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MANUAL LATERALITY IN CALLITRICHIDS

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The University of Durham

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ABSTRACT

The current state of evidence for population-level and individual lateral motor asymmetries in nonhuman primates is evaluated in a review of the existing literature. It is accepted that the existence of a population-level left hand bias for simple reaching in prosimians is essentially proven. There appears to be an important association between increased postural demands and increased strength of preferences in prosimians, monkeys and apes. Simple reaching tasks are inadequate to reveal underlying preferences in the manually sophisticated monkeys and apes. More complex unimanual and bimanual tasks tend to elicit indications of a preference for use of the right hand for fine manipulation of objects. Few investigations of lateral preferences in Callitrichids have been conducted so far, and studies linking hand preferences to whole-body turning behaviour have been confined to prosimians, and then only using induced rather than spontaneous measures. There has been no attempt to systematically investigate laterality in manual grooming.

Observations of lateral preferences in spontaneous feeding, grooming and turning behaviour were conducted on 21 captive Callitrichid primates. Focal samples were recorded using a laptop computer and specially developed software. Results indicate no population-level laterality for any sampled activity. Most subjects passed objects more often from right to left hands. Preferences were variable in both strength and direction. Strength of turning preference was associated with strength of intermanual transfer and grooming preferences. It is suggested that use of a preferred forelimb for support when turning may be a predictor of lateral preference in these activities. Females made more consecutive left turns than males. This may be due to stronger right forelimb preference for supporting posture.

Manual Laterality in Callitrichids.

Jon Martin Watts

Thesis submitted for the degree of
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At
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Research Conducted in
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DECLARATION

None of the material contained in this thesis has previously been submitted for a degree at any university.

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INTRODUCTION

The traditional view that population-level asymmetries of hand preference and left hemisphere motor specialization are unique characteristics of man has recently been challenged by MacNeilage *et al* (1987). In their controversial review they claimed that there was evidence that nonhuman primates tend to prefer the left hand for visually-guided reaching movements and the right for fine manipulation. They went on to propose a "Postural Origins" model to account for this. The suggestion is that manual laterality evolved firstly from a left hand, right hemisphere preference for visually-guided hand movement in early prosimians, accompanied by a right forelimb specialization for postural support. The development in monkeys of a more upright posture decreased demands upon the right hand for support and allowed it to become specialized for fine manipulation and bimanual coordination.

However many commentators have felt that the evidence presented was rather weak. The MacNeilage *et al* review has provoked a resurgence of interest in nonhuman primate handedness and has stimulated a good deal of new research. The best of this recent work is characterized by the use of more appropriate measures, criteria and techniques and a shift of emphasis towards viewing handedness, not as a simple trait, but as a highly task and situation-dependent phenomenon.

This study examines the current state of evidence for nonhuman primate laterality. Observations are reported of the spontaneous feeding, grooming and locomotor behaviours of 21 captive Callitrichid primates, of six species, housed at London Zoo. Thirty two hours of focal observations were collected using a laptop personal computer running a data-logging program which was specially developed for this study.

LITERATURE REVIEW

Laterality in Animals and Humans.

It is a fact that roughly 90% of modern humans prefer to use the right hand for most unimanual activities. This functional asymmetry in motor behaviour is the most striking outward illustration of the underlying suite of lateralized functions in the cerebral hemispheres, which subserve our linguistic and emotional capabilities as well as our perceptual and motor abilities.

This functional lateralization is rather stable between different human populations (Salmaso & Longoni, 1985), and the prevailing view has been that this is a unique, and perhaps definitive, characteristic of humans (Warren, 1980).

It is now known that laterality in various forms is to be found in a variety of species (Rogers, 1993), and the evidence has been accumulating for many years. Friedman & Davis (1938) reported left-handedness for handling food items in several species of African parrots. Left-hemisphere control of singing has been demonstrated in a number of songbird species (Nottebohm, 1971, 1976). In chickens the right hemisphere is used for control of agonistic and copulatory responses (Howard, Rogers & Boura, 1980). The cat, rat, rabbit and mouse all apparently have larger right hemispheres (Kolb *et al*, 1982).

The numbers of such examples to be found in the literature and the diversity of species represented suggests that lateralization of functions and hemispheric specialization is a common adaptation in animals, and is likely to have arisen rather early in evolution, and repeatedly in different forms. The specific adaptaion at issue in this review, the preference of one hand for unimanual activities is best documented in humans. It would be puzzling indeed if some evidence for analogous, or perhaps homologous, manual specialization were not present among the extant, nonhuman primates. Yet such evidence has been surprisingly elusive and difficult to interpret. The case for an evolutionary precursor to human handedness is still very far from being proven.

