CHAPTER 7

LATERALIZED MOUTH OPENING AND EYE MOVEMENTS IN THE PRODUCTION OF FACIAL EXPRESSIONS AND VOCALIZATIONS

7.1   INTRODUCTION

The experiments reported in this chapter examined asymmetries of mouth opening and other facial features during the production of a fear expression and during the production of two types of vocalization. The aim was to determine whether the marmosets have hemispheric specialization for the control of negative emotional responses, as proposed in the previous chapter, and also to determine whether they might have hemispheric specialization for the production of vocal signals. Asymmetries of visual or vocal communication functions are now known to be present in a range of species but there have been no previous investigations of the lateralization of marmosets or of other New World primates.

Asymmetrical movements in the production of facial expressions and speech are indicative of hemispheric specializations for communication in humans. Negative emotional responses are expressed more intensely on the left side of the face in humans (e.g. Wolf and Goodale, 1987; Schiff and MacDonald, 1990; Kowner, 1995). Since each side of the face is controlled by the contralateral hemisphere, these results indicate that the right hemisphere is specialized for the control of emotional responses. During speech the right side of the mouth opens first and wider (Sackeim et al. 1978; Graves et al. 1985; Hager and van Gelder, 1985; Graves et al. 1990), reflecting the specialization of the left hemisphere for the production of speech (Sperry, 1964; Segalowitz and

Bryden, 1983).

Recent findings of lateralization for both production and perception of visual and vocal communication signals in a wide range of nonhuman species demonstrate that these hemispheric specializations are not unique to humans (for reviews see Rogers and Bradshaw, 1996 and Bradshaw and Rogers, 1996). Like humans, rhesus macaques (*Macaca mulatta*) have specialization of the right hemisphere for the production of fear expressions (Hauser, 1993). To measure hemiface asymmetries in rhesus macaques, Hauser (1993) recorded the side of the mouth that began to move first when the macaques produced fear expressions. He found that the left side of the mouth opens first during the production of fear expressions (Hauser, 1993). Left-left hemiface chimeras of the macaques producing a fearful expression were also perceived by human judges as more 'expressive' (Hauser, 1993) than right-right chimeras. It is possible that macaques also perceive the left hemiface of the fear expression as being more expressive, but this was not measured in the same study (Hauser, 1993). However, specialization of the right hemisphere for discriminating between faces of different individuals and for discriminating different emotional expressions has been shown to be characteristic of rhesus macaques by other researchers (Ifune et al. 1984; Hamilton and Vermeire, 1988), as outlined in Chapter 1 (pp. 37-39).

A number of researchers have found that Japanese macaques (*Macaca fuscata*) have specialization of the left hemisphere for perception of vocal communication signals (Dewson, 1977; Petersen et al. 1978; Heffner and Heffner, 1984; Petersen et al. 1984; Hauser and Andersson, 1994). Japanese macaques display a right-ear advantage, and thus left hemisphere specialization, for discriminating between subtypes of conspecific 'coo' vocalizations, a vocalization produced in a variety of social contexts (Heffner and Heffner, 1984; Petersen et al. 1984). Thus, it appears that hemispheric specialization for the perception of species-specific vocalizations may be present in nonhuman primate species and not humans only.

In fact, there is now evidence that the left hemisphere may be specialized for the

perception and production of species-specific vocalizations in a variety of species, including frogs (Bauer, 1993), mice (Ehret, 1987), gerbils (Hollman and Hutchison, 1994) and birds (Nottebohm et al. 1976). It has been shown that frogs, gerbils and birds have specialization of left hemisphere for the production of species-specific vocal signals. Bauer (1993) compared the number of release vocalizations (emitted when a male or nongravid female mounts another male) produced by frogs (*Rana pipiens*), following lesions of the left or of the right hemisphere. He showed that the number of vocalizations produced, when frogs were clasped with a human hand, was significantly reduced in individuals subjected to lesions of the left hemisphere, compared to those with right-hemisphere lesions, sham-operated animals and unoperated controls. Similarly, lesioning of the left 'higher vocal centre' in canaries (*Serinus canarius*) has been shown to significantly disrupt song production (Nottebohm et al. 1976). Although similar lesions of the right hemisphere had a slight effect on the song of the canaries, the effects of these lesions were considerably smaller than those made in the left forebrain (Nottebohm et al. 1976). Sectioning of the left hypoglossal nerve, which is the primary motor output pathway from the left 'higher vocal centre' in songbirds (Nottebohm, 1989), also significantly disrupts song production in chaffinches (*Fringilla coelebs,* Nottebohm, 1970), white-crowned sparrows (*Zonotrichia leucophrys,* Nottebohm and Nottebohm, 1976), white-throated sparrows (*Zonotrichia albicollis,* Lemon, 1973) and in Java sparrows (*Padda oryzivora,* Seller, 1979). Thus, the production of song appears to be controlled by the left hemisphere, via the left hypoglossal nerve, in many species of songbird.

Left hemisphere specialization for the perception of species-specific communication signals has been shown in mice (Ehret, 1987). Ehret (1987) tested lactating house mice on a 'choice test', requiring them to choose between an ultrasonic sound resembling the distress calls of their pups and an ultrasonic sound that bore no resemblance to a species-specific vocal signal. Subjects were tested binaurally or monaurally (i.e. by placing plugs in the left or right ear). In the binaural condition and when hearing with the right ear only (left-ear plugged), the mice approached the sound

of the 'distress call' (Ehret, 1987). By contrast, when the subjects could hear only with the left ear they approached the two sounds randomly (Ehret, 1987). Therefore, it would appear that when using the right ear, and thus left hemisphere, mice were able to recognize the communication signals of the pups, but when using the left ear, and right hemisphere, they could not. This result suggests that in mice the left hemisphere is specialized for the processing of species-specific communication signals (Ehret, 1987). The results with nonprimate species suggest that left hemisphere specializations for the processing of species-specific vocalizations are present in species that evolved as early as amphibia. These specializations seem to have been retained by birds, rodents and primate species, at least.

However, the left hemisphere does not process all types of vocal communication in humans, the right hemisphere is also specialized for processing some vocal signals. For example, it has been shown that the right hemisphere processes the emotional aspects of speech, including the emotional tone of speech (Ley and Bryden, 1982; Bryden and McRae, 1989). It is possible that the right hemisphere also processes the emotional information of vocal signals in macaques, but this has not been tested. There is some evidence that the right hemisphere might process the same types of vocal information in humans and nonhuman species. Indeed, the right hemisphere advantage in humans for discriminating between voicing contrasts, such as 'bah' and 'pah' (Molfese et al. 1983), has also been shown in dogs (Adams et al. 1987) and rhesus macaques (Morse et al. 1987).

It was proposed that, if marmosets have hemispheric specializations for communication functions, they might display greater opening of the right side of the mouth during social communication, as in human speech, and greater opening of the left side of the mouth during the production of negative emotional expressions, including vocalizations indicative of fear. The experiments reported in this chapter compared mouth asymmetries during the production of fear expressions and the 'tsik' call, a mobbing call given in the presence of a potential predator, with those made during the production of a social contact vocalization, the twitter call (Epple, 1968).

7.2   METHODS

To induce fear responses the 'snake model' (described in Chapter 6) was presented directly below a video camera (Sony Hi 8, CCD-TR2000E). The camera was positioned to ensure that the marmoset's face was facing it directly. Presentation of this stimulus elicited fear expressions and tsik vocalizations (Figures 7.1a and 7.1b). For the collection of data for the nonvocalizing and vocalizing expressions, each subject was filmed for 15 minutes per day over a minimum period of 5 days and a maximum of 15 days. The 11 subjects video recorded were adults (older than 22 months).

The twitter call was elicited in the presence of the experimenter with whom the marmosets were very familiar (Figure 7.1c). The marmosets often twitter when the experimenter enters their room. The same twitter call is given in intraspecific social communication (Epple, 1968). Video sequences in which a marmoset twittered and oriented to the experimenter, and thus the camera, were selected. Only faces that were oriented directly toward the camera were selected for analysis. Filming was continued until at least 10 video sequences with twitter calls had been recorded for each of the 9 subjects examined.

The vocalizations were recognized by ear and were checked by looking at sound spectrograms. Spectrograms of the tsik and twitter vocalizations are presented in Figure 7.2. It should be noted that the maximum frequency that could be analyzed using the equipment available was 23 kHz. It can be seen in Figure 7.2a, that the frequency of the tsik calls extends above 23 kHz. The spectrogram presented here shows the tonal structure of the tsik call (Figure 7.2a) but does not illustrate the frequency modulation as shown in the figure of Epple (1968). Epple (1968) has shown that the harmonics of the tsik call can reach up to 60 kHz to 80 kHz. She showed that tsik calls contain a number of harmonics, with the first at around 10 kHz and with others occurring at 10 kHz intervals (Epple, 1968). The twitter call has a frequency range of 5-15 kHz, and could be analyzed with the equipment available. As shown in Figure 7.2b, the contact twitter vocalization is composed of sequences of short notes (0.02-0.04 seconds) separated by intervals of 0.06-0.08 seconds (Epple, 1968).

a1.

a2.

b1.

b2.

c1.

c2.

Figure 7.1   Fear expressions and tsik and twitter vocalizations of marmosets.   This figure shows faces of marmosets when producing tie fear expression (Figure 7.1a1- a4), the tsik vocalization (Figure 7.1b1- b4) and the twitter vocalization (Figure 7.1c1-c4).   Note the distinct differences between the facial expressions.   In the ncnvocalizing fear expression the lower teeth are displayed and the ear tufts are flattened against the head, as can be seen clearly in a3.   For the tsik

a3.   **a4.**

b3.   **b4.**

c3.   **c4.**

vocalization, both the upper and lower teeth are shown and the tufts are either erect (b1 and b3) or flattened against the head (b2 and b4). In the twitter vocalization the teeth are not displayed. Also, compare the left side-of-mouth bias shown clearly in a2 and a3 when producing the fear expression with the right-side bias illustrated in c1 and c2 during the production of the twitter vocalization.
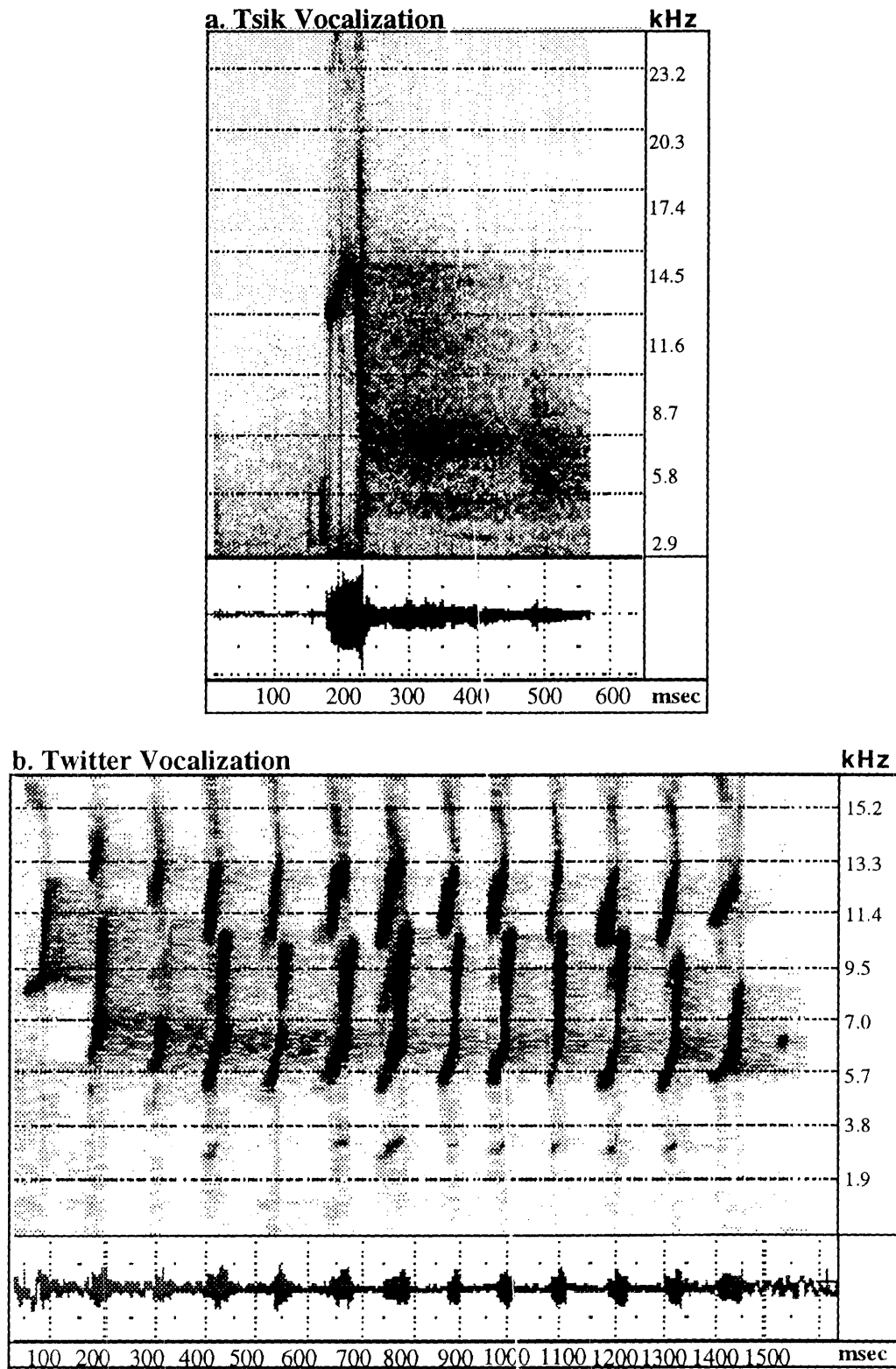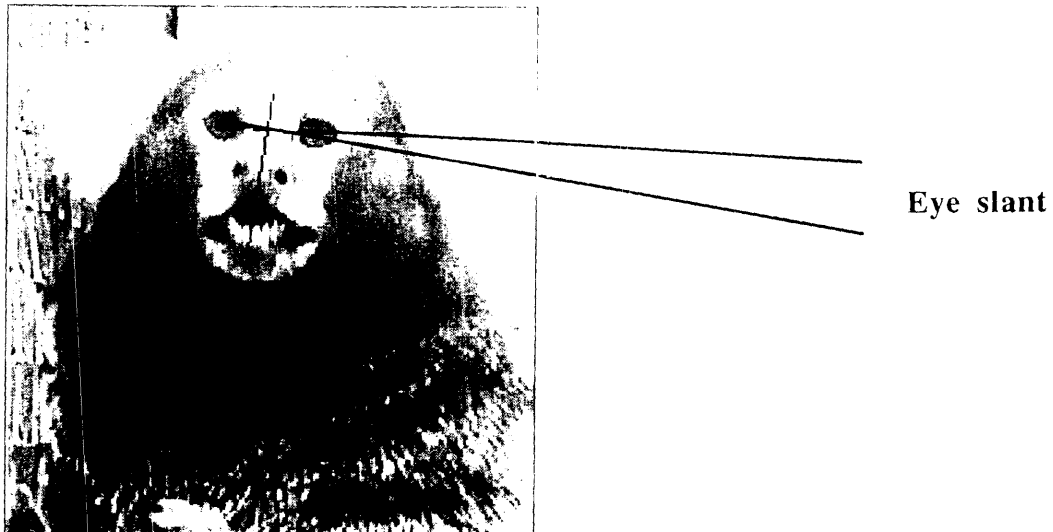
a. Tsik Vocalization

kHz
23.2
20.3
17.4
14.5
11.6
8.7
5.8
2.9

100   200   300   400   500   600   msec

b. Twitter Vocalization

kHz
15.2
13.3
11.4
9.5
7.0
5.7
3.8
1.9

100 200 300 400 500 600 700 800 900 1000 1100 1200 1300 1400 1500   msec

Figure 7.2 Spectrographic representations of tsik and twitter vocalizations. The acoustic structures of the tsik (a) and twitter (b) vocalizations recorded from the marmosets at the University of New England are presented. Frequency (kHz) of the vocalization components are shown on the y axis and the duration (msec) is presented on the x axis. As can be seen in this figure, the tsik vocalization has a tonal structure whereas the twitter vocalization is modulated temporally. The degree of background noise in these signals could not be avoided as the subjects would not vocalize in a soundproof chamber, so the signals had to be collected in their home cages.

Video images were analyzed using frame-by-frame analyses and a videocard program (Apple Video Player). The areas of the left and right halves of the mouth (hemimouth) and the distances from the midline of the face to the lateral corners of the mouth were used as measures of asymmetry. To determine the position of the midline of the face, a line was drawn between the inner canthi of the left and right eyes (Figure 7.3). The midpoint of the line was determined and a perpendicular line was drawn through this midpoint. The perpendicular line dissected the mouth. This line almost invariably passed through the philthral groove where the left and right sides of the top lip meet, confirming the method for halving the face. The midline did not pass through the philthrum in only 2 of 60 faces (20 of each type of expression) examined, or in 3% of cases. Even in the 3% of cases the midline was less than 1mm from the philthral groove.

To measure hemimouth area a line was drawn around the perimeter of the mouth and the area determined (cm^2). For the distance-to-midline measurements a line was drawn from the outer corner of the mouth to the midline (cm). Both area and distance were analyzed using Canvas, a Macintosh program. Measurement of the area (Figure 7.3b) and distance (Figure 7.3c) was replicated three times for each face analyzed. Also, when the outer canthi of the eyes were visible, the slants of the left and right eyes were determined (Overman and Doty, 1982). As shown in Figure 7.3a, to determine the slant of the eye a line was drawn between the inner and outer canthi of each eye. The angle formed between this line and the midline of the face was calculated (Figures 7.3a), and subtracted from 90° to obtain the degree of eye slant. Eye slant data were collected for the nonvocalizing fear expressions and tsik vocalizations only. It was not possible to collect enough information on eye slant for the twitter vocalization because, when the subjects approached the experimenter to twitter, they also moved nearer to the wire mesh wall of the cage and thus in more than half of the facial images analyzed the outer canthi of the eye could not be seen clearly. The wire mesh obstructed the image.

a.

Eye slant

b.   c.

Figure 7.3 Measurements of asymmetries in the production of facial expressions and vocalizations. To determine the midline of the face a line was drawn between the inner canthi of the left and right eyes. The midpoint of this line was determined and a second perpendicular line was drawn through this midpoint dissecting the mouth (midline). The procedures for measuring facial asymmetries are shown in Figures 7.3a, b and c. Eye slant (7.3a) was calculated by determining the angle between the line connecting the inner and outer canthi of the eyes and the midline of the face, and then subtracted from $90°$. The larger the eye slant measurement the greater the displacement of the eye. Area of hemimouth (7.3b) and distance-to-midline (7.3c) measurements were determined using Canvas, a Macintosh drawing program.

Determining a reliable method for collecting data for a large sample of faces

Full frame-by-frame (24 frames per second) analyses of the hemi-areas of the mouth for three production sequences of each type of expression were conducted to determine whether asymmetries vary during the production of facial expressions (Figures 7.4, 7.5 and 7.6). The term 'production sequence' refers to the detailed successive movements of the facial features when producing an expression. For sequences that were 15 frames in duration (or shorter) each frame was analyzed (Figure 7.5). For sequences that were longer than 15 frames in duration, the first and last 5 frames of each production sequence were analyzed and then every third frame between the 5th and 5th last frame was examined (i.e. frame 8, 11, 14 etc.; Figure 7.4). For the expressions with vocalizations, the beginning of a production sequence was defined by the initiation of mouth movement and the sequence continued until the mouth resumed its neutral position. Nonvocalizing fear expressions, however, were longer and not all of a production sequence was directed toward the camera (Figure 7.4). Therefore, these sequences were scored from the time when a subject first faced the camera and continued until the subject turned away. These analyses were used to determine which
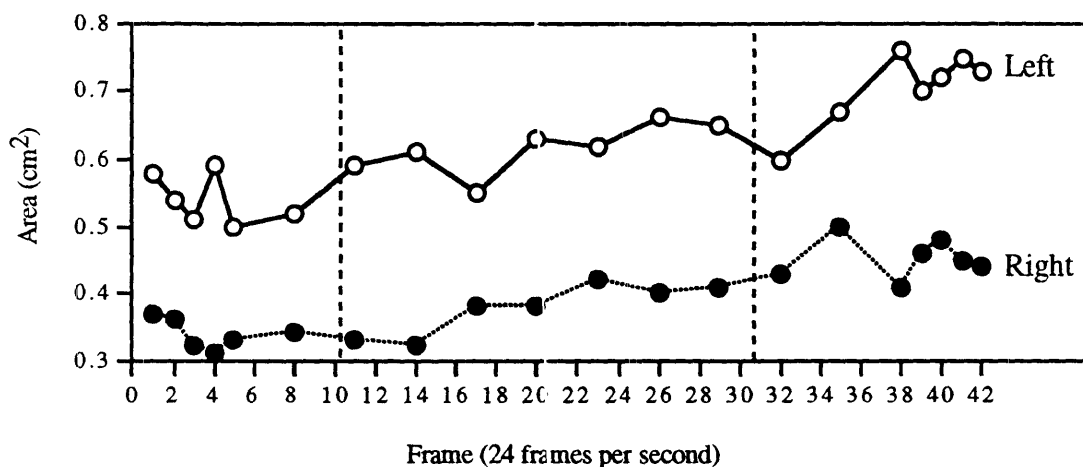

Frame (24 frames per second)

Figure 7.4 Area of mouth opening during the production of a fear expression. Frame numbers (24 frames per second) are presented on the x axis and the area of the hemimouth (cm²) is represented on the y axis. The left side of the mouth is plotted as (O) and the right hemimouth as (●). As the production sequence for this fear expression was longer than 15 frames in length, the first 5 frames and the last 5 frames were analyzed, as well as every third frame in between them (i.e. frame 8, 11, 14). In the collection of a larger sample of fear faces, a frame from the middle of a production sequence (enclosed in the dashed lines) was chosen. Note that the left hemimouth is consistently larger than the right hemimouth in this production sequence.

part of the production sequence, for each expression, would provide the most reliable measure of asymmetry in the total sequence.

An example of a production sequence obtained for a fear expression is presented in Figure 7.4. As can be seen in Figure 7.4, the nonvocalizing fear expression is a fixed expression of long duration (Figure 7.4) in which the lips are drawn laterally and the lower teeth only are bared (Figure 7.1a). The ear tufts are flattened back against the head (Figure 7.1a). The areas of both hemimouths are relatively constant throughout the production of the nonvocalizing fear expression.

When tsik calls are produced the mouth is opened maximally, both vertically and horizontally, to reveal both the upper and lower incisors (Figure 7.1b). As shown in Figure 7.5, the mouth opens and closes rapidly during the production of the tsik
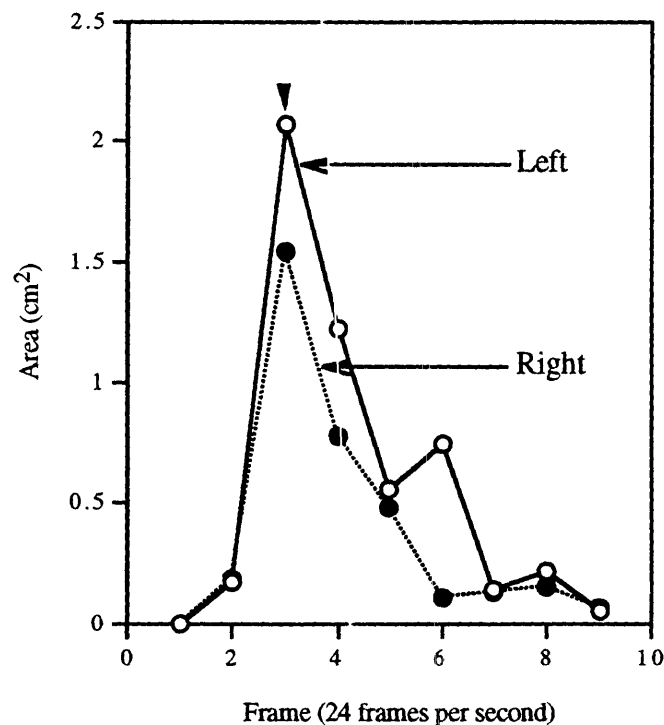

Frame (24 frames per second)

Figure 7.5 Area of mouth opening during the production of a tsik vocalization. An example of a production sequence for the tsik vocalization is presented. Frame numbers (24 frames per second) are on the x axis and the area of the hemimouth (cm^2) is represented on the y axis. The left side of the mouth is plotted as (O) and the right hemimouth as (●). ▼ denotes the maximal expression in the tsik vocalization, in the middle of the sequence, selected for collecting data for the larger sample size. The production sequences for the tsik vocalizations were considerably shorter than those for fear expressions. As can be seen in the figure, this sequence is only 8 frames in length and thus each frame was analyzed.

vocalization. Thus, production sequences for the tsik vocalization were of short duration, compared to the nonvocalizing fear expressions and the twitter vocalizations. The facial expression produced during the tsik call can also be distinguished from nonvocalizing fear expressions by the visibility of the upper incisors during vocalization (Figures 7.1a and 7.1b).

The mouth does not open and close for the production of the series of twitter notes and the area of mouth is relatively constant while producing the vocalization (Figure 7.6). The duration of the production sequences for twitter calls varied from 0.5 seconds to 2 seconds in length. The twitter call depicted in Figure 7.6 is approximately 1 second in duration.
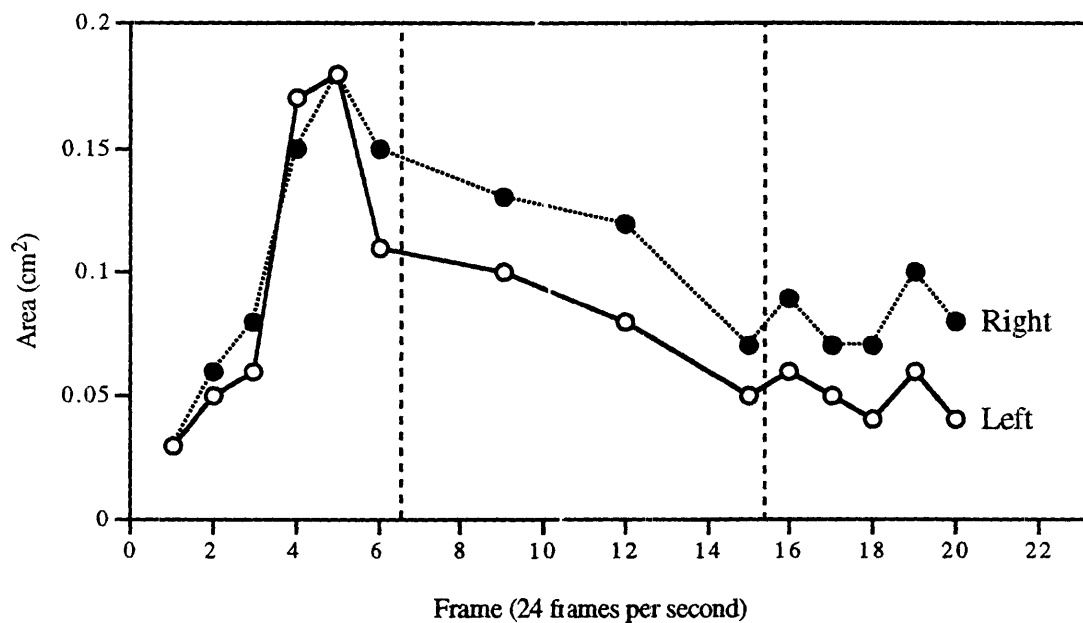

Frame (24 frames per second)

Figure 7.6 Area of mouth opening during the production of a twitter vocalization. A production sequence for a twitter vocalization is presented. Frame numbers (24 frames per second) are presented on the x axis and the area of the hemimouth (cm^2) is represented on the y axis. The left side of the mouth is plotted as (O) and the right hemimouth as (●). In contrast to the fear expression and tsik vocalizations, the right side of the mouth was opened wider than the left for most of the twitter vocalization sequence (frames 6-20). A face from the middle of the sequence (enclosed in the dashed lines) was reliably representative of the total sequence, and faces from this middle section were selected for collecting data for a larger sample size of faces.

The detailed frame-by-frame analyses revealed that a large mid-portion of a production sequence could be selected to represent reliably both the direction and magnitude of the asymmetry of expressions. Detailed frame-by-frame analysis of a large number of production sequences would have been too time consuming in a larger sample of subjects and it was not always possible to score all frames in many of these sequences because the subjects were not facing the camera directly for all frames. Faces that were not oriented directly toward the camera could not be analyzed. Therefore, subsequent data collection of a larger sample size of faces from more individuals involved determining the beginning and end of a production sequence, dividing the sequence into quadrants and selecting a frame from the second or third quadrant for further analysis (Figures 7.4 and 7.6). Selecting faces from the second and third quadrants of the sequences, rather than from only one third of the sequence, increased the probability of finding a clear image that was directly facing the video camera. Only frames with clear images were analyzed. The tsik vocalization was of short duration and it was always possible to select the frame in which the mouth was maximally opened (always in the second or third quadrant; Figure 7.5). Ten faces, each from a different production sequence, were analyzed for each subject and for each type of expression (nonvocalizing fear, tsik, and twitter), recording the left and right hemimouth areas and distance-to-midline measurements and the eye slant for each eye.

7.2.1 Asymmetries of Production of Facial Expressions and Vocalizations : Analysis of an Increased Sample Size of Subjects and Faces

Eleven adult marmosets (7 female, 4 male) were used to determine hemimouth size in the nonvocalizing fear expression. Nine of the same marmosets (5 female, 4 male) were used to examine hemimouth asymmetry in the production of the tsik vocalization. Another group of 9 subjects (6 female, 3 male), also part of the original group of 11 subjects, was used to determine asymmetries of mouth opening in production of the social contact call. It was possible to collect only 5 tsik expressions for one male subject and 5 twitter expressions for another male subject. However, the individual lateralization of these subjects was determined and they were included in the

group analyses.

Individual lateralization and group level biases were examined separately for each type of facial expression and separately for area, distance and eye slant scores. For each individual, Wilcoxon signed rank tests (T+) were used to compare the area, distance-to-midline and eye slant measurements of the left and right sides of the face determined for the 10 faces (or 5 faces in 2 cases) scored per individual. Both area and distance measurements, for the left and right hemimouths, were then standardized by determining the percentage that each hemimouth contributed to the total mouth measurement. To standardize the eye slant measure, the left-eye slant was divided by the eye slant of the left eye added to the eye slant of the right eye. The mean percentage use of the left and right sides of the mouth, and the mean percentage eye slant of each eye, was then calculated for each individual using the 10 faces selected for each expression. The mean percentage left and mean percentage right biases for each individual were used to assess whether group level biases were present for the production of the three different facial expressions.

To determine whether experimenter bias influenced the results of these experiments a second observer reanalyzed the hemimouth area of 50 faces of each expression. The second observer was naive with respect to the expectation for each face. An inter-observer correlation coefficient of 0.95 (p<0.001) was found for the hemimouth area scores, showing that experimenter bias had not effected the lateralization determined.

7.2.2 Comparisons between Lateralization for the Production of Facial Expressions and Side-of-Mouth Preferences for Chewing

The relationships between percentage left-hemimouth biases displayed for the production of the three types of facial expression and percentage left side-of-mouth preferences for chewing (Chapter 4) were examined using Spearman rank correlations.

7.3 RESULTS

7.3.1 Asymmetries of Production of Facial Expressions and Vocalizations : Analysis of an Increased Sample Size of Subjects and Faces

Nonvocalizing fear expression .

For each individual the mean hemimouth area, distance-to-midline and degree of eye slant (expressed as percentage left ±SEM) displayed for the fear expression is presented in Figure 7.7 a-c (see also Appendix A, Table N). As shown in Figure 7.7a, when the areas of the left and right hemimouths were compared, using the 10 scores collected for each individual, 8 of the 11 subjects displayed significant individual biases for a larger left side of the face (Wilcoxon, p≤0.05). The 3 remaining subjects displayed larger left than right-sided expressions but their biases were not significant (Figure 7.7a). For the measure of distance-to-midline, 10 subjects displayed bias (Figure 7.7b). The remaining subject displayed a larger left than right-sided expression but his bias was not significant (Figure 7.7b).

Wilcoxon signed rank analyses comparing the mean percentage of left and right-sided expressions across individuals confirmed that there were significant biases for both the area and distance-to-midline measurements at the group level (Wilcoxon, area and distance-to-midline, $T^+= 11$, p= 0.003 for both measures).

Analysis of the asymmetries of eye slant revealed that 7 of the 11 individuals displayed a larger angle for the left eye rather than the right (Wilcoxon, p≤0.05; Figure 7.7c). This suggests that, during the production of the fear expression, the outer canthi of the left eye was lifted higher than the right eye, even though the mean difference was only equal to 2.79± 0.27%. A significant group bias for the left eye to be lifted higher than the right was found (Wilcoxon, $T^+= 10$, p= 0.004; Figure 7.7c).

Tsik vocalization

Nine marmosets were sampled when producing the tsik vocalization and a significantly larger area of the left side compared to the right side was found for 6
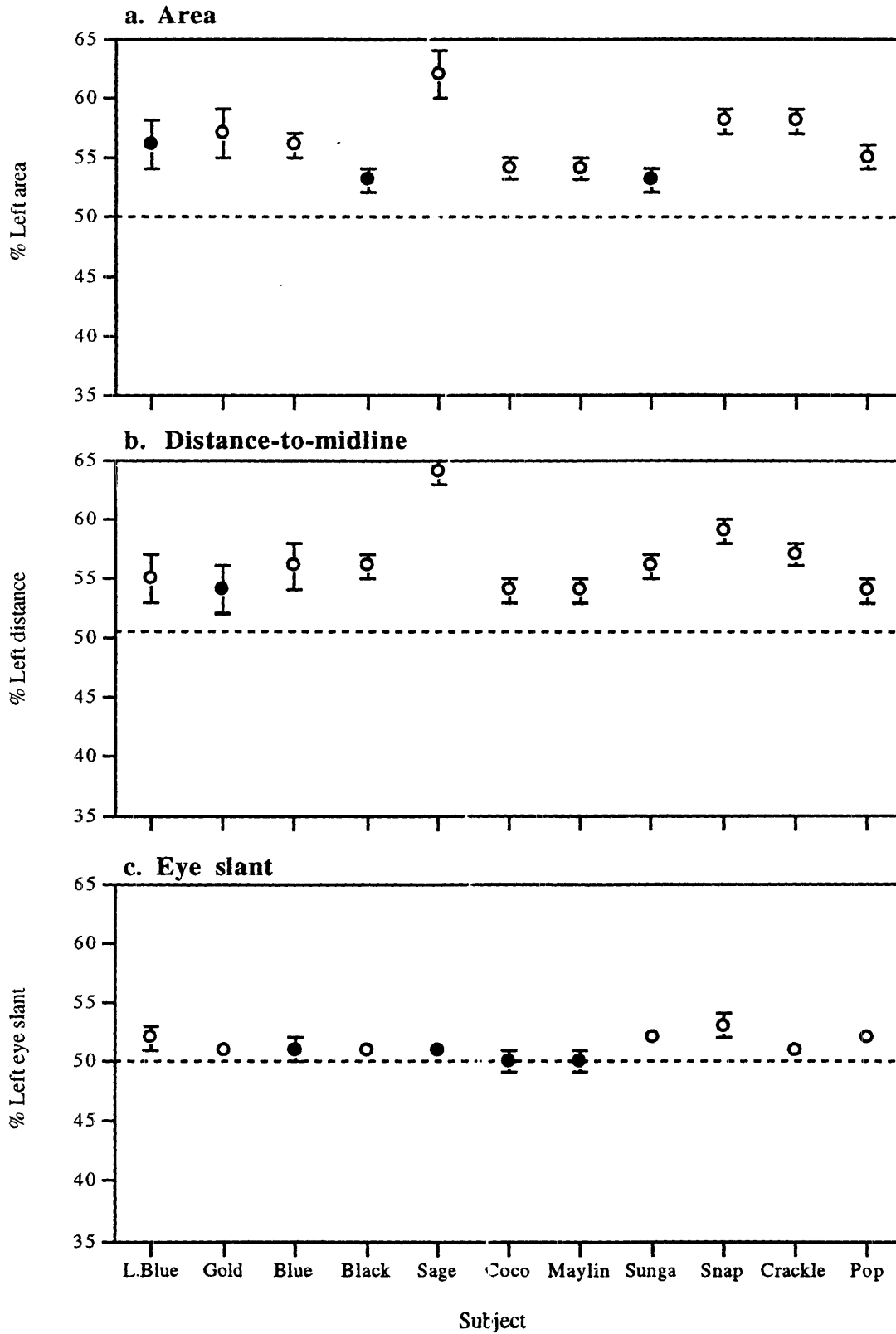
Figure 7.7 Distribution of percentage left biases in the production of the fear expressions. In Figure 7.7a the mean percentage left area (±SEM) for each subject (x axis) is presented. White symbols (O) indicate that the bias is significant (p≤ 0.05) and the black symbols (●) denote nonsignificant biases. The mean percentage left hemimouth area is shown on the y axis. Figure 7.7b shows the mean percentage left distance-to-midline scores (±SEM), and Figure 7.7c the mean percentage left eye slant scores (±SEM), presented in the same way as Figure 7.7a. Note that the majority of subjects displayed greater left than right-side measurements, although the magnitude of the bias was small particularly for the eye slant measurement. No subject displayed a right-side bias.

subjects (Figure 7.8a; Appendix A, Table O). Only 5 subjects displayed significant left-side biases for the distance-to-midline measurement. However, as can be seen in Figures 7.8a and 7.8b, all of the subjects displayed a tendency for more left than right-sided expressions and there was a significant left-side bias at the group level for both hemimouth area (Wilcoxon, $T^+= 9$, p= 0.007; Figure 7.8a) and distance-to-midline measurements (Wilcoxon, $T^+= 9$, p= 0.007; Figure 7.8b). Although the bias toward the left side was only small (mean difference = 5.3% for area, 4.2% for distance), the direction was consistent across faces and across individuals.

There was no lateralization of eye slant when producing the tsik expression. Only 3 of the 9 marmosets lifted the left eye significantly higher than the right during the production of the tsik vocalization and the remaining subjects did not display significant biases (Figure 7.8c).

Twitter vocalization

In contrast to the results for both the fear expression and the tsik vocalization, when the marmosets produced the contact twitter the right hemimouth was larger than the left (Figure 7.9a; Appendix A, Table P). At a group level there was a significant bias for greater area on the right side of the face (Wilcoxon, $T^+= 9$, p= 0.007, Figure 7.9a) and 6 of the 9 individuals displayed significant right-side biases. The magnitude of the bias for larger opening of the right side of the mouth was small (mean difference= 9%), but it was consistent across faces. However, for the distance-to-midline measurement there was no evidence of a group bias (Wilcoxon, $T^+= 4$, p= 0.59, Figure 7.9b) and only one individual displayed a significant right side-of-mouth bias.

7.3.2 Comparisons between Lateralization for the Production of Facial Expressions and Side-of-Mouth Preferences for Chewing

Asymmetries found during the production of fear expressions and vocalizations were not related to side-of-mouth preferences in chewing. There was no correlation between the percentage left-hemimouth area in the production of the nonvocalizing fear expressions and side-of-mouth preferences for chewing the twig (Spearman rank, $r_s=$
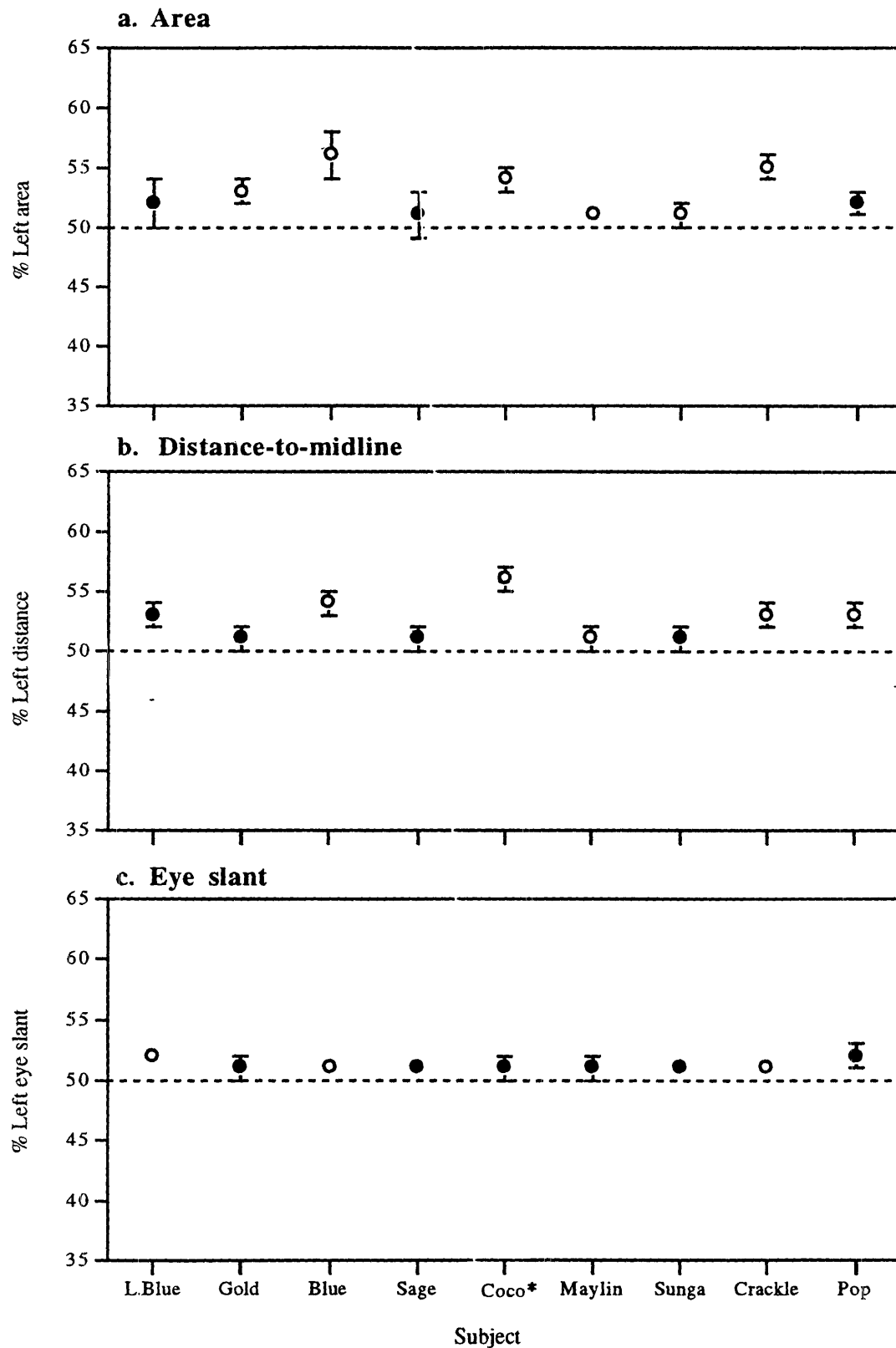
Figure 7.8 Distribution of percentage left biases in the production of the tsik vocalization. White symbols (O) indicate that the bias is significant (p≤ 0.05) and the black symbols (●) denote nonsignificant biases. In Figure 7.8a the mean percentage left area (±SEM), shown on the y axis, is presented for each subject (x axis). Figure 7.8b shows the mean percentage left distance-to-midline scores (±SEM), and Figure 7.8c the mean percentage left eye slant (±SEM), graphed in the same way as 7.8a. Biases displayed during the production of tsik vocalizations were less than those shown in the fear expression, but most individuals displayed greater mouth opening on the left side, rather than the right side. * indicates that only 5 faces could be collected for this subject (Coco).
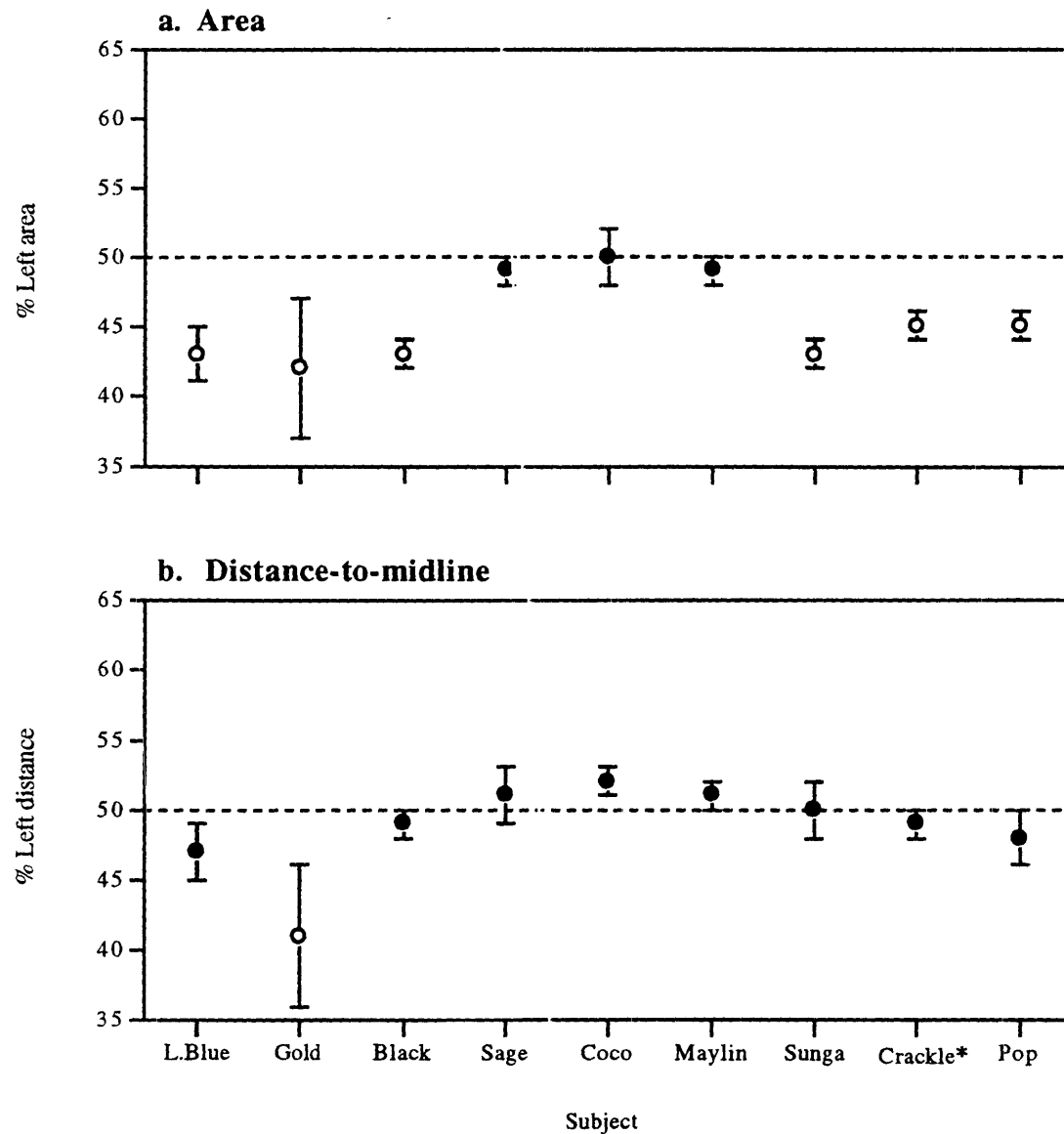
a. Area

b. Distance-to-midline

Subject

Figure 7.9 Distribution of percentage left biases in the production of the twitter vocalization. In Figure 7.9a the mean percentage left area (±SEM), shown on the y axis, is presented for each subject (x axis). Mean percentage left distance-to-midline measurements (± SEM) are shown in Figure 7.9b, graphed in the same way as Figure 7.9a. White symbols (O) indicate that the bias is significant ($p \leq 0.05$) and the black symbols (●) denote nonsignificant biases. Note that most individuals displayed a larger mouth opening on the right side of the mouth compared to the left side. * shows that only 5 twitter faces could be collected for this subject (Crackle).

-0.02, p= 0.95) or the bar (Spearman rank, r_s= -0.31, p= 0.32). Side-of-mouth preferences for chewing the twig and the bar were also not related to percentage left-hemimouth biases in the production of the tsik vocalization (Spearman rank; twig, r_s= 0.08, p= 0.81; bar, r_s= 0.10, p= 0.78). There was no relationship between percentage left hemimouth area in the twitter vocalization and side-of-mouth preferences for chewing (Spearman rank; twig, r_s= 0.07, p= 0.85; bar, r_s= -0.38, p= 0.28).

7.4   DISCUSSION

In producing the fear expression, with or without vocalization, marmosets pull the left side of the mouth further laterally than the right and the lips are opened wider on the left than on the right side of the mouth. There is also a greater angle of the left eye, compared to the right. As the magnitude of difference between the left and right eye slants was only equal to 2.79%, however, it is probable that they were caused by greater movement of the left side of the mouth. Nevertheless, the side-of-mouth biases would appear to reflect specialization of the right hemisphere for production of negative emotional expressions and vocalizations in marmosets, as is known to be the case in macaques (Hauser, 1993) and humans (Wolf and Goodale, 1987; Schiff and MacDonald, 1990). By contrast, the left hemisphere appears to be specialized for the production of vocalizations for social communication (not associated with fear responses) because the right side of the mouth was opened wider than the left when the marmosets produced the twitter call. The lack of individual biases for the distance-to-midline measurement in the twitter expression, however, indicates that during this vocalization the mouth is not drawn out further at the right corner, a result analogous with mouth position in humans for speech production (Graves et al. 1985; Wolf and Goodale, 1987; Graves et al. 1990). Although during the production of fear vocalizations the magnitude of the bias to the left side for the area measurement was only 5.3%, and the magnitude of the bias to the right side during social contact vocalizations was only 9%, these biases were significant.

Vocal production utilises motor control of both sides of the mouth and therefore

output from both hemispheres, but the output from the hemispheres is not equal. Depending on the nature of the vocalization being produced, the left or right hemisphere appears to assume a greater, or dominant, role in motor control of the mouth opening. In other words there is at least some degree of lateralization of control of vocalizations. Possibly the laterality of motor control reflects distinct and complementary specializations of the hemispheres for processing social signals or for generating them. Asymmetries revealed in studies of production and perception of communication signals might be indicative of the hemisphere that is responsible for extracting and producing the most important information in the signal and is largely responsible for performing the response (Allen, 1983). It may be that in the twitter call information about the social identity of the caller is predominant, whereas in the fear call the communication of the emotional context might be most important.

The absence of correlation between side-of-mouth preferences in chewing and asymmetries of mouth opening in the production of facial expressions indicate that these two types of mouth function are likely to be controlled by different neural mechanisms. The lateralized production of visual and vocal signals might not be simply due to lateralized motor control of the facial musculature. As side-of-mouth preferences in chewing are dependent on hand preferences for simple food holding, it is probable that there is also no relationship between specializations for communication functions and hand preferences for simple food holding. Thus, the lateralized production of emotional expressions and vocalizations is not simply due to generalized asymmetries of motor function. In fact, the results of this study show that hemispheric specializations for communication occur in the absence of handedness, footedness and mouthedness for chewing. Specialization of the left hemisphere for processing vocalizations in mice (Ehret, 1987) also occurs in the absence of pawedness (Collins, 1975, 1985, 1991). This suggests that specializations of communication did not evolve from limb preferences or from chewing biases, as has been proposed by several other researchers (Searleman, 1980; MacNeilage et al. 1987; Peters, 1988b; MacNeilage, 1997).

Bernston et al. (1993) found right hemisphere dominance for perception of auditory stimuli with affective significance in a juvenile chimpanzee. Measuring ERP (event-related potentials) signals, from the left and right hemispheres, they demonstrated right lateral dominance when the young chimpanzee perceived conspecific threat vocalizations and also when a primary caregiver spoke the subject's name (Bernston et al. 1993). Human studies also suggest that affective sounds such as laughing, shrieking and crying may be controlled by the right hemisphere (Carmon and Nachson, 1973). Thus, the complementary lateralization of production of alarm versus social vocalizations in the marmosets may reflect hemispheric differences based on the affective significance of the acoustic signals. It may be that the differential specialization of the hemispheres found in marmosets reflects separate processing and production of positive versus negative emotional responses, as has been suggested to occur in humans (e.g. Davidson and Tomarken, 1989; Schiff and MacDonald, 1990). However, this hypothesis is very controversial and a number of studies have shown that the right hemisphere is specialized for the perception and production of emotional signals regardless of their emotional valence (e.g. Gainotti, 1989; Wittling and Pflüger, 1990). Therefore, it is possible that the differences in the lateralization of the production of positive and negative signals in marmosets reflects differential modes of perceptual or cognitive processing of auditory signals, rather than there being lateralization based on emotional valence.

It is possible that the hemispheric differences in modes of auditory processing were the evolutionary precursors of hemispheric specializations for communication functions. Indeed, Ross (1983) suggested that the specializations of the left and right hemispheres for analytic versus holistic processing of perceptual stimuli, respectively, might relate to the hemispheric asymmetries found for communication in humans. *Analytic* processing is defined as the processing of the 'segmental components, features or elements' of a stimulus, whereas *holistic* processing involves the whole stimulus configuration and analysis of the interrelationships between the component parts (Bradshaw and Nettleton, 1981). In marmosets, the complementary specializations of

the left and right hemispheres for the production of fear versus social contact vocalizations could be due to differences in the acoustic structures of the emotional and contact vocal signals examined in this study. The tsik vocalization of the marmoset has high frequency modulation, whereas the twitter has temporal modulation (Epple, 1968). In humans the right hemisphere is specialized to analyze the pitch, timbre and intensity of auditory signals (Curry, 1968; King and Kimura, 1972; Sidtis, 1981; Ley and Bryden, 1982), whereas the left hemisphere is specialized for the discrimination of acoustic information related to rhythm and temporal order (Gates and Bradshaw, 1977; Schwartz and Tallal, 1980; Tallal et al. 1995). There is also evidence for an analogous division of function between the hemispheres during song and speech production in humans (Bogen and Gorden, 1971; Gorden and Bogen, 1974; Ross, 1985; Cadalbert et al. 1994; Gandour et al. 1994; Fox et al. 1996). Specialization of the left hemisphere for the discrimination of acoustic signals differing in temporal cues has been found in rats (Fitch et al. 1993) and in macaques (Gaffan and Harrison, 1991) also. Moreover, Petersen et al. (1978) found that for the discrimination of species-specific vocalizations using pitch as the cue, one Japanese macaque (*Macaca fuscata*) displayed a left-ear (right hemisphere) advantage, whereas another did not display an advantage for either ear on this task. Thus, hemispheric specializations underlying production of the two types of vocalization examined in this study appear to be consistent with those for perception in other species, but the meaning of the calls (alarm vs social) may also be important.

The relative importance of hemispheric specializations for communication functions in marmosets needs to be addressed. It is possible that in a complex communication system there is an advantage for a division of function between the left and right hemispheres for processing and producing visual and vocal signals in different ways. It has been suggested that the hemispheres might collaborate in the processing of a stimulus, with each hemisphere processing the stimulus simultaneously using different types of analysis (Allen, 1983; Andrew, 1991; Sergent, 1995). There is some evidence to suggest that co-operation between the hemispheres might increase the speed

and accuracy of perceptual processing when different types of information must be processed simultaneously (Hellige, 1993; Robertson, 1995). Thus, the distribution of processing across the hemispheres might serve to produce a faster and more accurate response than if one hemisphere only was processing all of the information.

Collaboration between the hemispheres might also be of benefit in increasing the amount of information perceived and produced during vocal communication. In the perception of a tsik call by marmosets, for example, it may be not enough to know that the sender is afraid. It might be advantageous to gain information about the identity of the sender. In this situation the right hemisphere might assess the emotional state and the position of the sender, while the left hemisphere processes information about the identity of the caller. If there is referential communication in marmosets, the left hemisphere might also categorize the object of threat, although at present there is no evidence for referential communication in callitrichid species (Snowdon, 1993). Differential hemispheric specializations for communication functions might be beneficial in the evolution of a complex communication system for increasing the amount of information conveyed in vocalizations.

On the basis of the results of this study, it is suggested that in the evolution of a complex vocal communication system, specialization of the right hemisphere for control of negative emotional responses may have been complemented by left hemisphere control of positive emotional (social contact) vocalizations. These results demonstrate hemispheric specializations similar to those known in humans for the production of both emotional expressions and vocalizations.

It appears that hemispheric specializations for communication functions may have evolved very early in phylogeny, as left hemisphere dominance for the production of vocal signals has been found even in a species of frog (Bauer, 1993). This specialization seems to have been retained by species throughout the evolutionary continuum as outlined in the introduction of this chapter. It is tempting to suggest that complementary specialization of the hemispheres may be an evolutionary precursor of

the hemispheric specializations for the control of emotional responses and speech production in humans.

7.5 SUMMARY

These experiments are highly suggestive of marmosets having hemispheric specializations for the production of visual and vocal signals which are expressed in asymmetries of mouth opening. They appear to have specialization of the right hemisphere for the production of negative emotional expressions, with or without vocalization, and a specialization of the left hemisphere for production of a contact vocalization not associated with fear. The findings of complementary biases for the production of fear calls versus social contact vocalizations indicates that the type of call examined can influence lateralization, even within individuals. The opposite asymmetries of hemimouth areas for different calls also shows that the lateralizations found in these experiments do not simply reflect differences in the way individuals move the mouth when vocalizing. Thus, specializations for communication are not simply due to asymmetries in the control of the facial musculature. Instead, they may depend on underlying hemispheric specializations for both processing and producing different types of perceptual information.

CHAPTER 8

GENERAL DISCUSSION

There are two types of hemispheric lateralization. The first type of lateralization is present at the individual level only, whereas the second type occurs at a group level. Lateralization at the group level occurs when the majority of individuals display the same direction of preferences on a task. Studies of rats provide examples of both types of hemispheric lateralization. Individual rats and mice display paw preferences when reaching for food, but half of the individuals display strong left-paw preferences while the other half display strong right-paw preferences (Collins, 1975; Wishaw, 1992). By contrast, group level biases are found for the performance of tasks in which rats are tested monocularly. Specialization of the right hemisphere for spatial navigation has recently been shown in male rats when they were tested in a Morris swim maze with an eye patch covering the left or right eye (Cowell et al. 1997). The performance of subjects using the left eye only (right-eye patched) or the right eye only (left-eye patched) was measured in terms of latency to find a hidden escape pattern using spatial cues to search. Rats using the left eye only took less time and travelled a shorter distance to find the platform than those using the right eye only (Cowell et al. 1997). Lesioning studies with rats have also shown that the right hemisphere is specialized for the control of negative emotional responses. Garbonati et al. (1983) found that handled rats with an intact right hemisphere (lesioned left hemisphere) displayed higher levels of 'muricide' (mouse killing) than handled rats with an intact left hemisphere only or whole-brain controls. Thus, rats display lateralization at the individual level only for the control of the paws in reaching and at the group level for perceptual processing and

for the control of negative emotional responses.

The results of the present study indicate that marmosets also show two types of hemispheric organization, which are similar to those found in rats. In marmosets, hand preferences for simple food holding and visuospatial reaching are present in individuals but there is no consistent bias for one direction of preference at the group level (Table 8.1). Strong group biases were found or the tests of eye preference, provided the marmosets were viewing stimuli that did not increase their arousal (Table 8.1). Group biases for the production of negative emotional responses were also found in marmosets (Table 8.1). Thus, hemispheric specializations, indicated by group level biases, are present in marmosets and rats, despite the fact that they are not manifested in hand preferences when reaching for food.

Table 8.1 Summary of results for marmosets

Function	Individual Preferences	Group Bias	Distribution	Chapter
Simple food holding	+	-	Bimodal	3
Visuospatial reaching	+	-	Bimodal	4
Side-of-mouth for chewing	+	-	Bimodal	4
Hand and foot preferred for initiating locomotion	+	-	No bias/ most ambipreferent	5
Eye preferences for viewing neutral stimuli	+	+	Right eyedness	6
Eye preferences for viewing arousing stimulus	+	-	No bias/ most ambipreferent	6
Asymmetry in production of fear expression	+	+	Left side-of-mouth bias	7
Asymmetry in production of social contact vocalization	+	+	Right side-of-mouth bias	7

+ means present, - absent.

LATERALIZATION PRESENT AT THE INDIVIDUAL LEVEL ONLY

Individual preferences were found for simple food holding and visuospatial reaching. Some subjects also displayed leading-limb preferences for walking, leaping and landing, although most subjects were ambipreferent (Table 8.1): there were no group biases on any of these measures. The absence of handedness for simple food holding, and for walking, confirms the results of previous studies on marmosets (Box, 1977a; Matoba et al. 1991). Apart from adding more data, however, the results reported in this thesis extend previous findings by showing that hand preferences for different tasks may not be random or independent. Significant relationships were found between different forms of manual function in the marmosets.

Hand preferences for simple food holding and visuospatial reaching

The significant relationships found between preferences expressed for different types of manual function suggest that the preferred hand used in one task influences the hand used preferentially in another task. Thus, hand preferences on different tasks are not independent, as Fagot and Vauclair (1991) have suggested. As illustrated in Figure 8.1, differential and opposite lateralization of the hemispheres was found for the control of simple food holding and visuospatial reaching, confirming the earlier results of Hook-Costigan and Rogers (1995) with an increased sample size of subjects from the same colony.

For most of the marmosets, one hemisphere controls the limb used for simple food holding and the other hemisphere controls the limb used for visuospatial reaching (Chapter 4; Figure 8.1). This division of function is present at an individual level only. While some individuals display left-hand preferences for simple food holding and right-hand preferences for visuospatial reaching, others prefer to use the right hand for simple food holding and the left hand for visuospatial reaching (Figure 8.1).

Hand preferences for simple food holding influenced side-of-mouth preferences used in chewing. The subjects displayed significantly stronger side-of-mouth preferences on tests in which hand-mouth co-ordination was required compared to tests

Differential lateralizations for control of the hands (and the mouth) in individual marmosets

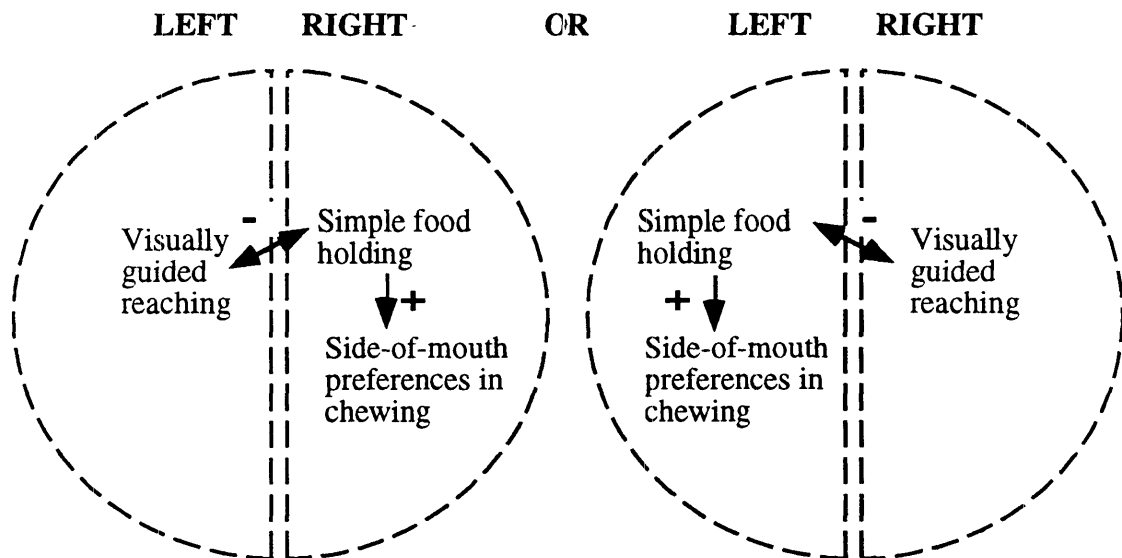**LEFT   RIGHT   OR   LEFT   RIGHT**

Figure 8.1 Lateralization of limb preferences and side-of-mouth preferences for chewing are present at an individual level only in marmosets. The dashed line used to depict the hemispheres illustrates that there is no hemispheric specialization for these functions. One hemisphere controls limb use for simple food holding, the other controls visually guided reaching, but not all individuals are lateralized in the same way as illustrated by the mirror images. There are relationships between the functions connected by the arrows. + signs show that there is a positive relationship between simple food holding and side-of-mouth preferences, while the - symbols indicate that there is a negative relationship between simple food holding and visuospatial reaching. Hand preferences for simple food holding caused side-of-mouth preferences for chewing in marmosets.

of chewing in which hand use was not required. The results of this study do not, therefore, support the hypothesis of Peters (1988b), which states that side-of-mouth preferences might have led to the evolution of hand preferences for simple food holding. Instead, it would appear that hand preferences cause side-of-mouth preferences, rather than vice versa. This could also be the case in the gentle lemur, *Hapalemur griseus*: Stafford et al. (1993) found that hand preferences for simple food holding were directionally congruent with side-of-mouth preferences for chewing in the gentle lemurs, although they did not examine side-of-mouth preferences on tests in which hand use was not required.

marmoset colony at the University of New England and is observed in wild marmosets (Rosenberger, 1978; Stevenson and Rylands, 1988; Rylands and de Faria, 1993). This behaviour demands high levels of postural control and lateralized mouth use for gouging with the lower incisors (Hershkovitz, 1977; Rosenberger, 1978; Rylands and de Faria, 1993). During feeding on gum exudate on a vertical trunk of a tree, at least one arm must be positioned above the head to allow lateral placement of the head against the trunk (Figure 8.2). Marmosets gouge with the side of the mouth on the same side as the higher arm (Figure 8.2). Although MacNeilage (1991) points out that in this clinging posture the higher side of the body would bear more of the load, it should be noted that the lower arm would also be involved in postural control. The lower arm would control the force with which the body was pressed against the branch and would increase gouging ability by exercising strength. Thus, it cannot be presumed that the higher arm is also the stronger arm. However, the preferred side of the mouth is likely to be used for chewing, and thus the arm bearing most of the load might be the one used for simple food holding. Increased use of the preferred hand and side of mouth in feeding might increase asymmetries between the arms and the sides of the mouth. Visual mechanisms might be involved also because lateral placement of the head against a branch largely occludes visual input to one eye (Figure 8.2). While one side of the body may bear most of the load and may be used for gouging, the contralateral eye might be used to monitor the environment to detect approaching prey, predators or conspecifics (Hook-Costigan and Rogers, 1995). The hand on the same side as the viewing eye might thus be used for visuospatial reaching. Co-ordination of this species-typical behaviour may result in a division of function between the hemispheres (and hands). For example, once an individual establishes a hand preference for simple food holding, and subsequently a side-of-mouth preference for chewing, the need for co-ordination between the two sides of the body in gum exudate feeding may influence the hand used preferentially for visuospatial reaching, thus improving performance of this co-ordinated behavioural act. Note that this differs from the hypothesis of MacNeilage et al. (1987), which suggests that asymmetries of postural control when feeding on a vertical substrate lead to handedness in prosimians and New World

this co-ordinated behavioural act. Note that this differs from the hypothesis of MacNeilage et al. (1987), which suggests hat asymmetries of postural control when feeding on a vertical substrate lead to handedness in prosimians and New World primates.

In Chapter 3 it was suggested that differences in foraging strategies between marmosets and tamarins might have led to handedness in tamarins, *Saguinus oedipus*, and not in common marmosets, *Callithrix jacchus*. As discussed in Chapter 3 (p. 99), tamarins have been reported to use more manipulative foraging strategies than marmosets. Garber (1993) indicates that tamarins use their hands to 'explore crevices and knotholes' and 'jump rapidly to ground to seize cryptic prey'. By contrast, marmosets spend a significant proportion of their time foraging for gum exudate

Figure 8.2 This drawing illustrates a typical posture adopted by marmosets when gouging for gum exudate. The higher position of one arm on the vertical tree trunk is accompanied by gouging with the lower teeth on the ipsilateral side of the mouth. Although the eye on the side next to the branch is not fully occluded in this drawing, it should be noted that in most cases the eye is pressed closer to the trunk of the tree and thus is closed.

crickets, cicadas and cockroaches (Stevenson and Rylands, 1988; Rylands, 1993). On the basis of these descriptions of the differences in the foraging strategies of marmosets and tamarins, it was suggested (Chapter 3, p. 99) that there may be no selective advantage for handedness in marmosets. Tamarins might display right handedness for simple hand use because of the increased manipulative demands of foraging strategies, whereas marmosets may not have handedness as their foraging strategies do not demand high levels of manipulation or visuospatial processing. In the absence of a selective advantage for one direction of lateralization, manual specializations might be disadvantageous. As Steklis and Marchant (1987) pointed out, absolute specialization of one hand for visually guided reaching and the other for postural support might be inefficient and disadvantageous when foraging in an arboreal environment. Steklis and Marchant (1987) suggested that the ability to capture insects with the left hand only, would be very inefficient as an individual might not be able to capture prey flying past on the right side. Moreover, if such an individual did snatch with the right hand for an insect in flight, the individual might fall, because the left side of the body would be insufficiently adapted for postural support (Steklis and Marchant, 1987).

In individual marmosets, adoption of particular postures during gouging may override any initial bias for left-hand preferences in visuospatial reaching. In those subjects that use the right side of the body to bear most of the weight of the body, and the left hand for visuospatial reaching, performance of gum exudate feeding might enhance pre-existing preferences for visuospatial processing. Thus, the strength of hand preferences for visuospatial reaching might be increased. By contrast, in subjects that use the left arm to bear most of the weight, and the right hand for visuospatial reaching, performance of gum exudate feeding might decrease the strength of hand preferences for visuospatial reaching. There was some evidence to support this hypothesis in the present study. Subjects that displayed left-hand preferences for taking food from a rotating disc (7 revolutions/ minute) displayed significantly stronger lateralization than subjects that displayed right-hand preferences on this task (Mann-Whitney U, U= 6, p= 0.01). In the absence of demands for high levels of visuospatial

lateralization than subjects that displayed right-hand preferences on this task (Mann-Whitney U, U= 6, p= 0.01). In the absence of demands for high levels of visuospatial processing motor habits may mask pre-existing specializations of the left hemisphere.

It is likely that the right hemisphere (left hand) is specialized for the finer and more complex aspects of visuospatial performance in marmosets, as in a variety of other species (Chapter 4, p. 141), but the feeding strategies of marmosets may not depend greatly on visuospatial abilities. If marmosets were forced to perform detailed tracking with one or the other hand, as used by Lorincz and Fabre-Thorpe (1996) to test cats, they might be more accurate when using the left hand. Lorincz and Fabre-Thorpe (1996) tested cats on a task requiring them to track a moving spot of light on a computer screen with one forepaw. The accuracy of the left and right forepaws of the cats when reaching for the spot of light was compared, and time taken for execution of the task using the left or right forepaw was scored. During early learning of this tracking task the left paw was found to be significantly more accurate than the right and the onset of movement of the left paw was faster than the right paw. Use of similar detailed tracking tasks with marmosets may also reveal superior performance of the left hand in the majority of subjects, and thus right hemisphere specialization, in this species for visuospatial processing.

Other studies of nonhuman primates have found small, but consistent, hemispheric advantages when measuring performance asymmetries between the hands (Preilowski, 1979; Ward et al. 1993; Fragaszy and Adams-Curtis, 1993; Preilowski, 1993). For example, Fragaszy and Adams-Curtis (1993) tested 3 crab-eating macaques (*Macaca fascicularis*) on a task requiring them to reach and sequentially depress two buttons to obtain juice. The first button, located 3 cm from the subjects, activated a 'ready' signal (a tone) and the second button (the target button) was located 7.5 cm (near) or 14 cm (far) behind the ready button. The performance of the each hand was evaluated using two measures: reaction time (time taken to release ready button after tone was heard) and movement time (time from releasing ready button and pressing target button). Subjects were tested on unimanual, using the left or right hand only, and

it was found that the right hand moved and completed the task significantly faster than the left (Fragaszy and Adams-Curtis, 1993). The right-hand advantage found might indicate specialization of the left hemisphere for 'planning' and executing sequential motor movements. Preilowski (1979) also found that 8 rhesus macaques (*Macaca mulatta*) were able to produce a specific force between the fingertips when using the right hand, compared to the left. The right-hand advantage found for producing a specific force between the fingertips might be indicative of a left hemisphere advantage for control of fine motor movements in macaques. The studies with primates, and with cats, demonstrate that group level advantages for one hand, and thus hemisphere, are revealed in the performance of complex manual tasks, at least in the initial stages of learning of a task. It is possible that marmosets would also display group biases for the performance of more detailed manual movements.

The tests used in the present study may not have been complex enough to demand use of underlying hemispheric specializations in marmosets. It should be noted, however, that the tests used in these experiments would be characteristic of natural foraging behaviours, for example reaching for fruit from a suspended posture, and thus it is suggested that they would elicit hemispheric specializations if they were advantageous in the performance of species-typical behaviours. As they do not, it might be concluded that there is no selective advantage for hemispheric specialization for these manual functions in marmosets. Hand preferences might simply develop from a slight tendency for an individual to use one hand more than the other, eventually resulting in a strong individual bias through the formation of motor habits. In fact, there was a strong positive correlation between percentage left-hand use in infancy and in the juvenile stages of development, although most infants did not display a significant hand preference for simple food holding (Chapter 3, p. 74). It may be that the infant's tendency to use one hand led to the development of significant hand preferences in the juvenile stage of development. However, if habit is the cause of hand preferences for simple food holding in marmosets, it might be expected that the infant marmosets would not have displayed any tendency for increased use of one hand in simple food holding, or should have been closer to ambipreferent. Instead, even as

marmosets would not have displayed any tendency for increased use of one hand in simple food holding, or should have been closer to ambipreferent. Instead, even as infants the marmosets displayed a mean strength of preference of 60%. There is a definite need to extend research on the development of hand preferences and the factors that affect them in marmosets to further understanding of the significance of individual hand preferences.

Hand and foot preferences during locomotory activities

Leaping and landing require visuospatial processing for the accurate assessment of the spatial position of a landing substrate, coupled with sufficient strength of the limbs for propulsion in leaping or for absorbing the energy of contact with a substrate in landing (Hunt et al. 1996). Thus, it could be proposed that opposite lateralizations for visuospatial processing versus propulsion might prevent conflict between the hemispheres during leaping and landing, producing optimal co-ordination of this motor behaviour. However, marmosets do not perform locomotory behaviours in a lateralized way. Most subjects did not display significant leading-limb preferences for leaping or landing (Chapter 5). Even in those individuals that did display limb preferences for initiating locomotory behaviours the strength of preferences was significantly weaker than those found for other forms of limb function, including simple food holding (Chapter 5). The decreased strength of hand and foot preferences during locomotion might reflect the necessity for both sides of the body to be capable of performing either visuospatial or propulsive motor actions. Inability of one side of the body to provide sufficient force for leaping from one branch to another might limit the direction in which an arboreal primate would be able to locomote and thus be disadvantageous. Indeed, there is also no evidence of handedness for leading-limb use in brachiation in the three arboreal hylobatid species (Hylobates syndactylus, H. concolor, H. lar) that have been studied (Stafford et al. 1990). This is suggestive evidence that absolute specialization of the hemispheres for limb control in locomotion is, possibly, disadvantageous in an arboreal environment.

walking is in contrast to the strong evidence for lateralization in other species, including ruffled lemurs, bonobos, chimpanzees, orangutans and gorillas (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). Perhaps the absence of handedness and footedness for initiating walking in marmosets is related to their adaptation to an arboreal environment, and the lessened significance of this form of locomotory behaviour (Chapter 5, p. 163).

Although marmosets did not display right footedness for initiating walking, as shown in other primate species, they did display a diagonal gait for walking. Use of a diagonal gait for walking has been described as characteristic of many primate species (Napier, 1976; Hunt et al. 1996). In this study the diagonal relationship between hand and foot use in locomotion was also found for leaping and landing. Thus, the evidence presented in this study shows that use of this locomotory pattern has not only been retained throughout evolution for walking, but also for different modes of locomotory behaviour. These findings suggest that the diagonal relationship between hand and foot movements in locomotion may represent an important motor pattern for performance of these behaviours. Indeed, the use of a diagonal gait would distribute weight equally across the two sides of the body and, therefore, would be important in maintaining balance during walking and leaping. Also, during leaping the foot that is last to leave the platform, and provides the propulsive force to push off from the surface, propels the body in the opposite direction. Thus, the diagonal relationship between hand and foot use would allow a subject to grasp the landing substrate with the forelimb that is first to reach the surface. This diagonal pattern of movement appears to have been retained throughout primate phylogeny, possibly facilitating the performance of locomotory behaviours.

Comparisons with other primate species

The absence of handedness in marmosets does not support the 'postural origins hypothesis' proposed by MacNeilage et al. (1987). As discussed in Chapter 1, MacNeilage et al. (1987) suggested that New World primates, along with prosimians and Old World monkeys should use the right hand for postural support and should show left handedness when reaching for food. There was a tendency for marmosets to land with the right hand contacting the surface first which would suggest that the right arm is

stronger in marmosets and may be used for postural control, as MacNeilage et al. (1987) proposed. However, this bias is not manifest for handedness. That is, marmosets do not display left handedness for simple food holding and visuospatial reaching. Also, asymmetries of strength were shown to be balanced between the two sides of the body in marmosets. Most of the marmosets tended to leap with the left foot leaving the platform last and thus providing propulsion for this motor behaviour. The indication of a stronger right arm and a stronger left leg suggests that both sides of the body may be involved in postural control in marmosets. It is interesting to note that the use of the more demanding posture was associated with increased use of the left hand in juvenile marmosets, as the 'postural origins theory' would predict. Moreover, increased use of the tripedal posture was related to increased use of the right hand in juvenile marmosets. Whether asymmetries of strength between the two arms are influencing hand preferences in the juvenile marmosets or hand preferences are influencing posture is unknown. However, the absence of left handedness in marmosets suggests that asymmetries of postural control cannot be the underlying determinant of hand preferences, at least in marmosets, as MacNeilage et al. (1987) proposed. Another variable must have influenced the posture in which the juvenile marmosets chose to feed, or alternatively the hand with which they chose to feed. It is possible that underlying perceptual and cognitive specializations influence the development and expression of hand preferences. Hand preferences for feeding in New World primates may be indicative of the different perceptual or cognitive demands of the foraging strategies characteristic of a species. As mentioned previously in Chapter 3, there is evidence to suggest that hand preferences might be indicative of cognitive (Horster and Ettlinger, 1985; Hopkins et al. 1992; Hopkins and Washburn, 1994), social (Stafford et al. 1990) or temperamental differences (Hopkins and Bennett, 1994; Watson and Ward, 1996) between left and right-hand preferent subjects.

As outlined in the introduction (pp. 5-9), there is evidence to suggest that tamarins, muriquis and capuchins (in some studies) are right-handed when reaching for and holding food. Squirrel monkeys, like marmosets, do not appear to have handedness for feeding activities and spider monkeys display left handedness in feeding (Chapter 1, pp. 5-9). Since handedness for simple food holding has been found in some studies, it cannot be said that hand use in feeding is simply too easy to elicit manual specialization, as suggested by Fagot and Vauclair (1991). It could be suggested that

right handedness had evolved in tamarins and that marmosets were in transition from left-handed ancestors toward right handedness, as there is evidence that many prosimian species display left handedness during feeding (Ward et al. 1990) and that the tamarin, *Saguinus oedipus*, closely related to marmosets, displays right handedness for holding and picking up food (Diamond and McGrew, 1994; King, 1995). However, it is recognized that the results obtained for one species of marmoset (*Callithrix jacchus*) and one species of tamarin (*Saguinus oedipus*) might not apply to all marmosets and tamarin species. Moreover, there is no convincing evidence to suggest that marmosets evolved earlier than tamarins; there is only speculation that this may have been the case (Ferrari, 1993).

It is noted that all of the studies of lateralization in marmosets have been conducted with captive populations. It would now be interesting to compare the lateralization of captive and wild populations of marmosets. There is a definite need to extend these studies to further clarify the effects of experience and environment on limb preferences. Experience was shown to effect the rate of development of lateral preferences (Chapter 3) and the strength of lateral preferences (Chapters 3, 4 and 5) in marmosets. Thus, differences in the experiences of wild and captive marmosets could influence their limb preferences. It is also possible that different experiences in captivity might have caused inconsistencies of hand preferences found across studies (e.g. in capuchins, as discussed in Chapter 1, pp. 8-9). Comparisons between the lateralization of species in captive and wild conditions and records of the circumstances in which lateralized behaviours occur would contribute to our understanding of the factors influencing the evolution of handedness.

LATERALIZATION PRESENT AT THE GROUP LEVEL

Eye preferences in marmosets and asymmetries of perceptual processing

Even though there were no group biases for limb preferences or side-of-mouth preferences for chewing in marmosets, there was a consistent and strong group bias for right eyedness when viewing nonarousing stimuli (Figure 8.3). There was no evidence of a relationship between hand preferences and eye preferences. Thus, it was reasoned
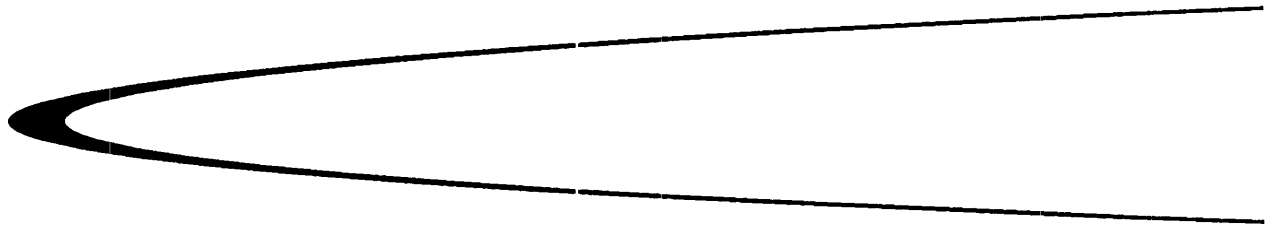
Hemispheric specializations in marmosets

Figure 8.3   The second type of lateralization in marmosets is present at the group and, possibly, population level. As illustrated by use of the solid line, unlike the dashed line in Figure 8.1, the results of the present study indicate that marmosets might have specialization of the left hemisphere for the production of a species-specific contact call and right eyedness, whereas the right hemisphere is specialized for production of negative emotional expressions.

in Chapter 6 (pp. 224-225) that right eyedness in marmosets reflects underlying asymmetries of perceptual processing. Although in primate species each eye transmits information to both of the cerebral hemispheres, on the basis of morphological differences between the nasal and temporal hemiretinas of each eye and of the crossing and noncrossing fibres, it was suggested that the more detailed visual image would be transmitted to the hemisphere contralateral to a viewing eye. This means that each eye transmits qualitatively superior input to its contralateral hemisphere than it does to its ipsilateral hemisphere. Thus, eye preferences in primates may not be entirely dissimilar to those found in birds (Andrew, 1988; Andrew, 1991) and rats (Mittleman et al. 1988; Cowell et al. 1997), even though primates have ipsilateral as well as contralateral projections from the retina.

Thus, the right eyedness of the marmosets when viewing neutral stimuli might reflect a left hemisphere specialization for the categorization of objects. Although further research would be necessary to confirm this hypothesis, evidence of left hemisphere specializations for categorization in other species does suggest that this may be the case. Left hemisphere specializations for categorization have also been reported in chicks (Andrew, 1988; Andrew, 1991) and in rats (Bianki, 1982). In fact, it has been suggested that, in chicks and rats, the left hemisphere processes select cues that can be

used for categorization of stimuli, while the right hemisphere is used for processing the details of each particular stimulus, including its position in space (Bianki, 1983; Bianki, 1988; Andrew, 1991). The monocular viewing preferences of marmosets appear to parallel those found for chicks. On tasks requiring chicks to categorize food and nonfood objects (i.e. grains and pebbles), those using the right eye learnt to categorize faster than those using the left eye (Andrew et al. 1982; Mench and Andrew, 1986; Zappia and Rogers, 1986). It is suggested that the difference in performance between chicks using the left versus the right eye, may be due to specialization of the left hemisphere for the classification of objects. Use of the right eye by marmosets may also reflect underlying left hemisphere specializations for categorizing objects (i.e. banana versus other stimuli). By contrast, the right hemisphere appears to mediate attack behaviours in chicks and these negative emotional responses are intensified when chicks use their left eye to view a threatening stimulus (Rogers et al. 1985). Rogers et al. 1985) treated chicks with the hormone testosterone, which elevates attack responses, and then observed their responses to a threatening stimulus (a human hand simulating another chick attacking) when they could see with their left or right eye only. When the chicks were tested using their left eye only their attack responses were elevated, but when they were tested using the right eye only they displayed comparatively few attack responses. These data suggest that the left eye system (right hemisphere) is specialized for the discrimination of threatening stimuli in chicks, as in marmosets. The similarities between monocular viewing preferences in marmosets and asymmetries found in chicks suggest that hemispheric specializations for perceptual processing may have been present in the evolutionary precursor of birds and mammals.

Humans also have specialization of the left hemisphere for categorizing objects (Gross, 1972; Bradshaw et al. 1977; Jones, 1979; Sergent et al. 1992). Sergent et al. (1992) used positron emission tomography (PET) scans to determine the cortical regions of the brain that were activated in human subjects when they were required to identify whether a visual object belonged to a natural or man-made category. They found that the temporal regions of the left hemisphere tended to be activated during this task (Sergent et al. 1992). Thus, it would appear that hemispheric specializations for perceptual processing are present in a wide number of species. Right eyedness for viewing neutral stimuli in marmosets, and also in humans, may have evolved from pre-existing hemispheric asymmetries for categorization. However, the inconsistency of the

data on eye preferences in primate species must be addressed, taking into account the effects of arousal on lateralization, before any firm conclusions on the evolution of eye preferences can be reached (Chapter 6, pp. 222-223).

Andrew et al. (1982) suggested that the visual constraints inherent in species with laterally placed eyes, together with completely crossed optic fibres (e.g. fish, lizards and birds), might have been the primary reason for the evolution of hemispheric specialization. In species with laterally placed eyes, both eyes can view different visual environments (Deckel, 1995; Wallman and Pettigrew, 1985; Schaeffel et al. 1986), which means that the separate hemispheres can process different visual information simultaneously. The absence of a corpus callosum in fish, lizards and birds (summarized in Deckel, 1995 and Bradshaw and Rogers, 1993) also results in slower or reduced transfer of information between the hemispheres, and thus interhemispheric interactions in these species might be significantly reduced. As Bradshaw and Rogers (1993) suggest, these anatomical and behavioural characteristics of fish, lizards and birds would provide strong pressure for the evolution of lateralization of brain function in these species, because each eye and hemisphere may act as an independent processing unit. Hemispheric specializations might have evolved to prevent the conflict of responses that could arise when stimuli are simultaneously perceived by the left and right eyes (Andrew et al. 1982). Asymmetries of perceptual processing that evolved in lizards may have been retained by rats and mice and could, possibly, be the evolutionary precursors of hemispheric specializations found in primates. As noted previously, monocular viewing tests with rats have revealed a hemispheric specialization for spatial processing in this species (Cowell et al. 1997). Hemispheric specializations for perceptual processing are, therefore, present in rats. The finding of right eyedness in marmosets, despite the absence of handedness in this species, might also support the hypothesis that asymmetries of perceptual processing, rather than handedness, were the evolutionary precursors of hemispheric specializations in primates. Moreover, as outlined in Chapter 1, macaques and baboons show evidence of hemispheric specializations for perceptual processing (e.g. Hamilton and Vermeire, 1988; Vauclair and Fagot, 1993), but there is inconsistent evidence for handedness for feeding in these species (e.g. Fagot et al. 1991; Vauclair and Fagot, 1993). There is a definite need to extend research on asymmetries of perceptual processing in nonhuman primate species, including the common marmoset.

Previous hypotheses on the evolution of hemispheric specializations in nonhuman primates have not considered the evidence of asymmetries of perceptual processing in nonprimate species (MacNeilage et al. 1987). However, it is possible that the handedness found in studies of visuospatial reaching, tactile perception and tool use are indicative of asymmetries of perceptual processing rather than motor specializations. Nondemanding manual tasks such as simple food holding might not utilize underlying hemispheric specializations and thus may not reveal handedness. Handedness might be found on tasks that demand higher levels of cognitive or visuospatial processing, such as that used by Lorincz and Fabre-Thorpe et al. (1996) with cats, as discussed previously. It should be noted, however, that in some species, including the tamarins, foraging strategies might demand higher levels of perceptual processing or manipulative control and this demand might lead to handedness for simple food holding.

Asymmetries of production of facial expressions and vocalizations

The group level biases found for asymmetries of mouth opening in the production of visual and vocal signals (Chapter 7) indicate that hemispheric specializations for communication functions have evolved in marmosets. As mentioned previously, the marmosets displayed a group bias of greater opening of the right side of the mouth during the production of nonvocalizing and vocalizing (tsik vocalizations) fear expressions. Thus, marmosets appear to have right hemisphere specialization for the control of negative emotional responses This is consistent with evidence for rhesus macaques (*Macaca mulatta,* Hauser, 1993), and humans (Wolf and Goodale, 1987; Schiff and MacDonald, 1990; Kowner, 1995), as discussed in Chapter 7. Moreover, it would seem that specialization of the right hemisphere for the control of negative emotional responses evolved very early in evolution and was retained in later evolving species. The dominant role of the right hemisphere in agonistic responses has been shown in lizards (Deckel, 1995) and toads (Robins et al. in preparation). This right hemisphere specialization has also been found in rats (Garbonati et al. 1983), chicks (Bullock and Rogers, 1986) and in gelada baboons (*Theropithecus gelada,* Casperd and Dunbar, 1996). Thus, the finding of right hemisphere dominance for the production of negative emotional expressions in marmosets is not only consistent with the data from humans and other primates but also with other nonprimate and nonmammalian species.

There is now evidence to suggest that specialization of the left hemisphere for processing species-specific vocal signals was also present in species evolving as early as amphibia (Bauer, 1993), and that this specialization may also have been retained by later evolving species including nonhuman primates, as outlined in Chapter 7 (pp. 230-232). The results of Chapter 7 suggest that marmosets also have specialization of the left hemisphere for the production of the contact twitter vocalization. There was a group bias for greater opening of the right side of the mouth during the production of twitter calls. Although the magnitude of bias was only small and only a small sample size could be tested, the right side-of-mouth bias was consistent for individuals and across individual faces. It is acknowledged that this research needs to be extended. However, even the indication of differential specialization of the hemispheres in marmosets for producing different types of calls suggests that, not only did the left hemisphere specialization for processing contact calls evolve prior to humans, but a complementary right hemisphere specialization for producing the emotional aspects of vocal signals might have evolved as well. It is possible that the differential hemispheric specializations for producing fear and contact vocal signals reflects a division of function between the hemispheres based on emotional valence, as has been suggested for humans. The right hemisphere may be specialized for the production of negative emotional signals, whereas the left hemisphere is specialized for the production of positive emotional signals. The contact vocalization of the marmoset, the twitter call, may be indicative of a positive emotional state, but this is not known. Also, as discussed in Chapter 7 (p.250), the hypothesis that the hemispheres are divided on the basis of emotional valence in humans, with the right hemisphere mediating negative emotions and the left hemisphere mediating positive emotions, is controversial. Thus, although it is possible that the type of emotion underlies the differential specializations of the hemispheres in marmosets and humans, further research is needed before any conclusions can be reached. It would now be interesting to determine whether different types of calls are lateralized in different ways in marmosets. Marmosets display a variety of species-specific calls that differ in their acoustic structure and meaning (Epple, 1968; Stevenson and Rylands, 1938; Snowdon, 1993). It may be possible to elucidate the mechanisms underlying the differential specialization of the hemispheres through further comparison of the lateralization of production of variety call types.

On the basis of lateralizations present at the group level in marmosets, it has

On the basis of lateralizations present at the group level in marmosets, it has been argued that hemispheric specializations for the processing of different types of sensory information and for communication have been highly conserved throughout evolution. It may be that hemispheric specializations present in marmosets evolved from asymmetries of perceptual processing present in species that evolved as early as amphibia or even fish. Most studies of nonhuman primate species, however, have measured handedness when looking for evidence of hemispheric specializations analogous to those found in humans. Handedness was considered to be the evolutionary precursor of hemispheric specializations in nonhuman primates and in humans (MacNeilage et al. 1987). Given that many studies, including the ones presented in this thesis, have found no evidence for handedness in nonhuman primate species, and considering evidence from nonprimate species, it is unlikely that manual specializations were the evolutionary precursors of hemispheric specialization. On the basis of evidence collected thus far, it appears that limb preferences are species-specific and are not always indicative of hemispheric specializations, because the latter have a long evolutionary history. The findings of this thesis underscore the importance of examining a variety of functions in individual species before concluding whether hemispheric specializations might be characteristic of the species.