01$. The y axis on Figure 3.2b ranges from 50-100 because it illustrates the mean lateral bias for a preferred hand, regardless of the direction of hand preference.

compared with unimanual, hand use (Figure 3.2a). Strength of preferences appeared to stabilize at 10-12 months (Wilcoxon tests, p> 0.05 for all comparisons; Figure 3.2b).

The distribution of unimanual hand preferences

The number of left, right and ambipreferent subjects observed within the group was compared to the number expected in each category by chance (null hypothesis) at each age. Individuals hand preferences at each age are presented in Figure 3.3 and the distribution of hand preferences at the group level for simple food holding at each age is summarized in Figure 3.4. As infants (0-2 months), only 3 out of 13 individuals displayed significant hand preferences for simple food holding (Figures 3.3 and 3.4; Appendix A, Tables A and B). All three preferred to use the right hand (Figure 3.3). The 3 individuals with significant hand preferences displayed 19 to 58 incidences of unimanual hand use. Two infants were not included in these analyses because they did not display more than 15 incidences of unimanual hand use (Figure 3.3). There was no significant difference between the number of right-hand preferent infants and the number of ambipreferent infants (χ^2 (1)= 3.77, p>0.05).

It was possible to collect a minimum of 100 unimanual hand use scores for each individual on each of the tests after 0-2 months. By 5-8 months of age, as juveniles, most of the subjects displayed significant hand preferences: 7 subjects displayed left-hand preferences, 6 were right-hand preferent and only 2 were ambipreferent (Figures 3.3 and 3.4). There was no evidence of a group bias at this age. Instead a bimodal distribution of preferences was found (χ^2 (2)= 1.2, p> 0.50; Figure 3.4). As most subjects did not display significant preferences at 0-2 months it was considered necessary to examine further the relationship between percentage left-hand use found in the infant and juvenile periods. As can be seen in Figure 3.5, there was a significant positive correlation between the percentage left-hand use displayed by the subjects at 0-2 months of age and the percentage left-hand use displayed at 5-8 months of age (Spearman rank, r_s= 0.87, p= 0.003). The lack of significant hand preferences during

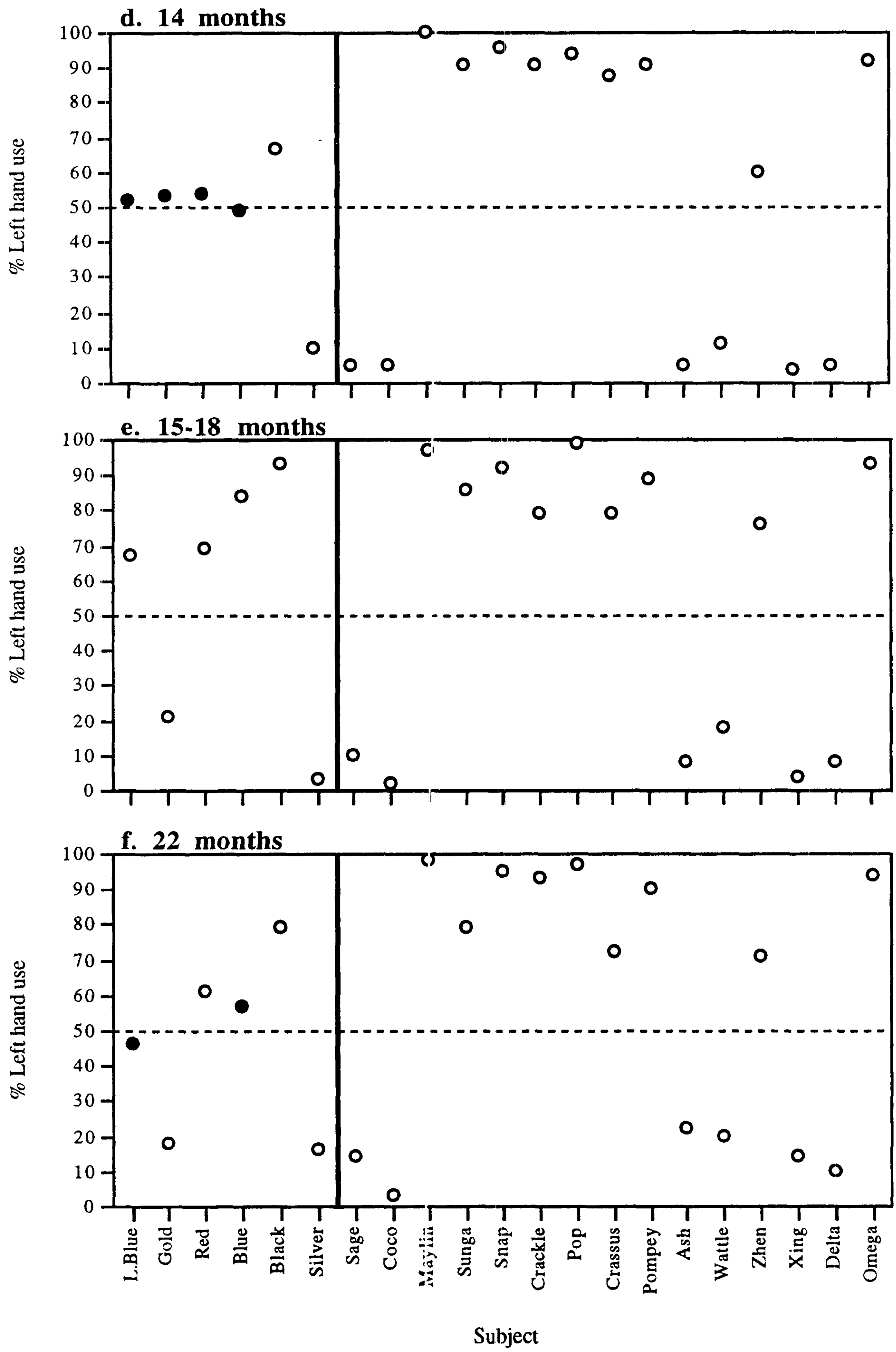

Figure 3.3 Individuals' hand preferences for simple food holding from 0-2 to 22 months of age. Each graph displays individual's hand (O) preferences on the simple food holding tests: a. 0-2 months, b. 5-8 months, c. 10-12 months, d. 14 months, e. 15-18 months, f. 22 months. Subjects are presented on the x axis and their percentage left-hand preference for simple food holding is shown on the y axis. The white symbols (O) indicate a significant hand or foot preference, and the black (●) symbols represent ambipreference. The thick black line dividing the subjects is used to divide the Experience Groups: Experience Group 1 (reader's left) and Experience Group 2 (reader's left).

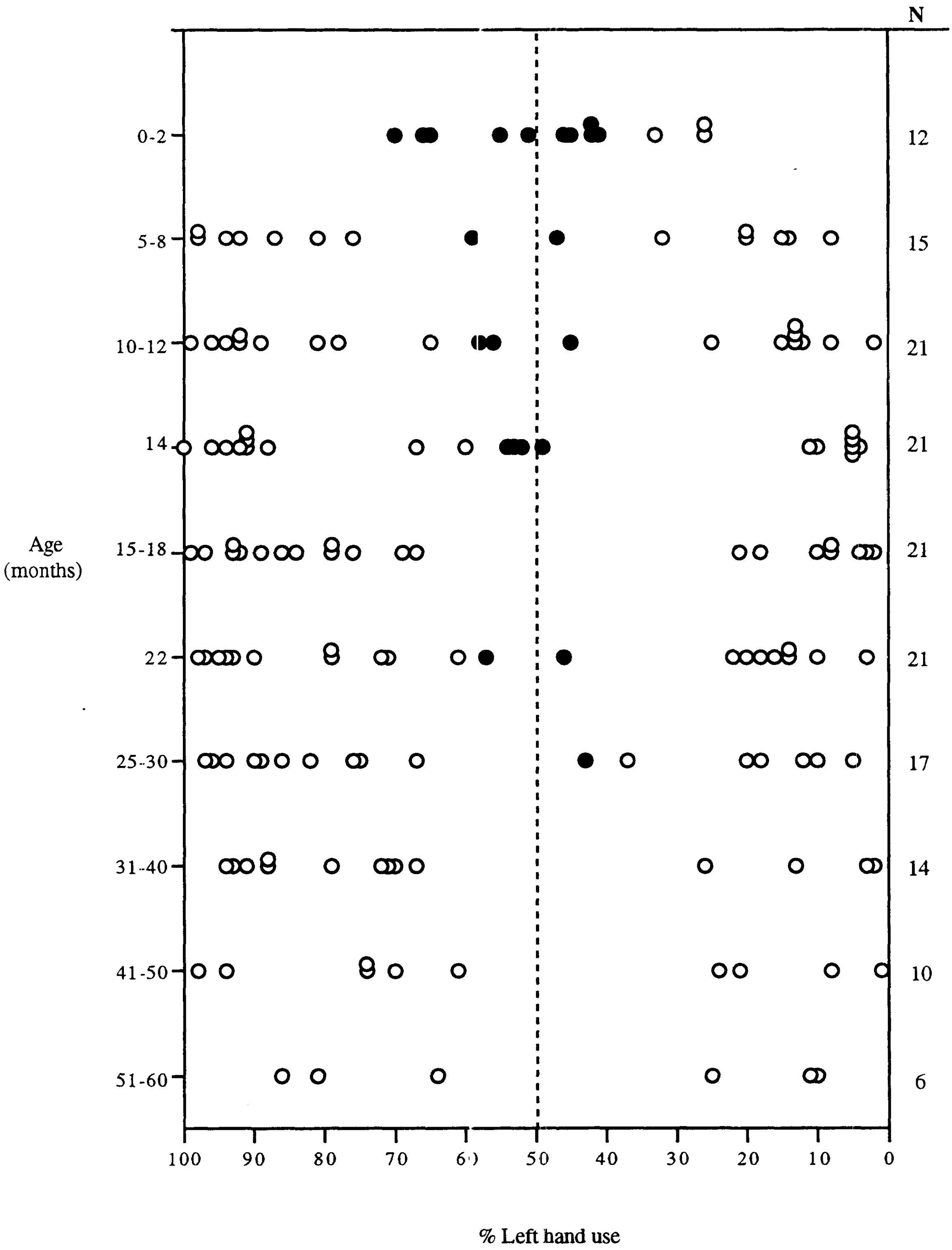

Figure 3.4 Distribution of hand preferences for simple food holding from 0-2 to 60 months of age. The ages at which the subjects were tested are shown on the y axis and percentage left-hand use is presented on the x axis. It should be noted that these axes are opposite to those shown in the previous figures. Each symbol represents an individual's preference. White symbols (O) indicate that the hand preference is significant (p≤ 0.05) and the black symbols (●) denote nonsignificant hand preferences. It can be seen that the data was symmetrically distributed at all ages. Note that the x axis has been reversed so that subjects with a left-hand preference are on the left of the reader and those with a right-hand preference are on the right side of the reader.