Early investigations into handedness in nonhuman primates (e.g. Warren, 1953; Cole, 1957; Hall & Mayer, 1966) have certainly shown that some, or perhaps most, individuals of a number of species do become lateralized to favour one hand for a given task, often markedly so. However these studies have also suggested that the direction of lateralization was rather labile, ontogenetically for the individual, and the choice of preferred hand was essentially a random one. They did not indicate the presence of species-specific adaptations for use of a preferred hand, but rather imply individual peferences arising from early experience and reinforcement. Indeed these studies, as well as many more recent ones, typically find that a given population has approximately equal numbers of dextral and sinistral members, with a variable proportion of ambidextrous animals, depending on the stringency of the statistical criterion used to assign handedness.

The notion that nonhuman primates do not show population-level deviation of hand preference in the human sense has pervaded the psychobiological literature. Theories advanced to explain the "unique" behavioural and anatomical asymmetries found in humans tended to reinforce this view to the extent, that for many researchers, it has been considered more or less axiomatic. This has inhibited further research into the essential facts. Annett (1980) for example, presents the "Right Shift" theory in which handedness is under the control of a single Mendelian gene. The 20% of humans who are presumed to lack the "rs+" allele are normally distributed along a continuum, from very left- to very right-handed, with most being of mixed handedness to some extent. The other 80%, who do have the rs+ allele form a right skewed distribution. When superimposed one group upon the other, the overall picture is of a human population with many right-handers, a sizeable proportion with mixed handedness and rather few strongly lateralized left-handers. A situation very close, in fact, to what is actually observed. The "Right Shift" gene, Annett argues, is a unique human attribute. The theory also implies that handedness is a simple, single trait, which much recent evidence strongly suggests is not the case (e.g. Healey *et al*, 1986).

It has also been suggested that shared use of tools was the major functional, proximate advantage and shaping force in the evolution of lateralized limb use. (Frost, 1980; Bradshaw & Nettleton, 1982), although it is not made clear whether the undoubted existence of large numbers of right-handed stone tools (Oakley, 1972; Dart, 1949) should be regarded as cause or effect. It is further claimed that this stimulated the specialization of the left hemisphere for language. Calvin (1982) claims that stone throwing, rather than toolmaking, may have shaped hominid brain evolution.

In a review of several sets of data accumulated prior to 1980, Warren (1980) characterizes hand preferences observed in nonhuman primates as being: i) Symmetrically distributed in the population, with no significant difference between the numbers of left- and right-handers. ii) Dependent on the task and other situational constraints. (See also Deuel & Dunlop, 1980) iii) Dependent on learning and practice. iv) Independent of other functions known to be lateralized, such as accoustic signal processing.
Furthermore, Warren claimed that the various forms of cerebral laterality obseved in nonhuman species are best viewed as analogues, rather than homologues to human specialization.

Warren's view can be challenged on several grounds (See Fagot & Vauclair, 1991). His account is only acceptable in the absence of statistically asymmetrical distributions. Later in this review it will be shown that such distributions do occur. Asymmetrical distributions have also been demonstrated in field studies and captive studies with naive subjects and measures of spontaneous behaviours, where task and situational constraints are minimal. Independence of hand preference from hemispheric asymmetries is no longer tenable in the light of evidence that there is a relationship between hand preference and specific lesions in the contralateral hemisphere in monkeys (Garcha *et al*, 1980, 1982), and also between hand preference and relative competence of each hemisphere in a visual discrimination task.

In a comprehensive review of studies up to the time, MacNeilage *et al* (1987) suggested that there was, in fact, evidence of population-level hand preferences among nonhuman primates. They argued that the difficulty in identifying handedness was due to the mixture of two different forms of manual specialization. The evolutionary scenario under which this manual specialization arose has become known as the "Postural Origins" theory. This was a significant improvement over earlier theoretical models of (human) handedness insofar as it furnishes a framework for the generation of testable hypotheses for a range of nonhuman primate motor behaviours.

The suggestion of MacNeilage and his associates is that a left-hand preference for visually-guided reaching and grasping arose among the early quadrupedal prosimians. As a consequence, this required a right-forelimb specialization for postural support. With the adoption of a more upright posture by monkeys, demands upon the supporting forelimb were reduced, allowing the right hand to become specialized for bimanual coordination and fine manipulation, thus complementing the activities of the left.

The evidence presented by MacNeilage *et al* from previous studies was limited, and in the opinion of many commentators (e.g. Corballis, 1987; Guiard, 1987; Steklis & Marchant, 1987), simply too weak to be convincing. It should be borne in mind however, that the studies drawn upon did not form a truly coherent corpus of evidence, sice a wide variety of tasks, methods and statistical criteria were employed. Often these used captive and immature animals and arcane, and possibly misleading testing regimes. most unhelpful of all perhaps, was the lack of a theoretical framework such as that which the reviewers themselves were advocating.

Despite its limitations, and the paucity of firm evidence, the MacNeilage *et al* paper opened a new debate on primate laterality and handedness, and stimulated a good deal of interest and research.

Laterality in Prosimians.

The first hypothesis suggested by the Postural Origins idea is that a left-hand preference for visually-guided prehension should be expected among prosimians. There now seems some reason to believe that such is the case. Ward *et al* (1990) assessed hand preferences for simple food reaching in a population of 194 lemurs (*Lemur* Spp.). Hand preferences were present in 80% of the animals tested, with a significant bias towards use of the left hand. Further evidence of left-handednes in lemurs is documented by Forsythe & Ward (1988) and Masataka (1989).

The relationship between laterality and posture implied by MacNeilage *et al* has been investigated by Forsythe *et al* (1988). They report that hand preference of ruffed lemurs (*Varecia variegata variegata*) was much more severely lateralized to the left when the animals were required to use a forelimb for postural support while reaching for food, as compared with a free-foraging condition. The preferential use of the right forelimb for support was an essential feature of the postural origins scenario.

Sanford & Ward (1986) reported left hand preferences in seven out of eight bushbabies (*Galago senegalensis*). Sanford *et al* (1984) found bushbabies more strongly left-preferent when reaching for food from a bipedal stance, which required that the wire of the cage be grasped with the other hand.

Another type of behaviour which may provide evidence for lateral biases related to handedness and posture is turning (ie. Rotational movement about the long axis of the body) . In rats, for example, turning biases have been found to be related to differences in dopamine levels between the right and left basal ganglia (Glick & Shapiro, 1985) and to be correlated with paw preferences and deviations of tail posture (Glick, 1973; Ross *et al*, 1981). In humans also, turning preferences are related to hand preference and sex in adults (Bracha *et al*, 1987), while children of both sex turn preferentially to the left (Gospe *et al*, 1990). An examination of turning preferences in nonhuman primates may therefore prove fruitful.

Mouse lemurs (*Microcebus murinus*) and bushbabies (*Galago moholi*) turn predominantly to the left (Dodson *et al*, 1992), as do bushbabies of the species *G. senegalensis* (Larson *et al*, 1989). Turn preferences in these two studies were much stronger than, and on the whole, not correlated with hand preference. However in *G. moholi*, hand and turn prefence was correlated for females, the females in this case being right hand preferent. A similar right hand bias was found in small eared bushbabies (*Otolemur garnettii*) by Milliken *et al* (1991).

In respect of prosimians at least, there is evidence to support the general thrust of the postural origins theory. Population-level preferences have been demonstrated in reaching and turning behaviours for several species. In particular the relationship between hand preference and postural support requirements is very compelling. Though there may well be felt to exist some contradictory or ambiguous evidence, the view of Warren (1980) that population-level lateral biases do not exist in nonhuman primates is clearly no longer sustainable.

Laterality in Monkeys.

Among monkeys and apes, which engage in far more fine manipulation and bimanual activities as part of their natural repertoire than prosimians do, the position is less clear. Of the 25 studies of simple food reaching in monkeys summarized in a review by Fagot & Vauclair (1991), only one demonstrated a clear population-level bias at $p<.05$ for this activity (Itani, 1957 for *Macaca fuscata*). There are additional difficulties in showing hand preferences in simians. In the first place the studies reviewed by Fagot & Vauclair employ a variety of statistical criteria for assigning handedness, as well as a range of testing conditions. Some studies used free-ranging subjects, others used animals restrained using equipment such as the Wisconsin General Test Apparatus. The lack of a consistent strategy such as that employed by Jeannette Ward and her colleagues, across a number of studies of prosimians, has clearly limited the usefulness of this work. Moreover, since the monkey studies have been carried out by many researchers over many years, without any particular theoretical framework it is not very surprising that few strong claims have been made. It should also be borne in mind that animals possessed of an upright posture, more highly developed hands and skilled bimanual cordination, under the MacNeilage *et al* model might be expected to show less strong hand preferences for simple grasping tasks. It may well have been failure to appreciate this possibility that led workers to dismiss the notion of nonhuman primate laterality for so long.

Early attempts to study laterality in monkeys concentrated almost exclusively on tests of simple food reaching in Macaques. Usually the findings were fairly inconclusive, with roughly equal numbers of left- and right-preferent subjects (e.g. Cole, 1957; Warren, 1953; Furaya, 1963). So many differerent criteria have been used to assign the handedness of individuals that a comparison of the type that Fagot & Vauclair have performed is of less value than it might have been. A lax criterion of >50% hand use simply means that no animals, or at most very few, will be assigned as ambipreferent (e.g. Lehman, 1970, 1978, 1980). Wheras a rigid criterion of say >80% will cause a greater proportion of the sample to be declared ambipreferent. If we ignore all those individuals in the 25 studies which are reported to be ambipreferent, in effect focussing on those animals which are known to have made more than 50% of reaches with a particular hand, we find that 12 studies have more right-handers than left, and 13 studies have more left-handers than right, hardly conclusive evidence for a left-hand bias for visually guided reaching in monkeys as a whole. However, more recently, Kubota (1990) showed that among Japanese monkeys of the Arashiyama-R troop, 19 animals showed a consistent left-hand preference in reaching for food pellets, with 5 right-handed and 20 ambipreferent individuals. In this instance the strength of hand preference was positively correlated with age. In another case, Lehman (1980) found that the strength of hand preference exhibited by cynomolgus monkeys (*Macaca fascicularis*) tended to increase with repeated food-reaching trials.

Investigating a more demanding unimanual activity, Kawai (1967) found that Japanese macaques (*M. fuscata*) caught thrown food items more frequently with the left hand than with the right, though most catches were made with both hands. Deuel & Schaffer (1987) observed catching behaviour in 25 Japanese macaques and found 15 left- and 8 right-handed catchers. King *et al* (1987, 1988) showed that squirrel monkeys (*Saimiri scuireus*) preferred to use the left hand when catching live fish (11 left-handers and 3 right-handers). The same monkeys displayed no group-level preference when reaching for stationary food items. Somewhat earlier Subramoniam (1957) reported consistent use of the left hand in a prosimian, the slender loris (*Loris tardigradus*) when capturing stationary but live insects. Interestingly, Hatta & Koike (1991) have found that eight mother macaques (*Macaca* Spp) took up their babies very preferentially with the left hand in response to a simulated threatening emergency. It seems plausible therefore to suggest that while for simple grasping activities monkeys are reasonably adept with either hand, under conditions of high cognitive or emotional load, either the left hand is more efficient or reliable, or perhaps the right hand is to be preferred for postural support.

Reaching for food is a basic skill common to all primates (Jolly, 1972) and is developed very early in infancy (Fagot & Vauclair, 1991). The ability of either hemisphere in the monkey to process a visually-guided unimanual reaching task is confirmed by studies in which commisurotomized animals with the optic chiasm severed are able, when monocular vision is imposed, to perform such a task, regardless of which eye (and thus hemisphere) was available (Lehman, 1968; Lund *et al*, 1970). Deuel & Dunlop (1980) report that when lesions in the hemisphere contralateral to the preferred hand of individual monkeys are created, they use the hand which is guided by the intact hemisphere.

The possibility that the left hand may be more effective or dependable under certain circumstances has been investigated in humans. It has been shown that a proportion of strongly right-handed people make ballistic hand movements more accurately with the left hand (Guiard *et al*, 1983), as the lorises and squirrel monkeys do.

In the manually sophisticated monkeys and apes it may be necessary to study hand use in more demanding tasks to bring out any true population-level laterality that may exist. When presented with a task which required the manual alignment of a plexiglass panel with a small window and a small aperture containing a food reward, Fagot & Vauclair (1988a) found that baboons preferred to use the left hand to make the adjustment. Hoerster & Ettlinger (1985) found that 78 monkeys spontaneously using the left hand learnt a tactile discrimination task in fewer trials than 77 right hand preferent monkeys. This would suggest some asymmetry for tactile performance. However 82 monkeys without consistent hand preferences learnt the task significantly faster than either group.

The effect of posture, already discussed in relation to prosimians, has been investigated by Fagot *et al* (1991). Of

29 monkeys performing a tactile discrimination task in a hanging posture, 21 had a left-hand bias, 4 a right-hand bias and 4 had no bias. The effect of posture was systematically tested using both visual and tactual discrimination tasks. A left-hand bias was demonstrated for tasks undertaken in hanging or sitting postures, but an almost symmetrical distribution was found when animals were in the tripedal posture. Biases were also noted to be stronger for tactile than for visual tasks.

Increasing task demands further, Westergaard (1991) has studied hand use in the manufacture and use of probing tools by lion-tailed macaques (*Macaca silenus*) and tufted capuchins (*Cebus apella*). This task was designed to be functionally similar to the manufacture and use of termite "fishing" tools, as described by Goodall (1986) for wild chimpanzees. Though the monkeys used both hands and teeth to modify tools and used bimanual actions for parts of the feeding task, insertion of the tool into the hole and removal were usually performed with one hand. The majority of subjects preferred the left hand for these activities. This has been the first quantitative analysis of hand preference by monkeys in a task involving the manufacture and use of tools.

In common marmosets (*Callithrix jacchus*), Box (1977) found a robust preference for the use of the left hand to take and hold food items in 6 of 8 animals. Investigating the same species, Matoba *et al* (1991) found that, while their subjects, 23 family groups of adult male and female with one infant, did not show a population-level bias, many individuals were hand-preferent. Infant hand preference were correlated with those of their mothers but not with the fathers'. It is well known that in marmosets, both parents contribute substantially to the care of offspring. It is unlikely then that this is the result of preferential imitation of imitation of maternal behaviour, unless, as the authors speculate, it is related to the degree of involvement in care of individual fathers, which can be very variable.

The degree of precision of grip needed to acquire an object may influence the choice of hand which is used. According to the hypothesis of MacNeilage *et al* (1987) the right hand might well be preferred for precise prehension and manipulation of small food items. In a mixed species group of capuchin monkeys (*Cebus apella, C. capuchinus, C. albifrons*) comprising 31 individuals, Masataka (1990) found 25 animals to be right-hand preferent for picking up very small, scattered food remnants. This activity required a precision grip, with a degree of thumb opposability, which picking up a larger object does not.

It is becoming clear that handednes is not a straightforward, unidimensional phenomenon. It has been shown that hand-preference is dependent upon the cognitive, sensory and emotional demands of the situation in which a task is performed. Practice is responsible, to some extent, for reinforcing hand preference, but maternal preference may also be a predictor. Both postural demands and the degree of grip precision required can influence the strength and direction of preferences. Hand preference may be related to whole-body turning biases, and as a consequence, to the half of the visual field into which new spatial information first arrives, this relationship may be more important for female animals than for males.

Laterality in Apes.

The search for an analogue of human lateralized behaviour among animals must surely include the apes. These animals exhibit the most elaborate manual behaviour of all, even to the extent that some engage in the making and use of tools. This activity was once thought to be exclusively and definitively human, and perhaps involved in the human development of both handedness and language. As our closest extant relatives, it is among apes that we might expect to find the best indications. There is anatomical evidence of asymmetry between cerebral hemispheres in gorillas (Groves & Humphrey, 1973). This certainly looks like the result of a selective pressure to develop functional lateralization of some sort. Whether this can be detected in measures of overt behaviour, and whether it pertains to hand use is, of course, open to question.

In a study of 10 captive gorillas at Barcelona Zoo, Spain, Fagot & Vauclair (1988b) found a symmetrical distribution of hand preferences for simple reaching (3 left, 3 right, 4 no preference). However 7 of 8 gorillas tested on a task requiring the precise alignment of two openings were found to prefer the left hand. A task and result similar to those of their baboon study (Fagot & Vauclair, 1988a). These authors stress the importance of considering the type of task employed in the assessment of hand preferences. They suggest a distinction between the handedness of an individual when simply reaching and manual specialization for novel or complex tasks.

Stafford *et al* (1990) have investigated lateralization of hand use for both feeding and brachiation in gibbons (*Hylobates Spp.*). For food reaching they discovered that adult females were strongly right-hand preferent, wheras males had no across-group bias. Among the females there was a significant correlation between strength of of right hand preference and age. In terms of absolute strength of hand preference, females were more strongly lateralized than males. There were no group preferences for leading limb when brachiating, although three subjects changed hands depending on whether or not they were vocalizing at the time.

Heestand (1986) reported that a heterogenous population comprising 29 gorillas, 20 chimpanzees, 3 orangutans and 13 siamangs exhibited overall a right hand preference for leading limb in quadrupedal locomotion.

Olson *et al* (1990) have assessed hand preferences for gorillas orangutans and gibbons in retrieving objects, both from the floor and from slightly above head height, the latter requiring a bipedal stance. On the floor retrieval task the distribution of preferences was:

	LEFT	RIGHT	NO PREF.
GORILLA	2	5	5
ORANGUTAN	3	4	5
GIBBON	6	2	0

In the bipedal reaching condition the distribution was:

	LEFT	RIGHT	NO PREF.
GORILLA	2	10	0
ORANGUTAN	3	4	5
GIBBON	6	0	0

The gibbon and gorilla engage more often in bipedal locomotion in the wild than does the orangutan. The authors suggest a correlation between the degree of bipedal behaviour a species exhibits and its readiness to show a population-level hand preference when reaching from a bipedal stance. The effects of such a posture on strength of hand preference have already been noted for prosimians. Interestingly the gibbons were left-preferent, as the bushbabies were, and the gorillas were right-preferent as seen in the very bipedal humans.

Hand use in gorillas has been investigated in a number of recent studies. Annett & Annett (1991) observed 31 captive animals and counted the numbers of unimanual reaches made while feeding. They found a full range of hand preferences from strongly right to strongly left, with most animals showing intermediate levels of preference. This is what would be predicted by Annett's (1985) "Right Shift" theory for a nonhuman primate species lacking the exclusively human rs+ gene. However it is clear, that for apes at least, the observations of gross motor activity which they recorded are precisely those which are least likey to reveal any functional asymmetry.

Byrne & Byrne (1991) have reported observations of hand use in the gathering and feeding behaviours of 44 wild gorillas. They note that feeding on different wild plant species requires a different technique for gathering, preparing and consuming each. Each type of food demands a specific sequence of coordinated actions of hand and mouth. More complex tasks evoked stronger individual hand preferences than simple tasks. The distribution of hand preferences was symmetrical overall, with a slight tendency to favour the right hand for fine manipulation. Once again there was a relationship between the hand preferences of mothers and offspring. Processing efficiency was only slightly greater with the preferred hand.

Lockard (1984) observed the spontaneous foraging behaviour of 8 lowland gorillas and reported 5 right-handers, 1 left and 2 ambidextrous. Fischer *et al* (1982) found 4 female lowland gorillas they studied all to be right-handed for a reaching task, with 96% right hand usage overall for the group. An interesting observation was made by Schaller (1963), who noticed that in 8 adult male mountain gorillas he studied, 59 out of 72 chest-beating displays were seen to be initiated with the right hand. Dimond & Harries (1984) found face touching to be an activity for which the left hand seems to be preferred, with 4 of 8 gorillas studied being left-preferent and the remainder showing no preference.

Cunningham *et al* (1989) watched the development of behavioural lateralization in an infant orangutan. Initially food reaching was predominantly done with the right hand, though a shift to the left occurred after 61 weeks of age. The infant was observed to have a left-hand preference for touching her own face or body.

Given the very close genetic relationship between ourselves and the chimpanzee (*Pan troglodytes*), this would appear to be the most promising species in which to look for human-like behavioural asymmetries. Bard *et al* (1990) studied the presence, strength and direction of lateral biases in 12 hand-reared chimpanzees during the first 3 months of life. Of the 10 animals in which hand to mouth movements were recorded, 8 showed a right-hand preference. Grasping of one hand by another was also recorded , and was found to be inversely related to the hand to mouth bias. The hand used to make a defensive grasping action to remove an object placed over the face, tended to be the same as that used for the hand to mouth behaviour. Walking reflexes were elicited by leaning an infant gently forward from a standing posture. The first foot to move tended to be ipsilateral to the prefered hand-to-mouth hand. Strength of lateralization was found to increase as the subjects matured. The authors noted that these behaviours were expressed under conditions of emotional arousal.

Aruguette *et al* (1992) investigated laterality in spontaneous touching behaviour in 27 chimpanzees. These animals displayed a right-hand preference for touching inanimate features of their environments, which was more strongly expressed in males than in females, but exhibited no hand preference when touching their own faces or bodies.

In a study of 67 wild chimpanzees in the Tai Forest Reserve, Boesche (1991) found no significant population asymmetry in non-tool using behaviours such as reaching and grooming, but a right hand preference among males for dipping leaf wadges, and more right hand preferences for nut-cracking among young subjects than among adults.

Lutz-maki & MacNeilage (1991) conducted an experiment with 13 chimpanzees in which 10 were found to use the right hand to pull upon a spring-loaded rope, while 2 preferred the left and one showed no preference.

A study by Hopkins *et al* (1989) required 3 chimpanzees and two rhesus monkeys to perform a simple reaching task, and a fine manipulation task in which a joystick was used to move a cursor on a screen to obtain a reward. Variable preferences were found on the reaching task. However all five subjects used the right hand for the joystick task on between 96% and 100% of trials. In a subsequent test where animals were given 100 joystick trials with each hand, all were quicker with the right hand, trials with the left taking between 1.3 and 3.5 times as long.

While lateral preferences for some activities reported for apes seem to be fairly consistent across studies, right hand preferences for fine manipulation for example, preferences on simple reaching tasks are very variable. In a recent review, Marchant & McGrew (1991) have been critical of the methods used in laterality studies of apes. They advocate the use of a wider range of tasks, comparison between spontaneous and induced measures, more trials per subject, and systematic investigation of the significance of age as a variable influencing lateral preferences. These suggestions, of course, may equally well be applied to studies involving monkeys and prosimians.

Summary and Conclusions.

There is now sufficient evidence that humans are not unique among animals, either in the possession of structural and functional brain asymmetries, or in exhibiting population-characteristic lateral biases in observable aspects of their overt motor behaviour. Thus explanations of the evolution of handedness in humans which, explicitly or implicitly, view the phenomenon as a *de novo* development of our species alone, or perhaps of our hominid ancestors, must be treated with great caution. Taxonomic chauvanism has, from time to time, driven humans to apply a label to their species to emphasise its uniqueness and special qualities, and in some way, to be definitive of what we are. Debunking such images of ourselves is a fine and instructive exercise. Since "Man, the Toolmaker" was overthrown by the observations of Jane Goodall, other images have been first touted and then undermined. We know that humans are not the only species to copulate face to face, commit murder, practice systematic genocide, recognize themselves in a mirror or carry out acts of tactical deception. Even the extent to which humans are regarded as unique in their capacity for language has undergone almost continual qualification and redefinition. It is puzzling that, for so long, the view of humans as "The behaviourally lateralized animal" held currency, but at any rate it ought now to be abandoned.

The seminal review of MacNeilage *et al* (1987) and their "Postural Origins" scenario has encouraged researchers to refocus their attention on nonhuman primates as possible models for stages in the evolution of human handedness.

A consensus is emerging that the extant prosimians present a fair model for the early stage of manual lateralization. Studies have demonstrated a general left-hand prefence for visually guided reaching, which appears strongly linked with a right forelimb preference for postural support.

In monkeys the position is less clear, with little evidence to support a population-level laterality for reaching tasks. It is intriguing to speculate that monkeys may represent an intermediate stage in manual specialization. Their more upright posture and more sophisticated manual behaviour allows, and requires extensive use of both hands. There are indications that they may prefer the right hand under certain circumstances, for example very finely controlled manipulative tasks, but resort to the left for gross motor actions, ballistic movements, and possibly under conditions of high emotional arousal. This combination of preferences is not at all incompatible with the postural origins idea, and it will be interesting to discover whether or not they continue to be borne out by future studies.

Several studies have now shown that apes are right-handed for tasks, and sub-tasks which require a high degree of precision. There has been however some contradictory and ambiguous evidence. It is certain that when assessing preferences in such manually and cognitively adept animals as these, a clear understanding of the task requirements is of critical importance. Also significant is the effect of situation, experience and, possibly "culture". It seems unlikely that an unassailable population-level laterality for gross motor actions exists among apes. This might indicate that they do not serve as an appropriate model for hand use in hominids. What does seem feasable at least, is that early hominids found an adaptive advantage in being right-handed, which apes did not.

Among monkeys, there has been a great emphasis upon studies of Old World species. Relatively few studies have involved New World monkeys and there have been very few indeed of Callitrichids. If we are to gain a balanced understanding of hand preferences in simians, it is neccessary to bring as diverse as possible a range of taxa and behaviours under scrutiny. There have been very few studies of laterality in manual grooming activity. This study reports observations of hand use in both feeding and grooming, and and also turning behaviour in six Callitrichid species, five of which, as far as this author is aware, have not been investigated before.

METHODS

Subjects

The animals used in this study were occupants of Regent's Park Zoo, London. They comprised a heterogenous sample of 21 Callitrichid primates as detailed below.

Subject	**Species**	**Sex**	**Enclosure**
1	*Leontopithecus rosalia rosalia*	F	1
2	*L. rosalia rosalia*	M	1
3	*L. rosalia rosalia*	M	2
4	*L. rosalia rosalia*	F	2
5	*Callithrix argentata*	F	3
6	*C. argentata*	M	3
7	*L. rosalia rosalia*	F	4
8	*L. rosalia rosalia*	M	4
9	*L. rosalia rosalia*	F	5
10	*L. rosalia chrysomelas*	M	5
11	*Saguinus imperator*	M	6
12	*S. imperator*	F	6
13	*Callimico goeldii*	M	7
14	*Saguinus oedipus*	F	8
15	*C. goeldii*	M	9
16	*C. goeldii*	F	9
17	*Cebuella pygmaea*	M	10
18	*C. pygmaea*	F	10
19	*C. pygmaea*	M	10
20	*L. rosalia rosalia*	F	11
21	*L. rosalia chrysomelas*	M	11

The population thus contained 11 male and 10 female animals. All subjects were adults of breeding age, with the exception of #19 which was a sub-adult, though very similar in size to his parents with whom he was housed. Most subjects were housed as male-female pairs. Subjects 9 and 20 had been given contraceptive implants as they were housed with males of a different subspecies with which breeding was not desired, though copulation was observed between the two *L. rosalia* subspecies on several occasions. The *C. pygmaea* adult pair had an offspring present, as has been mentioned.

Subjects 13 and 14 were members of larger communities, being housed with three and five conspecifics respectively. They were the only occupants of their enclosures to be included in the study due to difficulty experienced by the observer in individually identifying their cage-mates.

Maintenance of Animals.

Enclosure #1 was a large showpiece enclosure of approximately 16m^2 floor area and 5m high, fronted with glass. Two sleeping refuges were accessible via holes in artificial concrete tree trunks. The area contained several large branches and a decorative mixture of living and artificial plants, as well as a small stream and pool of water. The indoor area was adjacent to a larger wire cage outside, of approximately 28m^2 ground area and 5m high containing several bushes and trees as well as branches and a framework of steel poles for climbing. The animals were free to move between areas via a communicating door. The remaining ten enclosures were contained within the Clore Pavillion, the Zoo's small mammal house. These were somewhat variable in shape but were about 8m^2 in floor area and 3m high, with enclosure #2 being slightly larger and #10 slightly smaller. All were glass-fronted,had a translucent skylight in the roof and a small sleeping box. Numerous branches, stumps and logs were provided, as well as a mixture of natural foliage both growing and cut, with some artificial plants also. The floors were covered with a layer of shredded bark pieces which facilitated waste removal.

The animals were fed three times daily on a mixed diet of fresh fruit and vegetables chopped into 1-2cm pieces and primate chow. This was supplemented by the occasional release of live invertebrate prey into the enclosures (usually beetles and cockroaches, various spp.). Some enclosures were equipped with wooden hanging feeders from which peanuts could be obtained by inserting a digit into one of several holes. Water was provided in a large ceramic dish placed on the floor of each cage.

Observations.

A record of spontaneous feeding, grooming and locomotor behaviour was made using focal animal sampling only. Observation sessions lasted 20 minutes. Between four and seven sessions were conducted on each animal, yielding a total of 32 hours of focal data from 97 sessions. Data recorded for each animal was balanced, as far as practicable, for time of day, though observation was carried out only between 1000 and 1700 hours.

Observations were recorded using a Sharp PC6200 laptop personal computer with a backlit LCD screen, 640kb of RAM and a 20mb hard disk. The data-logging software (program name HANDY) was written specifically for this project, using TURBO Pascal Version 7 (Borland International Inc. 1983, 1992). The HANDY program is extremely straightforward in use. It uses single-key inputs from the operator to denote the type and time of occurence of relevant behavioural acts, providing continual visual feedback to the user. The program allows for the marking and correction of known errors (wrong key presses etc), and stores the information as ASCII files on the computer's internal hard disk, for later analysis. Complementary Pascal routines were written to convert data files to a suitable format for analysis using the statistical package MINITAB. Further information about development of the HANDY program is given in Appendix I.

An initial period of four days trial observations was made between 01 and 04 April 1993. This was to allow for practice of the observing technique and evaluation of the HANDY program. As the technique was found to take a few days to master and some small errors were found in the software, these data have been discarded from the study. The main observations took place between 14 April and 12 May 1993.

The observer stood, as quietly as possible, before the glass front of the enclosure, with the computer placed on a convenient ledge at about waist height to record observations. During the first few days some animals occasionally appeared curious about the observing procedure, moving towards the front of the cage to investigate the computer and observer. However all animals adjusted to the situation rather quickly, ignoring both computer and operator thereafter. At no time was any overt expression of fear shown towards the observer, as would be indicated by sudden flight into cover, alarm cries or piloerection, though all these reactions were seen in response to the behaviour of noisy Zoo visitors who shouted, cried, made sudden movements or banged on the glass.

The technique of entering information, having been practiced in the preliminary sessions, proved to be very easy to carry out. It was possible to "touch-type" data accurately during periods of intense activity, though at quieter times it was found preferable to obtain visual feedback from the computer screen by occasional downward glances. The revised HANDY program was extremely robust in execution, with no runtime errors experienced during any of the 97 sessions. Operator errors were very few and were nearly always easy to spot and correct. Unfortunately it was not possible to obtain an objective evaluation of observer reliability, but the simplicity of the procedure and the restricted range of clearly-identifiable acts recorded gives grounds for confidence in this respect.

Actions Recorded.

Fifteen distinct event classes were recorded. These were defined as follows:

1) Pick

The unimanual act of prehension or grasping of an object, usually a food item. Recorded as left or right.

2) Drop

Discarding an object which had been held with one hand. Recorded as left or right.

3) Turn

An act of continuous body rotation about the long axis of the body through an angle of 135 degrees or more. Estimation of angle is acknowledged to be somewhat subjective, but turns of lesser magnitude were thought to be unduly influenced by the location of the animal and the geography of the cage. The purpose was to gain information about the preferred direction of turns which the animal could have reasonably made in either direction. Recorded as left or right.

4) Rake

The act of running the digits of one hand through the pelage of a cagemate so that the coat is parted as though by a comb. A single hand movement from first contact to removal was recorded as one rake. Recorded as left or right.

5) Probe

The act of touching a cagemate using one or more digits during grooming. Usually, but not always, seen in conjunction with raking behaviour. From contact to loss of contact constitutes one act. Recorded as left or right.

6) Manipulate

A bimanual activity in which an object is held in one hand and acted upon by the other, for example to remove dirt. From the moment the second hand contacts the object until one hand is removed constitutes one act. Recorded as left or right according to the hand that is used to act upon the object. (i.e. the non-holding hand)

7) Self-groom

Unimanual scratching, probing or raking movements directed towards the actor's own body. Usually seen as a rapid succession of similar movements, sometimes lasting for several seconds. Though truly this activity naturally occurs in bouts, for the purpose of the analysis a self-groom is considered to be an instantaneous act. One act is taken to be a series of movements directed to the same part of the body with the same hand terminated by a period of fifteen seconds during which no like movements take place. Thus an act is separated from others by either a pause, a change of hand, or a change in the area towards which it is directed. Recorded as left or right.

8) Grip

Grasping part of a cagemate's body, usually a limb or the head. Usually performed in conjunction with raking or probing. Recorded as left or right, at the instant of first contact.

9) Mouth

Movement of a single hand containing an object towards the mouth. Recorded, ideally, at the moment the object is mouthed. Not recorded as left or right since this can be determined from the immediately preceeding events. This behaviour is not recorded in circumstances where the hand used could be ambiguous, for example if the animal currently has an object in each hand, or if it mouthes an object held bimanually.

10) Swap

The act of transfering an object from one hand to the other. Direction is not recorded as it is discernable from the context.

11) Release

Relinquishing of a grip upon cagemate. Direction not recorded since the gripping hand is already known.

12) Unseen

Indicates the moment when visual contact with the subject is lost.

13) Seen

Indicates the moment when visual contact is reestablished with a previously unseen subject.

14) ERROR

Used when the observer realizes that he has just made an incorrect keypress. Indicates that the previous entry is wrong. