Behavioural Lateralization in the Marmoset (*Callithrix jacchus*)

A thesis submitted for the degree of Doctor of Philosophy of the University of New England

By

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DECLARATION

I certify that the substance of this thesis has not already been submitted for any degree and is not currently being submitted for any other degree or qualification.

I certify that any help received in preparing this thesis, and all sources used, have been acknowledged in this thesis.

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PUBLICATIONS AND COMMUNICATIONS ARISING FROM THE RESEARCH PRESENTED IN THIS THESIS

Refereed papers

Hook-Costigan, M.A. and Rogers, L.J. Eye preferences in common marmosets (*Callithrix jacchus*): Influence of age, stimulus and hand preference. *Laterality,* in press.

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Published Abstracts

Hodgkinson, M.A. and Rogers, L.J. (1994). Handedness, mouthedness and eye preference in the common marmoset (*Callithrix jacchus*). *Handbook and Abstracts of the XVth Congress of the International Primatological Society*, 203.

Hook-Costigan, M.A. and Rogers, L.J. (1995). The lateralization of motor and sensory function in the common marmoset (*Callithrix jacchus*). *Proceedings of the Australasian Society of Animal Behaviour,* 22, 15.

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SUMMARY

Lateralization of 21 common marmosets (*Callithrix jacchus*) belonging to the colony at the University of New England was determined on a range of tasks. Hand preferences were measured during feeding. The hand preferred by subjects to hold food and take it to the mouth (simple food holding) was scored. Hand preferences were also measured on tests of visuospatial reaching that varied in the postural and spatial demands that they placed on the subjects. Leading-limb preferences (hand and foot) were recorded for walking, leaping and landing. Two types of mouth function were examined: side-of-mouth preferences for chewing, on tests in which hand use was or was not required, and asymmetries of mouth opening in the production of a fear expression and species-specific vocalizations. The marmosets' eye preferences for viewing various stimuli were also determined. The presence or absence of hemispheric specialization, indicated by a group bias in the direction of lateralization, was determined for each function. Also, relationships between individual preferences displayed on the separate tasks were examined with a view to understanding factors influencing the development and evolution of lateralization.

Individuals displayed strong hand preferences for simple food holding. These preferences developed by 5-8 months of age and remained consistent throughout the duration of this study, until 22 months of age for most subjects. However, there was no evidence of a group bias for simple food holding and therefore no handedness. Instead, preferences were bimodally distributed. Individuals also showed hand preferences on all of the tests of visuospatial reaching but, as for simple food holding, there was no group bias. Despite the absence of handedness on all tasks, it was found that most marmosets used one hand for simple food holding and the other for visually guided reaching. Thus, differential specialization of the hemispheres was present at an individual level, one hemisphere controlling simple food holding and the other visuospatial reaching.

Preferences for simple food holding were related to side-of-mouth preferences in chewing. Most individuals displayed significant preferences to chew on one side of the mouth when hand-mouth coordination was required, but not when they chewed on a twig that could not be manipulated by the hands. Thus, hand preferences for simple food holding appear to lead to side-of-mouth preferences for chewing in marmosets. No group bias was found for the side-of-mouth preferences in chewing.

Task complexity influenced the strength of hand preferences. The hand preferences displayed on visuospatial reaching tasks that required subjects to adopt a suspended posture were significantly stronger than those found when subjects reached from a tripedal posture. Posture might also play a role in the development of hand preferences for simple food holding. For juvenile marmosets (5-8 months), a significant positive correlation was found between percentage left-hand preference for simple food holding and the percentage occurrence of feeding in a suspended posture. A significant negative correlation was found between percentage left-hand preference for simple food holding and the percentage occurrence of feeding in a tripedal posture. Whether posture influences hand preferences or vice versa cannot be discerned, but a number of possible explanations are discussed. Although some effects of gender were also found in the present study, this variable did not appear to effect limb or side-of-

mouth preferences as much as did early experience and posture.

Most subjects did not display leading-limb (hand and foot) preferences for walking, leaping or landing. Also, when leading-limb preferences were found, they were significantly weaker than preferences displayed for simple food holding, visuospatial reaching or side-of-mouth in chewing. Despite this, a significant positive correlation was found between hand preferences for visuospatial reaching and leading-hand preferences for landing. This suggests that there is a slight bias for the same hemisphere that controls visuospatial reaching, in individual marmosets, to control the leading-hand in landing. No group biases were found for a leading-hand or leading-foot in walking, leaping or landing.

Eye preferences were determined on a task requiring the subjects to look with one eye through a peephole at a variety of stimuli, including familiar food. Out of 21 marmosets, 20 displayed a strong right-eye preference for viewing familiar food. Age and practice did not influence eye preferences for viewing food. However, arousal did effect eye preferences: most subjects did not display eye preferences when they viewed a fear-inducing stimulus. It is reasoned that eye preferences in marmosets reflect asymmetries of perceptual processing. There were no relationships between eye preferences and hand or foot preferences, suggesting that eye preference is not simply a consequence of the postural demands of the task or limb preferences.

Although only 9-11 subjects could be assessed for asymmetries of mouth movement during the production of a fear expression and species-specific vocalizations, group level biases for the production of these communication signals were found. Marmosets displayed a larger left hemimouth during production of fear expressions and fear vocalizations and a larger right hemimouth in the production of a social contact vocalization. As each side of the face is controlled by the contralateral hemisphere in primates, these results suggest that marmosets have specialization of the right hemisphere for the production of fear responses and specialization of the left hemisphere for the production of a social contact vocalization. There were no relationships between asymmetries of mouth opening in the production of communication signals and side-of-mouth preferences in chewing, or between asymmetries of mouth opening and hand preferences.

There are two types of hemispheric lateralization in marmosets. The first type of lateralization is present at the individual level only. Hand preferences for simple food holding and visuospatial reaching are examples of this type of lateralization. The second type of lateralization occurs at the group level, with most subjects displaying the same direction of preference. Marmosets display a strong group bias for eyedness and group biases for the production of fear expressions and vocalizations.

Handedness was considered to be the evolutionary precursor of hemispheric specializations in primates (MacNeilage et al. 1987). However, group biases for eyedness and communication functions indicate that marmosets have hemispheric specialization, even though they do not have handedness. These results demonstrate the importance of examining a variety of functions before concluding whether hemispheric specializations are characteristic of a species.

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CHAPTER 3: THE DEVELOPMENT OF HAND PREFERENCES FOR SIMPLE FOOD HOLDING

DEFINITIONS OF TERMS USED

Bimodal distribution	Approximately fifty percent of subjects display strong preferences for left-sided responses and fifty percent display strong preferences for right-sided responses.
Eyedness	A bias is present at the group level for left or right-eye preferences in a monocular viewing situation. Thus, most individuals within the group display the same direction of preference for monocular viewing.
Handedness	Most of the subjects within the group display the same direction of preference for one hand on a task. Handedness was measured for three types of manual function: simple food holding, visuospatial reaching and during the initiation of walking, leaping and landing.
Footedness	Most subjects within the group show the same direction of preference for one foot. Foot preferences were recorded in the initation of walking, leaping and landing.
Mouthedness	Most subjects within the group display the same direction of preferences for chewing with one side of the mouth.
Preference	This refers to the lateral bias of an individual. Subjects could display a significant preferences or ambipreference (no bias for either left or right-sided responses). The significance of individual biases for use of one hand (side-of-mouth, foot, eye) was determined using a z-score test (Chapter 2, p.). Significant lateralization was accepted if $p \leq 0.05$.
Shifters/ Nonshifters	Shifters display opposite hand preferences for simple food holding compared to reaching from a suspended posture for food on a plate. Nonshifters display the same hand preferences on the two tasks.
Simple food holding	Holding food in one hand and then taking it to themouth (Chapter 3). Also referred to, by other authors, as a spontaneous behavioural act as it occurs without experimental manipulation (Rothe, 1973; Diamond and McGrew, 1994).
Strength of preference	This is the absolute preference (%) for one hand (side-of-mouth, foot, eye) displayed by an individual, irrespective of the direction of the preference (left, right or ambipreferent).
Visuospatial reaching	Hand use on tasks requiring the visual assessment of the spatial position of an object while reaching. Four visuospatial reaching tasks are used in this thesis and they will be referred to as bowl, plate, string, rotating disc (see Chapter 4).

LIST OF FIGURES

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