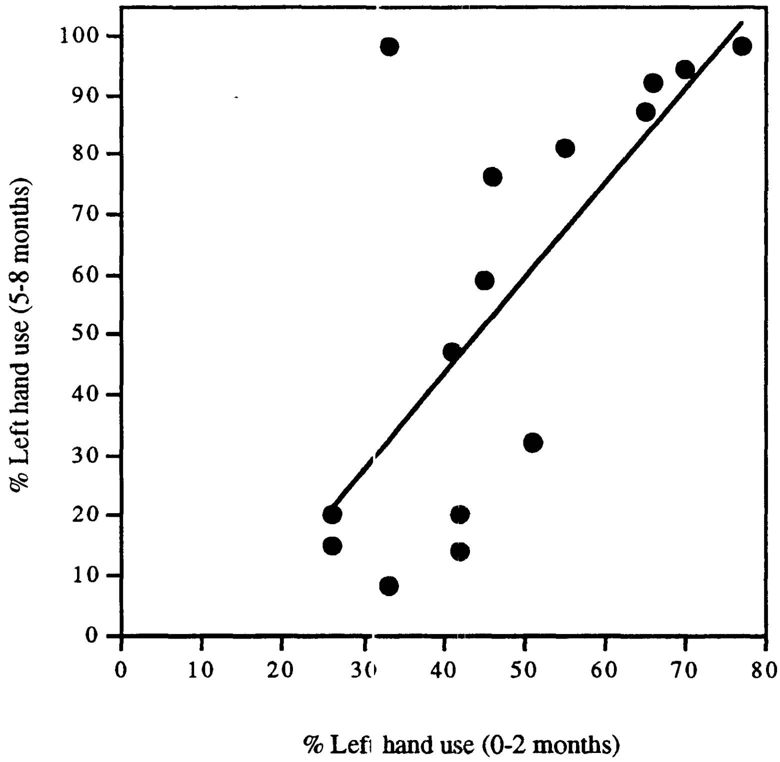

Figure 3.5 Relationship between hand use for simple food holding in the infant and juvenile periods. A significant positive correlation was found between the hand used by individuals to hold food as infants (0-2 months) and juveniles (5-8 months). Most individuals did not display significant hand preferences for simple food holding as infants, whereas they did as juveniles.

the infant period might have been influenced by the low incidences of unimanual hand use in this period.

All of the handed subjects maintained the direction of their hand preferences at 10-12 months and the two ambipreferent subjects displayed significant left-hand preferences. None of the subjects changed the direction of their hand preferences at 14, 15-18 or 22 months of age (Figure 3.3). From 10-12 to 22 months of age, 9 subjects were left-hand preferent and 6 were right-hand preferent. Thus, there was no evidence of handedness within the group on any of these tests (χ^2 (1)= 0.6, p>0.30; Figure 3.4). All of the subjects tested at ages older than 22 months displayed the same hand preferences for simple food holding as they had at the earlier ages.

The distribution of hand preferences in the group was also examined with the inclusion of the 6 subjects (founding marmosets) that had not been tested longitudinally but had been tested at most ages. No group bias indicative of handedness was found in the total group of 21 marmosets at 10-12, 14 and 15-18 months (χ^2= 3.71, 2.57, 1.19, respectively, p>0.10 in all cases). However, it was found that 3 of the 6 founding marmosets did not display significant hand preferences until 15-18 months of age (Figure 3.3). At 15-18 months all of the subjects expressed significant preferences: 13 subjects had left-hand preferences and 10 had right-hand preferences (Figure 3.4).

As can been seen in Figure 3.4, there was no evidence of a group bias for left or right handedness at any age from 22 months. At 22 and 25-30 months the distribution of hand preferences differed from chance when the number of left, right and ambipreferent subjects were compared (22 months, χ^2 (2)= 6, p<0.05; 25-30 months, χ^2 (2)=7.18, p<0.02; Figure 3.4). However, in both cases the numbers of left and right-hand preferent subjects did not differ significantly (χ^2 (1)= 0.2, 0.8, respectively, p>0.05). Instead the number of subjects with hand preferences was significantly greater than those with no preference (χ^2 (1)= 6.23, 7.36, p<0.01). There was no group bias for handedness at 31-40, 41-50 or 51-60 months (Chi-squared, p>0.10 for all comparisons; Figure 3.4). Thus, overall there was a bimodal distribution of hand preferences in the group at all of the ages tested, except at 0-2 months.

Direction of hand preference and development of unimanual and bimanual hand use

In order to see whether left and right-hand preferent individuals developed their unimanual hand preferences at the same rate, the 15 subjects examined longitudinally were categorized as left or right-hand preferent according to the lateralization that they displayed at 10-12 months of age. This age was chosen to divide the group as all of the subjects displayed significant hand preferences by 10-12 months: 9 subjects were left-hand preferent and 6 were right-hand preferent. Then percentage bimanual hand use scores displayed by left and right-hand preferent individuals were examined separately

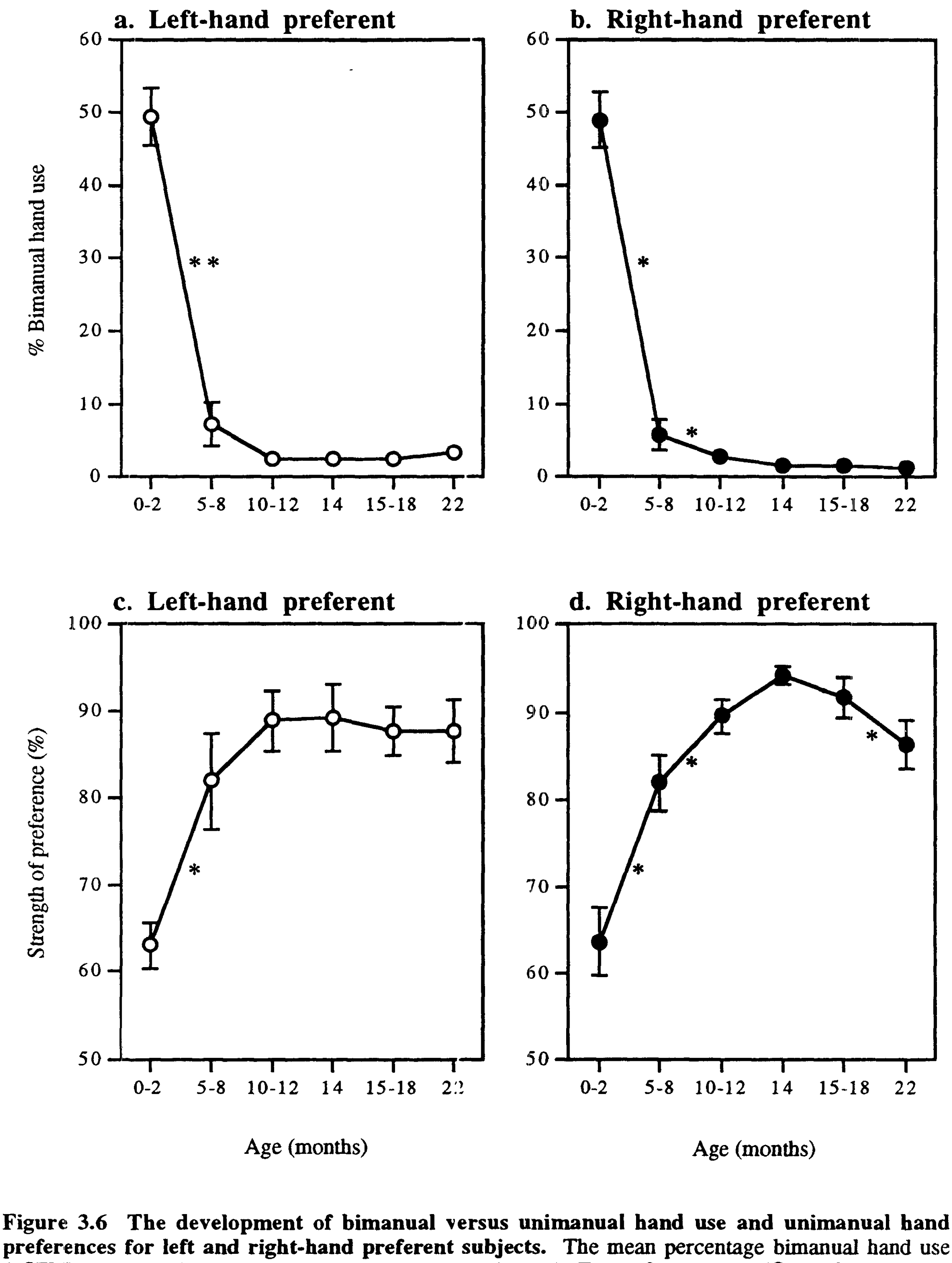

Figure 3.6 The development of bimanual versus unimanual hand use and unimanual hand preferences for left and right-hand preferent subjects. The mean percentage bimanual hand use (±SEM), versus unimanual hand use, at each age is shown in Figure 3.6a for left (O, N=9) and right-hand preferent (●, N=6) subjects separately. Figure 3.6b shows the development of strength of hand preferences as the mean strength of preference (±SEM) for the separate left and right-hand preferent subgroups. ** $p \leq 0.01$, * $p \leq 0.05$. The decrease in bimanual hand use between 5-8 months and the concurrent increase in strength of preferences between these ages was significant for the right-hand preferent group only.

across the various ages (Figures 3.6a and 3.6b). Both left and right-hand preferent subgroups displayed a significant effect of age on the incidence of bimanual food holding (Friedman statistic; left, F_r= 19.29, p= 0.01; right, F_r= 37.69, p< 0.001; Figures 3.6a and 3.6b). As shown in Figures 3.6a and 3.6b, both groups displayed significant decreases in bimanual hand use between 0-2 and 5-8 months (Wilcoxon; left, T^+= 9, p= 0.008; right, T^+= 5, p= 0.03). There was a significant decrease in bimanual hand use between 5-8 and 10-12 months of age in the right-hand preferent subgroup, and a tendency for a decrease in bimanual hand use during this period in the left-hand preferent subjects (Wilcoxon; left, T^+= 4, p= 0.08; right, T^+= 5, p= 0.04). This decrease in the right-hand preferent subgroup was equal to only 3%. No differences were found from 10-12 to 22 months in either hand preference group (Wilcoxon tests, p>0.05).

The effects of lateral preference on changes in the strength of hand preferences with age were also examined. Both groups displayed a significant effect of age on the strength of unimanual hand preferences (Friedman statistic; left, F_r= 22.07, p= 0.0005; right, F_r= 24.76, p=0.0002). As can be seen in Figure 3.6c and 3.6d, the development of unimanual hand preferences in left or right-hand preferent subjects followed a similar pattern from birth to 10-12 months. Between 0-2 and 5-8 months both subgroups displayed significant increases in the strength of their hand preferences (Wilcoxon; left, T^+= 1 p= 0.02; right, T^+= 0, p= 0.03). A significant increase in strength of hand preferences between 5-8 and 10-12 months was present in the right-hand preferent subjects only, but the left-hand preferent subjects showed a tendency for the same effect (Wilcoxon, left; T^+= 2, p= 0.08; right, T^+= 0, p= 0.04). After 10-12 months the left and right-hand preferent subjects differed from each other. From 10-12 months to 22 months the left-hand preferent subjects showed no change in their strength of hand preferences, whereas the strength of preferences in the right-handed subjects continued to increase up until 14 months and thereafter it decreased. The decrease in hand preferences observed in the right-hand preferent subjects between 15-18 and 22 months of age was significant (Wilcoxon, T^+= 6, p= 0.03). None of the right-hand preferent subjects lost their significant right-hand preferences at 22 months.

At 22 months both groups again displayed the same strength of hand preferences.

3.3.2 Development of Feeding Postures in Relation to Hand Use

Longitudinal development of preferred feeding postures

The percentage occurrence of the tripedal, seated and suspended postures from 5-8 to 22 months of age was examined for 11 individuals. The mean percentage occurrence of each posture (±SEM) is presented in Figure 3.7. Unfortunately, the posture assumed during feeding at 0-2 months was not always recorded and thus could not be included in these analyses.

Significant differences were found when the percentage occurrence of each of the three postures was compared with one another at each age (Friedman statistic, at each age $p<0.01$; Figure 3.7). *Post hoc* analyses revealed that the tripedal posture was adopted significantly more than the seated posture at each of the ages for which scores were available (Wilcoxon tests, $T^{+}=10, 11, 9, 9, 10$, increasing ages respectively,

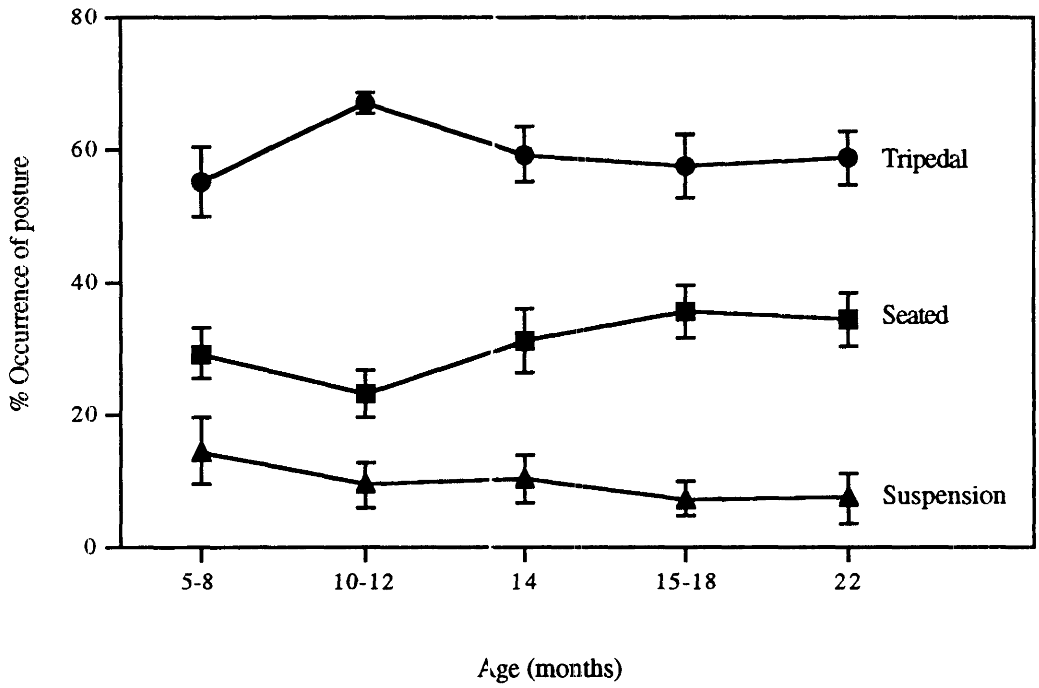

Figure 3.7 The percentage occurrence of the three postures in feeding throughout development. The mean percentage occurrence (±SEM) of the tripedal (●), seated (■) and the suspension posture (π) for the group of subjects scored from 5-8 to 22 months of age is presented. At all ages the tripedal posture was significantly preferred for feeding. The seated posture was also assumed more than the suspended posture at each age.

$p<0.05$ in all cases). The tripedal posture also occurred significantly more often than the suspended posture (Wilcoxon tests, $T^+= 9, 11, 10, 11, 10$, increasing age respectively, $p<0.02$ in all cases). The seated posture was adopted significantly more often than the suspended posture at 14, 15-18 and 22 months of age (Wilcoxon tests, $T^+= 9, 11, 10$, respectively, $p<0.05$ in all cases), but not at 5-8 or 10-12 months (Wilcoxon tests, $T^+= 8, 9$, respectively, $p= 0.08$ in both cases). The percentage occurrence of each of the postures did not vary significantly with age (Friedman statistic; tripedal, $F_r= 6.43$, $p= 0.17$; seated. $F_r= 6.24$, $p= 0.18$; suspended, $F_r= 2.02$, $p= 0.73$; Figure 3.7). As shown in Figure 3.7, there was a tendency for the percentage occurrence of the tripedal posture to increase between 5-8 to 10-12 months of age, but it was not significant (Wilcoxon, $T^+= 4$, $p= 0.08$). There was also a nonsignificant trend for increased use of the seated posture during feeding after 10-12 months of age.

The relationship between posture and unimanual versus bimanual hand use

To determine whether the percentage occurrences of the different feeding postures influenced the proportion of simple food holding acts that were bimanual, the percentage occurrence of each posture was correlated with the percentage bimanual hand use determined at each age. There was no relationship between the percentage occurrence of any of the postures and percentage bimanual hand use at any age. Spearman rank correlations revealed nonsignificant relationships between the percentage occurrence of the tripedal posture and percentage bimanual hand use at each age (Spearman rank, $r_s= 0.05, 0.01, 0.02. 0.26, -0.03$, with respect to increasing age, $p>0.40$ in all cases). There was also no relationship between adoption of the seated posture, which allows the subjects to use both hands, and bimanual food holding at any age (Spearman rank, $r_s= 0.05, 0.32, -0.14, 0.04, 0.24$, with respect to increasing age, $p>0.30$ in all cases). No correlation was found between the percentage occurrence of the suspended posture and bimanual hand use (Spearman rank, $r_s= 0.24, -0.03, 0.21, 0.02, 0.3$, with respect to increasing age, $p>0.40$ in all cases).

Direction of hand preference and the occurrence of postures assumed in feeding

The percentage occurrence of each posture was also determined for left and right-hand preferent subjects separately to see whether the development of preferred feeding postures differed for these subgroups. The mean percentage occurrence (± SEM) of each of the postures in the separated subgroups is shown in Figure 3.8. The subjects were separated into groups according to the hand preferences they displayed at each age. The two ambipreferent subjects at 5-8 months were not grouped with the left-hand preferent subgroup at this age as it was possible that their ambipreference might be related to the posture they adopted during feeding. From 10-12 months all of the subjects displayed consistent hand preferences: 7 subjects were left-hand preferent and 4 were right-hand preferent. The two ambipreferent subjects at 5-8 months were left-hand preferent from 10-12 months. As there were only four subjects in the right-hand preferent subgroup, however, the results of Wilcoxon signed rank tests did not always reach significance. Therefore, if all subjects displayed the same direction of preference ($p= 0.068$) for one posture over the other it was assumed that they significantly preferred the posture with the higher percentage occurrence.

Differences between the left and right-hand preferent subgroups were revealed. It was found that the left-hand preferent subjects did not display a preference for any posture at 5-8 months (Friedman statistic, $F_r= 2.80$, $p= 0.25$, in both cases; Figure 3.8), whereas the right-hand preferent subjects all preferred the tripedal posture to the seated and suspended postures at this age (Wilcoxon, in all comparisons $T^+= 4$, $p\leq 0.068$). There was also a significant difference between the left, right and ambipreferent subjects in the percentage occurrence of the tripedal posture at 5-8 months (Kruskal Wallis, $H= 7.57$, $p= 0.02$). It was found that right-hand preferent subjects assumed the tripedal posture during feeding significantly more than the left-hand preferent subjects (Mann Whitney U, $U= 0$, $p= 0.01$). Ambipreferent subjects were not used in pairwise comparisons. At 5-8 months the percentage occurrences of both the seated and suspended postures were greater in the left-hand preferent subgroup than in the right-hand preferent group, but neither comparison was significant (Kruskal Wallis; seated,

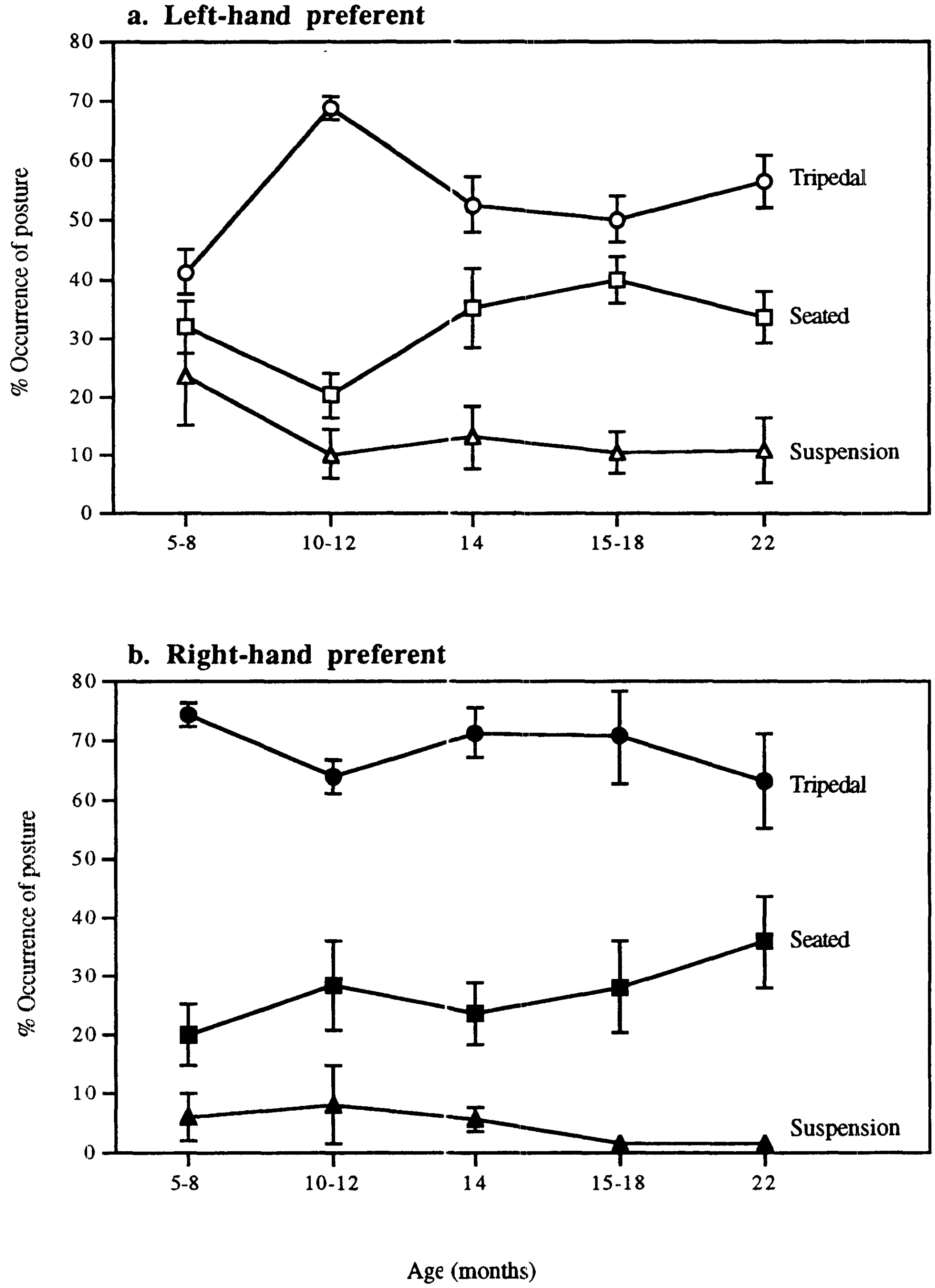

Figure 3.8 The percentage occurrence of the three postures during feeding for left and right-hand preferent subjects. Comparison was made between the percentage occurrence of the tripedal (O), seated (□) and suspended postures (Δ) throughout development by the left (O) and right-hand (●) preferent subjects. The mean percentage occurrence of each posture (± SEM) for the group of 7 left-hand preferent subjects and the group of 4 right-hand preferent subjects is presented.

H= 3.57, p= 0.17; suspended, H= 3.4, p= 0.18). At 14 and 15-18 months of age the percentage occurrence of the tripedal posture in the right-hand preferent subjects was also significantly greater than in the left-hand preferent subjects (Mann Whitney U; 14 mths, U= 3, p= 0.04; 15-18 mths, U= 2, p= 0.02). Although there were tendencies for left and right-hand preferent subjects to display different percentage occurrences of each posture, no further significant differences were found (Mann Whitney U, p>0.05 in all cases). The percentage occurrence of each of the postures did not vary with age in the right-hand preferent subgroup, whereas the postures adopted by left-hand preferent subjects did change with age (Friedman statistic; tripedal, F_r= -20.70, p≤0.01, seated, F_r= -10.40, p≤0.05; Figure 3.8). The percentage occurrence of the suspended posture did not vary with age in the left-hand preferent subgroup.

Between 5-8 and 10-12 months, the left-hand preferent subjects displayed a significant decrease in use of the seated posture (Wilcoxon, T^+= 5, p= 0.04) and significant increased assumption of the tripedal posture (Wilcoxon, T^+= 0, p= 0.04). The left-hand preferent subjects displayed a significant preference for the tripedal compared to the seated and suspended postures at 10-12 months (Wilcoxon; tripedal versus seated, 10-12 mths, T^+= 5, p= 0.04; tripedal and suspended, 10-12 mths, T^+= 5, p= 0.04). From 10-12 to 14 months the percentage occurrence of the tripedal posture in the left-hand preferent subjects significantly decreased (Wilcoxon, T^+= 5, p= 0.04), and the left-hand preferent subjects again did not display a preference for any posture (Friedman statistic, F_r= 2.80, p= 0.25). At 15-18 months, the tripedal and seated postures did occur significantly more than the suspended posture in the left-hand preferent subgroup (Wilcoxon; tripedal versus suspended, T^+=5, p= 0.04; seated versus suspended, T^+= 5, p= 0.04; Figure 3.8), but there was no significant difference between the percentage occurrence of the tripedal posture compared with the seated posture (Wilcoxon, T^+=3, p= 0.50). At 22 months the left-hand preferent subjects displayed preferences for the tripedal compared to the seated and suspended postures (Wilcoxon; tripedal versus seated, T^+= 7, p= 0.01; tripedal versus suspended, T^+= 6, p= 0.03). There was no significant difference between percentage occurrence of the seated posture and the suspended posture at 22 months (Wilcoxon, $T^{+}= 4$, $p= 0.06$; Figure 3.8). As can be seen in Figure 3.8, however, there was a tendency for the left-hand preferent subjects to prefer the seated posture at 22 months and in fact only one subject did not display this preference.

As shown in Figure 3.8, the right-hand preferent subjects preferred to feed in the tripedal compared with the seated posture and suspended posture at all ages (Wilcoxon, in all comparisons $T^{+}= 4$, $p \leq 0.068$). However, at 22 months the percentage occurrence of the tripedal posture was not significantly different to the percentage occurrence of the seated posture (Wilcoxon, $T^{+}= 3$, $p= 0.14$), only because one subject did not prefer the tripedal to the seated posture.

3.3.3 Relationships Between Unimanual Hand Preferences and Feeding Posture

Relationships between percentage left-hand use and feeding posture

Spearman rank correlations revealed significant relationships between percentage left-hand use and the percentage occurrence of the tripedal and suspended postures at 5-8 months of age. As shown in Figure 3.9a, there was a strong negative correlation between percentage left-hand use and the percentage occurrence of the tripedal posture (Spearman rank, $r_s= -0.78$, $p= 0.01$) and there was a close to significant positive relationship between the percentage occurrence of the suspended posture and percentage left-hand use (Spearman rank, $r_s= 0.75$, $p= 0.02$; Figure 3.9b). The latter correlation would have been significant had the stringent criterion of $p \leq 0.01$ not been adopted.

After 5-8 months the hand preference data was bimodally distributed and therefore could not be used in correlation analyses unless left and right-hand preferent subjects were treated separately. Subjects that were not included in the longitudinal sample were included in the analyses to increase the sample size. As there were only 4 subjects in the right-hand preferent subgroup at 10-12 and 14 months of age, the percentage left-hand use displayed by these subjects was not correlated with the percentage occurrence of any posture at these ages.

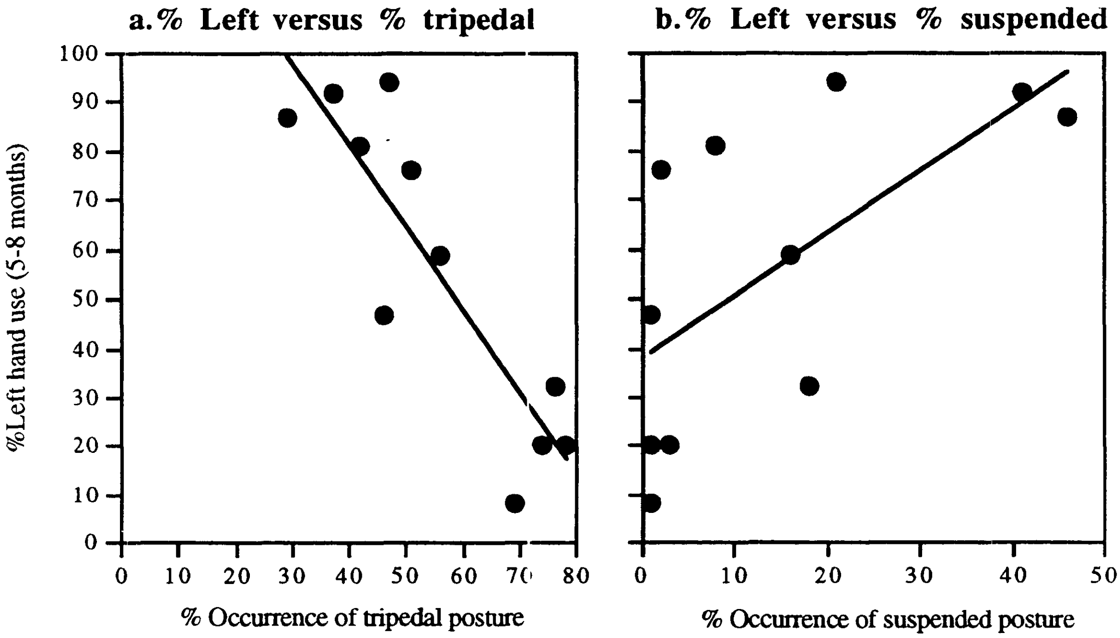

Figure 3.9 The relationship between posture and unimanual hand use at 5-8 months. The percentage left-hand use displayed by the juvenile subjects is presented on the y axis and percentage occurrence of the tripedal (a) or suspended posture (b) is denoted on the x axis. There was significant negative correlation between the percentage occurrence of the tripedal posture and percentage left-hand use at 5-8 months, but a tendency only for a positive relationship between the percentage occurrence of the suspended posture and percentage left-hand use.

At 10-12 months there was a tendency only for a positive relationship between percentage left-hand use and the percentage occurrence of the suspended posture in left-hand preferent subjects (Spearman rank, r_s= 0.64, p= 0.03). There was also a tendency for percentage left-hand use to decrease with increased occurrence of the seated posture at 14 months (Spearman rank, r_s= -0.72, p= 0.04). There was no correlation between percentage left-hand preferences and the percentage occurrence of the tripedal posture at either 10-12 or 14 months of age in the left-hand preferent group (Spearman rank, r_s= -0.10, 0.37, respectively, p= 0.70, 0.30). There was also no correlation between the percentage occurrence of the seated posture and percentage left-hand preferences at 10-12 months, and no correlation between the suspended posture and left-hand use at 14 months (Spearman rank; 10-12 mths, seated, r_s= -0.64, p= 0.07; suspended, 14 mths, r_s= 0.61, p= 0.08).

At 15-18 months of age there was no correlation between the percentage occurrence of any posture and percentage left-hand use for either left or right-hand preferent subjects. However, at 22 months of age there was suggestion of a negative relationship between the percentage occurrence of the seated posture and percentage left-hand use in the left-hand preferent subjects (Spearman rank, r_s= -0.75 p=0.03).

Comparison of the strength of hand preferences displayed by the marmosets in the different feeding postures

The Friedman statistic was used to compare the strength of preferences displayed in each posture allowing each individual to act as its own control (for age and experience). It was found that the posture assumed for simple food holding did affect the strength of hand preferences (Friedman statistic, F_r= 10.50, p= 0.005). The marmosets displayed stronger hand preferences when feeding in the stable tripedal posture compared with both the seated and suspended postures (Wilcoxon tests; tripedal versus seated, T^+=11, p= 0.003; tripedal versus suspended, T^+= 8, p= 0.03). Significantly stronger hand preferences were also observed when the subjects fed in the suspended rather than the seated posture (seated versus suspended, T^+= 4, p= 0.04). When the strength of hand preferences in each of the postures was compared for left and right-hand preferent subjects separately, it was found that effects of posture were present for the left-hand preferent subjects only (Friedman statistic; left, F_r= 7.40, p= 0.03; right, F_r= 3.50, 0.17; Figure 3.10). Subsequent Wilcoxon signed rank tests, with left-hand preferent subjects only, demonstrated that feeding in the tripedal posture elicited significantly stronger preferences compared with the seated posture in the left-hand preferent subgroup (Wilcoxon, T^+=7, p= 0.02; Figure 3.10). However, there was no significant difference between the strength of preference in the suspended posture compared with the tripedal and seated postures (Wilcoxon tests; tripedal versus suspended, T^+= 2, p= 0.18; seated versus suspended, T^+= 2, p= 0.07; Figure 3.10). All

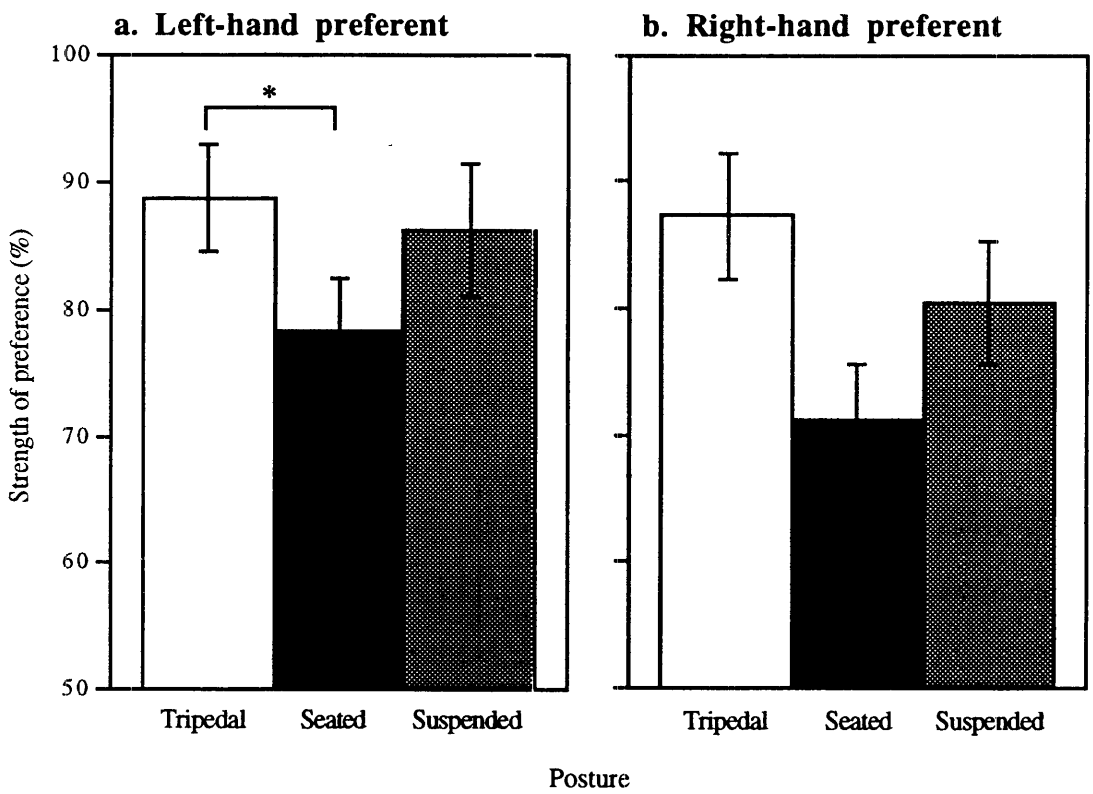

Figure 3.10 Comparison between the strength of hand preference for simple food holding in each of the postures. The strength of hand preferences displayed in the tripedal (□), seated (■) and suspended(▩) postures are presented separately for left and right-hand preferent subjects. It can be seen that left and right-hand preferent subjects displayed very similar effects of the postures on hand preference. * indicates that $p<0.05$.

of the right-hand preferent subjects also displayed stronger hand preferences in the tripedal compared with the seated posture and it is suggested that the lack of significance between postures in this group was simply due to the limited sample size. In fact, it can be seen in Figure 3.10 that the effect of posture on the strength of preference is similar for both left and right-hand preferent subgroups. Thus, it appears that the strength of preference displayed in each posture might not be affected by the direction of hand preference.

3.3.4 The Influence of Gender, Family Group and Early Experience on Hand Preferences

Gender and hand preferences

The number of female and male subjects that displayed left, right or no hand preferences is presented in Figure 3.11. There was a tendency for more males to be right-hand preferent and females to be left-hand preferent in this group of marmosets (Figure 3.11). However, Fishers exact tests did not reveal significantly different distributions between genders at any age ($p>0.10$ in all comparisons). Further comparisons, however, with Mann Whitney U tests showed that the females displayed significantly greater percentage left-hand use than males at 22 months of age (Mann Whitney U, $U=16.5$, $p<0.01$) and there was a tendency for significantly greater left-hand use in the female subgroup at 15-18 months of age (Mann Whitney U, $U= 27.5$, $p= 0.08$). There was no significant effect of gender on percentage left-hand use at 10-12 or 14 months of age (Mann Whitney U, $p>0.11$ in both comparisons). There was also no effect of gender on the strength of hand preferences at any age (Mann Whitney U, $p>0.31$ in all comparisons).

Family group

To investigate the effect of family group on the expression of hand preferences the direction and strength of preferences displayed at each age (0-2, 5-8, 10-12, 14, 15-18 and 22 months) were compared between the three family groups. There were no significant differences between the hand preferences (expressed as percentage left) in the groups at any age (Kruskal Wallis, $H= 1.9, 2.6, 4.6, 2.36, 0.6, 1.2$, in order of increasing age, $p>0.09$ in all cases).

There were also no differences between strength of preferences displayed by subjects in the separate family groups at 0-2, 10-12, 14, 15-18 and 22 months (Kruskal Wallis, $H= 4.7, 1.64, 2.67, 1.6, 4.9$, in order of increasing age, $p>0.09$ in all cases; Figure 3.12). However, as can be seen in Figure 3.12, there was a significant difference between family groups in the strength of hand preferences displayed at 5-8 months (Kruskal Wallis, $H= 8.40$, $p= 0.02$). Juveniles in Family Group 1 displayed stronger

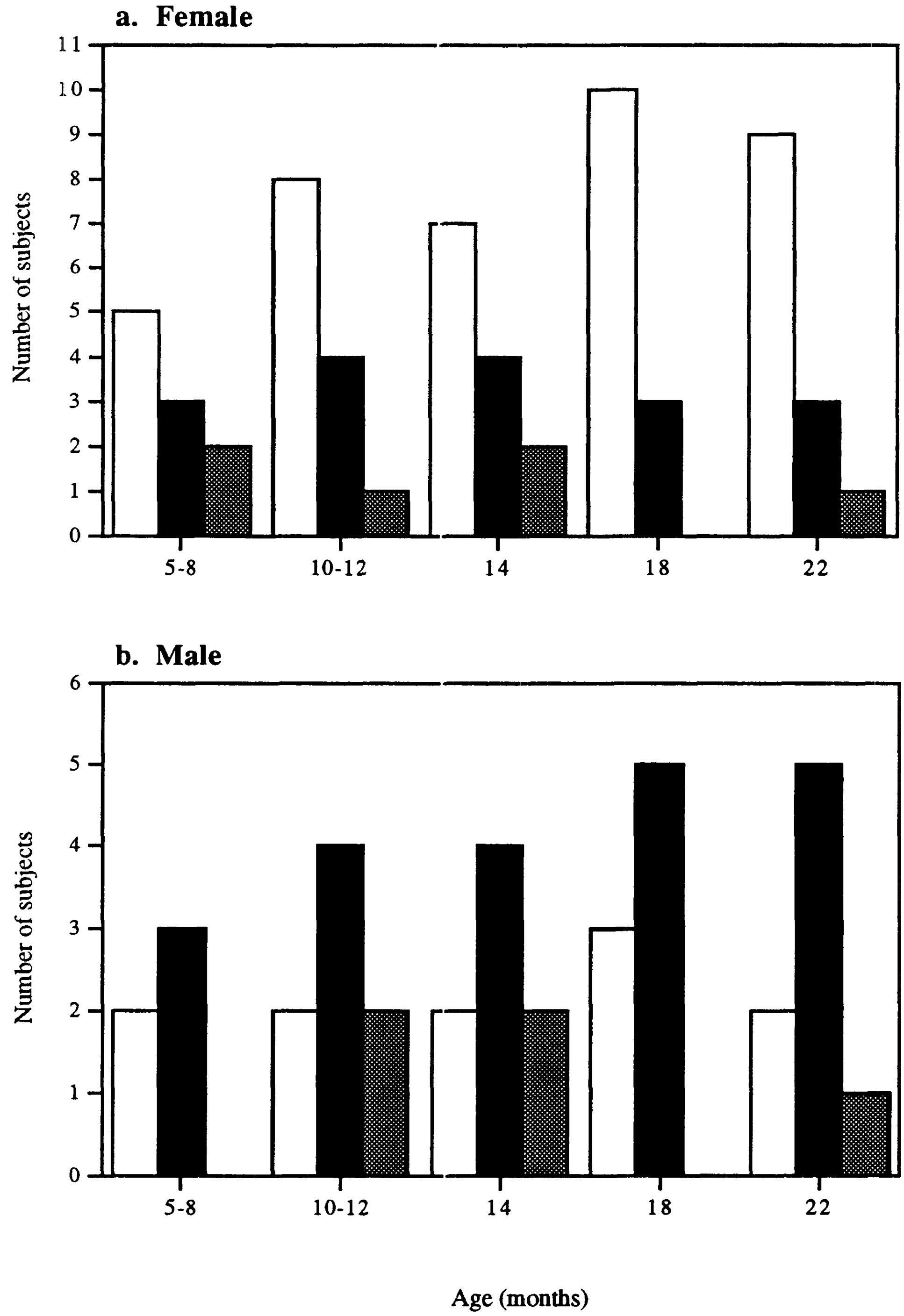

Figure 3.11 The distribution of hand preferences in the male and female subgroups. Figure 3.11a displays the distribution of hand preferences in the female subgroup and figure 3.11b the distribution in the male subgroup at each age. The number of subjects displaying left (□), right (■) or no significant hand preference (▩) is shown on the y axis.

hand preferences than those in Family Group 2 and Family Group 3 (Mann Whitney U, Group 1 versus 2, U= 0, p= 0.01, Group 1 versus 3, U= 3.50, p= 0.05; Figure 3.12). There was no difference between the strength of hand preferences displayed by juveniles belonging to the Groups 2 and 3 (Mann Whitney U, U= 6, p= 0.56).

It seemed that the strength of hand preferences of subjects in Group 1 may have developed earlier than those of the latter two groups. This hypothesis was confirmed when the percentage increase in strength of preference between 5-8 and 10-12 months

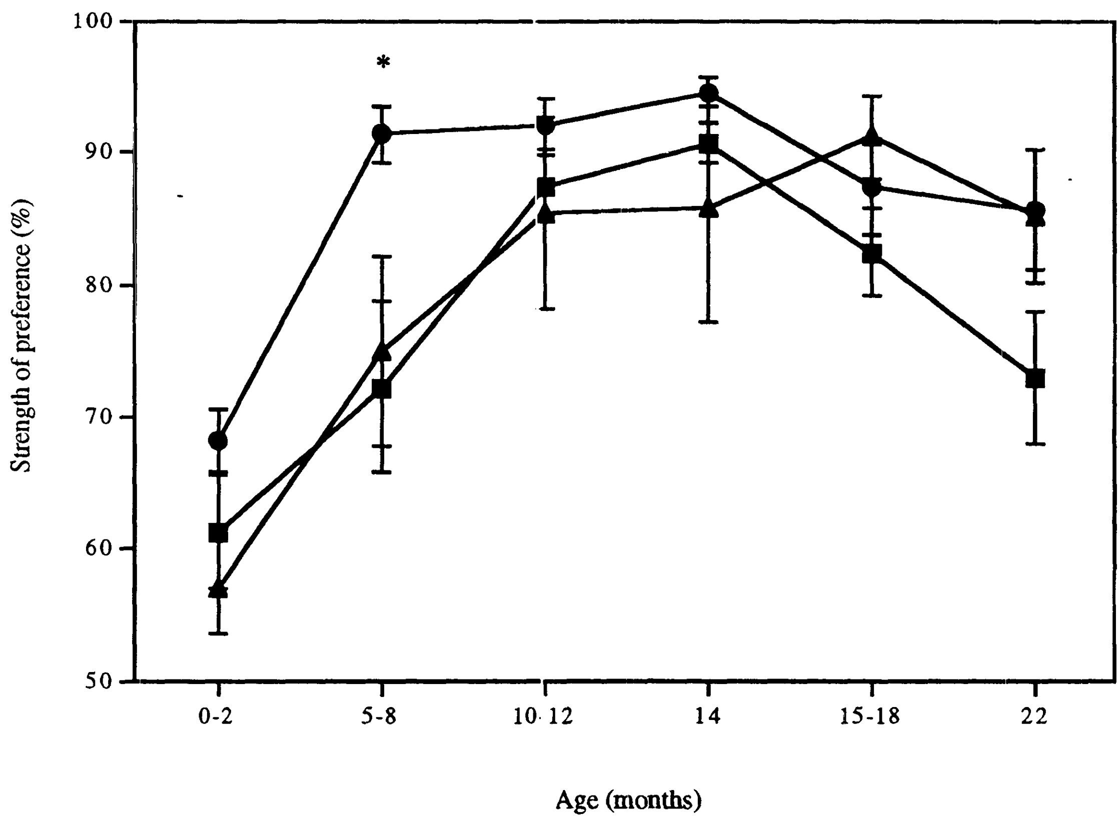

Figure 3.12 The effect of family group on the strength of hand preferences. The mean strength (± SEM) of preference (%) for each family group is graphed. The strength of individual preferences is defined as the absolute percentage use of the preferred hand regardless of the direction of the bias. Family Group 1 is represented by the circles (●), Family Group 2 by the squares (■) and Family Group 3 is plotted as the triangles (π). The ages at which the subjects were tested are depicted on the x axis. The asterisk denotes a significant difference between groups at 5-8 months (* p≤ 0.05).

of age was compared between family groups (Kruskal Wallis, H= 7, p= 0.03). *Post hoc* Mann Whitney U tests revealed that juveniles in Groups 2 and 3 (mothers= Red, Black respectively) displayed a significantly greater increase in strength of hand preferences between 5-8 and 10-12 months compared with juveniles in Group 1 (Mann Whitney U; Group 1 versus 2, U= 2, p= 0.02; Group 1 versus 3, U= 1, p= 0.01). This can be seen in Figure 3.12. There was no significant difference between the percentage increase in strength of preferences displayed by Groups 2 and 3 between 5-8 and 10-12 months (Mann Whitney U, U= 7, p= 0.77). However, there was also no significant difference between family groups in the degree of change in strength of preferences between 0-2 and 5-8 months (H= 3.5, p= 0.17). Although not significant, it can be seen in Figure 3.12 that subjects in Group 1 did display stronger preferences than those in Groups 2 and 3 at 0-2 months, and there does appear to be a steeper rate of increase between 0-2 and 5-8 months for subjects in Group 1.

Effect of early experience on hand preferences

Early experience did not affect the percentage left-hand use displayed by the subjects at any age (Mann Whitney U, p>0.36 in all comparisons). However, as shown in Figure 3.13, significant effects of experience on the strength of hand preferences were found at 10-12, 14 and 22 months of age (Mann Whitney U; 10-12 mths, U= 6, p= 0.002; 14 mths, U= 4, p= 0.001; 22 months, U=13.5, p= 0.03). Subjects in Experience Group 2 displayed significantly stronger hand preferences than subjects in Experience Group 1 at these ages. Comparisons between the strength of preferences displayed by subjects in the two Experience Groups at 15-18 months of age did not reveal a significant difference between the groups (Mann Whitney U, U= 29, p= 0.21).

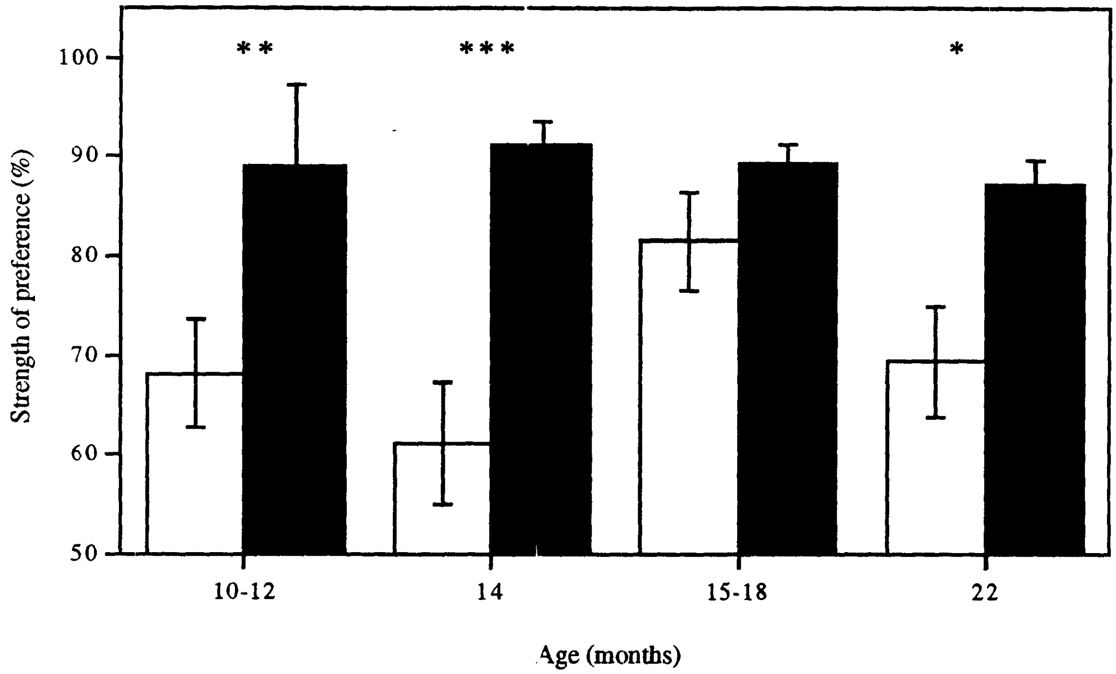

Figure 3.13 The effect of early experience on the strength of preferences for simple food holding. The mean strength of preferences for simple food holding displayed by subjects in Experience Group 1 (□) and Experience Group 2 (■) are presented at various ages (x axis). Comparisons between the strength of preferences displayed by subjects in the two groups showed that subjects in Experience Group 2 displayed significantly stronger preferences for simple food holding than subjects in Experience Group 1 at 10-12, 14 and 22 months (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$). There was no significant difference between the hand preferences displayed by subjects in the two groups at 15-18 months.

3.4 DISCUSSION

The development and distribution of hand preferences

Most of the infant marmosets (0-2 months) did not display significant preferences for simple food holding, although this result may have been due to the limited incidence of unimanual food holding observed during this period. Almost 50% of hand use for simple food holding in the infancy period was bimanual. Bimanual hand use significantly decreased (43%) between 0-2 and 5-8 months, and at 5-8 months all of the subjects displayed less than 10% bimanual hand use for simple food holding. This low incidence of bimanual food holding was maintained from 5-8 to 22 months. The decrease in bimanual hand use (i.e. increasing unimanual hand use) between 0-2 and 5-8 months of age in marmosets may reflect maturation and experience leading to increased neural control of the hands, as has been suggested by other authors (Ward et al. 1990; Adam-Curtis and Fragaszy, 1994). This hypothesis is also supported by the suggestion of an inverse relationship between bimanual hand use for simple food holding and the strength of unimanual hand preferences. The strength of unimanual hand preferences significantly increased between 0-2 and 10-12 months of age.

There were only slight differences between left and right-hand preferent subjects in the development of hand preferences for simple food holding. Both left and right-hand preferent subjects displayed decreasing bimanual hand use for simple food holding between 0-2 and 10-12 months with a concurrent increase in the strength of unimanual hand preferences. However, while the strength of unimanual hand preferences tended to plateau after 10-12 months in the left-hand preferent group, the right-hand preferent subjects displayed an increase in the strength of preferences until 14 months. Then between 15-18 and 22 months the right-hand preferent subjects displayed a significant decrease in the strength of their hand preferences, making the strength of preferences in the two subgroups equal. As there was no concurrent increase in bimanual hand use for the right-hand preferent group this change reflects increased left-hand use in these subjects. It was shown, however, that the right-hand preferent subjects still displayed significant right-hand preferences at 22 months.

The results of this study confirm those of previous studies with marmosets (Box, 1977a; Matoba et al. 1991) revealing a bimodal distribution of hand preferences at the group level. This study also extends previous studies by demonstrating that the bimodal distribution of hand preferences is present by the juvenile stage of development, even though previous hypotheses have suggested that immature primates might not display significant hand preferences (MacNeilage et al. 1987; Fagot and Vauclair, 1991). Also, despite the lack of significant hand preferences for simple food holding in infancy, it was found that the infant marmosets held food more often in the hand that they preferred later in life. The majority of marmosets tested longitudinally showed significant preferences for use of one hand in feeding by 5-8 months of age, and at 10-12 months all of the subjects tested displayed significant hand preferences. There was no change in the direction of hand preference with age for any subject. All of the subjects tested in the longitudinal analyses displayed the same hand preferences at 5-8 months and 22 months. Subjects tested at older ages (25-30, 31-40 and 41-50), also displayed the same significant hand preferences that they had displayed at 5-8 months. Thus, in this study it was demonstrated that hand preferences for simple food holding displayed by immature subjects are indicative of their lateralization in later life, and are retained over very long periods of time.

Gender did not affect the distribution of hand preferences significantly, possibly because of the small sample sizes, but it was shown that females displayed more left-hand use than males at 22 months. This result differs from the results of Matoba et al. (1991). Matoba et al. (1991) found no effect of gender on the direction of hand preferences. There is, in fact, very little evidence for an influence of gender on hand preferences in nonhuman primates. Most of the reports of gender effects on hand preferences are for prosimians, and they suggest that there are increased left-hand preferences in males compared to females (Milliken et al. 1989; Milliken et al. 1991a; Mason et al. 1995), which is opposite to the finding with the marmosets in this study. As Matoba et al. (1991) did not find an influence of gender on hand preferences with a larger colony of marmosets, it is proposed that gender might not influence hand preferences in marmosets directly. It is possible that the gender effects found in this study were secondary to another variable, such as the maternal influence found by Matoba et al. (1991).

Although examination of the maternal influence on hand preferences was not possible in the present study, the effects of lack of parental care and family group membership were considered. It was found that the lack of parental care and or/ stressful conditions prevented the development of stable hand preferences. Four of the six founding marmosets did not display significant hand preferences until 15-18 months of age. These subjects experienced less parental care and more stressful housing conditions in their first 6 months of life than subjects born and raised at the University of New England (Chapter 2, pp. 47-48). Moreover, it was found that subjects in the offspring group (Experience Group 2) displayed significantly stronger hand preferences that the founding marmosets at all ages except 15-18 months. Hopkins (1993) also found that early experience influenced the hand preferences of infant chimpanzees when reaching for food. He found that infant chimpanzees raised with their mother's displayed decreased percentage right-hand use when reaching for food compared with infant chimpanzees that were nursery raised (Hopkins, 1993). In the discussion of these results, Hopkins (1993) suggested that this difference was due to the nursery raised chimpanzees displaying stronger hand preferences. It was noted, however, that there was no interaction between the strength of hand preferences and rearing experience (Hopkins, 1993). Thus, the results with the infant chimpanzees indicate that rearing experience might influence the direction of hand preferences also. The significant differences found between the hand preferences displayed by marmosets, and chimpanzees, raised in different environments indicates that early experience might be very important in the development of preferences for simple food holding and reaching.

Furthermore, family group membership may influence the rate of establishment of stable hand preferences. Light Blue's offspring (Family Group 1) developed stable hand preferences, for both direction and strength, by 5-8 months of age. The significant increase in strength of hand preferences found between 5-8 and 10-12 months of age was due to subjects in Family Groups 2 and 3. Stabilization of the hand preferences of subjects in Family Groups 2 and 3 occurred by 10-12 months of age. Box (1975, 1982) noted striking 'temperamental differences' between marmoset family groups. Observations of the behaviour of the family groups included in this study also suggest distinct temperamental differences between groups. The three experimenters that worked with the marmosets at the University of New England indicated that Family Group 1 was the calmest group, and the most willing to participate in testing. The results of this study, therefore, suggest that even small amounts of instability in the social environment might delay the development of both the strength and direction of hand preferences in marmosets.

Comparisons with other nonhuman primate species

The age effects on hand preferences found in the longitudinal study are in accordance with those found for tamarins (King, 1995). Both species displayed increases in the strength of hand preferences with age and no effect of age on the direction of hand preferences. There is some discrepancy between marmosets and tamarins, however, in the timing of stabilization of hand preferences. King (1995) reported a significant positive correlation between strength of preference and age in tamarins ranging in age from 4 months to 11 years, whereas the marmosets observed longitudinally in this study displayed stable hand preferences for both strength and direction by 12 months of age. Evidence that marmosets (*Callithrix jacchus*) carry and provide for infants for a shorter period of time than the *Saguinus* species (Tardif et al. 1993) would be consistent with the finding that the rate of development of lateral biases differs between these primate groups. Tardif et al. (1993) proposed that there might be a relationship between the foraging patterns of a species and the duration of direct infant care required to produce viable offspring. They suggested that infant *Callithrix jacchus* may be able to forage independently earlier because in their natural habitat the dietary resources of this species are distributed in a small area. By contrast, the food resources of *Saguinus oedipus* are widely dispersed and, thus, infants may have to be carried for a longer period so that they may remain with their group. Differences in foraging patterns and the duration of direct infant care between the two species may, possibly, be consistent with differences in the rate of development of hand preferences.

Different foraging strategies may also explain the lack of handedness at a population level in marmosets, compared with tamarins that have right handedness (Diamond and McGrew, 1994; King, 1995). The fundamental difference between marmosets and tamarins is the evolution of modified lower anterior dentition for bark gouging in marmosets and not tamarins (Rosenberger, 1978; Ferrari, 1993). Although both tamarins and marmosets feed on plant exudates, the marmosets gouge holes while the tamarins use the holes made by other animals (Ferrari, 1993). The common marmoset (*Callithrix jacchus*) spends 15-29% of its foraging time gouging to extract gum exudate using the mouth as a foraging instrument rather than the hands (Rylands and de Faria, 1993). Less use of the hands in acquiring food might lead to less evolutionary selection for handedness in the gouging species of marmosets. This hypothesis could be examined by comparing the distribution of hand preferences of *Callithrix jacchus,* a gouging marmoset species, with a distribution in another marmoset species, such as *Callithrix humeralifer,* that spends less of its foraging time tree gouging (Rylands and de Faria, 1993).

Other differences in foraging strategies of marmosets and tamarins may also contribute to their differences in handedness. Rylands and de Faria (1993) describe the marmosets' foraging strategy as 'a stealthy stalk and pounce, foliage-gleaning method', while Garber (1993) indicates that tamarins 'explore crevices and knotholes, rummage through palm fronds, jumping rapidly to ground to seize cryptic prey'. These descriptions imply that the tamarins may employ a more manipulative strategy when foraging, perhaps leading to increased right handedness in these species as suggested by MacNeilage et al. (1987). The leaping and landing employed in the tamarins' foraging strategy may also affect their handedness perhaps leading to a division of function between the hands with one used to lead while leaping and the other, perhaps the right hand, to grasp the food object.

There appear to be distinct differences in the age effects on hand use found for marmosets and tamarins compared with prosimians (their evolutionary ancestors) and later evolving New World primates. For both prosimians and capuchins, there is evidence that the proportion of individuals with right-hand preferences increases with age (Forsythe and Ward, 1988; Ward et al. 1990; Ward et al. 1993; Westergaard and Suomi, 1993a; Westergaard et al. 1997). In the prosimians there seems to be a shift from ambipreference toward right-hand preferences during development (Ward et al. 1990). Ward et al. (1990) found that the strength of hand preferences, in a variety of lemur species, increased between 0-2 years and 3-6 years of age. They also found that there was a marked decrease in the proportion of ambipreferent subjects when groups tested at 12 and 24 months of age were compared. Again, the rate of development of hand preferences in the prosimians appears to be significantly slower than the marmosets. The slower rate of hand preference development in prosimians, compared with marmosets, may reflect the later development of independence in prosimian infants as in tamarins. Napier and Napier (1967) indicate that lemur infants are completely independent at 6 months of age, whereas marmoset infants begin to feed independently at around 1 month of age (Box, 1975; Missler et al. 1992; Yamamoto, 1993).

In capuchins, *Cebus apella*, there is a greater proportion of right-hand preferent individuals among adult groups compared with juvenile groups. Westergaard and Suomi (1993a) found that whereas all of the juvenile subjects they tested when reaching for food were left-hand preferent, 12 of 15 adults were significantly right-hand preferent. Increases in the strength of hand preferences with age have been found in capuchins also (Lacreuse and Fragaszy, 1996). However, distinction must be made between prosimians and capuchins. In the prosimians the shift toward right-hand preferences with increasing age appears to have been due to increased strength of preferences in ambipreferent subjects (Ward et al. 1990), whereas the data for the capuchins suggest a change in the direction of preferences with age (Westergaard and Suomi, 1993a). Nevertheless, as both of these species have been examined with cross-sectional analyses only, it is difficult to make a firm conclusion on the exact changes that occur with increasing age. At present the data collected for marmosets do not indicate directional shifts in hand preferences with increasing age, although it is acknowledged that the hand preferences of the marmosets may change in later life. In fact, one female subject displayed changed direction of hand preference, from left to right, between 41-50 and 51-60 months.

Relationships between feeding posture and hand preferences for simple food holding

Analysis of the longitudinal development of preferred postures in feeding indicated that posture may be related to hand preferences for feeding in marmosets, as MacNeilage et al. (1987) suggested. Although there was no relationship between the development of preferred feeding postures and the incidence of bimanual hand use, several significant interactions between unimanual hand preferences and the posture assumed in feeding were found. When the development of preferred feeding postures was examined across all subjects in the longitudinal analysis, it appeared that the tripedal posture was adopted significantly more often than both seated and the suspended postures. However, when preferred feeding postures across age were examined in left and right-hand preferent subjects separately, it was found that left-handed subjects had only a weak preference for the tripedal posture, and at 5-8 months of age there was no preferred posture. Right-handed marmosets displayed preferences for the tripedal posture rather than seated or suspended postures at all ages. Moreover, the percentage occurrence of the tripedal posture during feeding was significantly greater for right-hand preferent subjects than left-hand preferent or ambipreferent subjects at 5-8, 14 and 15-18 months. These results suggest that posture may play a role in the development of hand preferences. Whether posture influences hand preferences or vice versa cannot, however, be confirmed.

According to MacNeilage et al. (1987) the right side of the body is specialized for postural control in New World primates. It has been shown that muscle and bone weights differ between the left and right arms in frogs (Singh, 1971), rabbits (Singh, 1971), macaques (Dhall and Singh, 1977; Falk et al. 1988) and in humans (Pande and Singh, 1971; Chhibber and Singh, 1972). In macaques, and in humans, it has been shown that most muscles and bones tend to be heavier on the right side (Pande and Singh, 1971; Chhibber and Singh, 1972; Dhall and Singh, 1977; Falk et al. 1988). On the basis of these asymmetries, MacNeilage et al. (1987) proposed that the right side of the body should be used for postural control. There is some evidence to support this hypothesis. For example, Diamond and McGrew (1994) found that the tamarins lost their right-hand preferences when they assumed a vertical posture. As mentioned previously, they suggested that the decreased right handedness in tamarins when feeding in suspensory postures, compared to tripedal postures, might reflect a trade off between using the more efficient forelimb for maintaining posture against its use for performing the task (Diamond and McGrew, 1994). Thus, suggesting that the right side of the body might be specialized for postural control in tamarins.

It is proposed that, unlike the tamarins, posture does not influence the direction of hand preferences in adult marmosets, but that it might have a role in the development of hand preferences in marmosets. Use of the tripedal posture by the right-hand preferent juveniles might have led to a decreased need for postural control during simple food holding. MacNeilage et al. (1987) proposed that the role of the right limb in postural control might also have led to specialization of this limb for fine somatic sensorimotor control in New and Old World primates. Therefore, subjects that preferred to eat in a tripedal posture at 5-8 months might have used the right hand to hold food as it was better for holding and manipulating the object. A significant negative correlation was found between the percentage occurrence of the tripedal posture during simple food holding and percentage left-hand use in the juvenile subjects. Conversely, there was suggestion of a positive relationship, although not quite significant, between percentage left-hand use and the percentage occurrence of the suspended posture at 5-8 months. The left-hand preferent subjects' increased use of more demanding postures, such as the suspended and seated postures, at 5-8 months may have made it necessary for the right side of the body to be used for postural support leading to left-hand preferences for simple food holding, as proposed by MacNeilage et al. (1987).

The absence of a relationship between hand preferences and posture in the subadult or adult marmosets suggests that when hand preferences have been established, feeding postures no longer influence the direction of preference or vice versa. It is possible that the dominance of the right side of the body for postural control changes with experience. It has been shown that experience influences anatomical asymmetries in humans. Although human foetuses display a larger *pectoralis major* on the left arm (Pande and Singh, 1971), human adults have a heavier right *pectoralis major* muscle (Chhibber and Singh, 1972). This suggests that preferential use of the right arm by most human adults may modify the pattern of asymmetry present at birth (Pande and Singh, 1971). In the marmosets also, the influence of any postural asymmetries present at birth may be masked or even reversed with the establishment of a hand preference in feeding. It was found that both left and right-handed subjects displayed their strongest preferences in the stable tripedal posture after 10-12 months. Thus, it can be concluded that if posture is influencing the direction of hand preferences it must occur before 10-12 months of age

It is possible that hand preferences influence the feeding postures adopted by left and right-hand preferent subjects rather than vice versa. The left and right-hand preferent juvenile marmosets may choose to feed in different postures. Juveniles that chose to use the left-hand for simple food holding would be able to feed in any posture as they could always use the right side of the body for postural control leaving the left hand free for manipulating objects. By contrast, juveniles that preferred to use the right hand for simple food holding might be forced to adopt a tripedal posture in feeding, so that the need for postural control would be reduced. Preferences for the left or right hand for simple food holding might reflect underlying cognitive or temperamental differences between the juvenile subjects. Recent findings of cognitive (Horster and Ettlinger, 1985; Hopkins et al. 1992; Hopkins and Washburn, 1994), social (Stafford et al. 1990) and temperamental differences (Hopkins and Bennett, 1994; Watson and Ward, 1996) between left and right-hand preferent primates suggest that directional hand use may be indicative of other aspects of temperament or cognitive function on which selective pressures may operate. This would imply that the hand preferences of the subjects reflect underlying hemispheric specializations for perceptual or cognitive processes rather than motor specializations. It may be proposed that left-hand preferent marmosets feed more in suspended strategically-defensive positions to reduce the directions from which challengers may approach. That is, other individuals attempting to steal their food cannot approach from the frontal position when the marmoset is suspended and thus, if the defender of the food switched hands when approached laterally they could prevent their food from being taken. Right-hand preferent subjects might simply feed in the stable, and yet frontally vulnerable, tripedal posture. It has been shown that right-hand preferent chimpanzees tend to approach novel objects faster than left-hand preferent chimpanzees (Hopkins and Bennett, 1994), and it has been proposed that this approach-avoidance behaviour might reflect different affective states in these hand preference subgroups. While further research is needed to determine whether posture influences hand preferences or vice versa, or if both posture and hand preferences operate in conjunction, the data collected in this study indicate that posture does play a very important role in the development of hand preferences.

As mentioned, as adults all of the marmosets displayed stronger hand preferences when feeding in the stable tripedal posture in comparison to those displayed when feeding in both seated and suspended postures. Tamarins also display stronger hand preferences when feeding in tripedal postures compared to vertical postures (Diamond and McGrew, 1994). In fact, Diamond and McGrew (1994) reported that tamarins did not display right handedness when feeding in the vertical postures, yet they did when feeding in the tripedal posture. The influence of posture on the strength of preferences in marmosets and tamarins appears to be opposite to that found in other primate species including prosimians and capuchins. Sanford et al. (1984) demonstrated that bipedalism intensified hand preferences in the lesser bushbaby (*Galago senegalensis*). Westergaard et al. (1997) also found that capuchins (*Cebus apella*) exhibited right handedness when they reached for food from a bipedal posture but not from a tripedal posture. Only marmosets and tamarins have been reported to display their strongest hand preferences when feeding in stable, rather than unstable, postures.

Overall, it has been shown that the factors that effect hand preferences in the marmosets are, for the most part, consistent with those reported in the closely related tamarin species, *Saguinus oedipus*. Age, gender and postural effects on hand use are similar for the two species, although age and posture appear to have more influence on hand preferences in adult tamarins compared to adult marmosets. Also, it appears that the influences of age and posture on hand preferences in both marmoset and tamarins may differ from those of prosimians and capuchins (Sanford et al. 1984; Ward et al. 1990; Westergaard and Suomi, 1993a; Westergaard et al. 1997). Nevertheless, despite the similar effects of variables on lateralization in marmosets and tamarins, the distribution of hand preferences is very different in the two species. Marmosets have no handedness whereas tamarins have right handedness (Diamond and McGrew, 1994; King, 1995). Neither marmosets nor tamarins display the left handedness postulated by MacNeilage et al. (1987) for arboreal primates.

3.5 SUMMARY

Marmosets do not have handedness for simple food holding, instead hand preferences are bimodally distributed at the group level. This bimodal distribution of hand preferences for simple food holding was present in juvenile subjects (5-8 months) tested and was shown at all stages of development. Thus, hand preferences develop very early in marmosets and are retained for long periods of time. However, it was shown that several variables delay the development of hand preferences in marmosets. Lack of parental care, stressful housing conditions and even minor stressors such as temperamental differences between family groups delayed the development of hand preferences for simple food holding. Gender was also found to influence the direction of hand preferences displayed by the subjects, with females displaying increased percentage left-hand use, but it is suggested that this variable might be secondary to other effects such as parental influence.

Significant relationships were found between the postures adopted during feeding and the direction of hand preferences displayed by juvenile subjects, but not adult subjects. The relationship between increased suspension and increased left-hand use for simple food holding, together with the decreased left-hand use with increased feeding in a tripedal posture could suggest that in juvenile marmosets the right side of the body might be specialized for postural control, as MacNeilage et al. (1987) suggested. Alternatively, hand preferences for simple food holding might influence the posture preferred during feeding. There is no relationship between posture and hand preferences in adult marmosets.

Despite findings of interactions between posture and hand preferences in juvenile marmosets, which might concur with the hypothesis of MacNeilage et al. (1987), the lack of handedness in the marmosets does not support the proposal that New World primates should show left handedness in feeding (MacNeilage et al. 1987). It is proposed that manual specialization might have been lost or might not have evolved in marmosets. Decreased use of the hands in foraging, with increased use of the mouth for gum exudate feeding, might have led to the lack of handedness in common marmosets.

Other researchers have suggested that nonhuman primate species do not have hemispheric specialization if they do not have handedness (MacNeilage et al. 1987). On the basis of this assumption, the results of the experiments reported in this chapter would indicate that common marmosets do not have hemispheric specialization. However, as will be shown in the remaining chapters of this thesis, this is not the case.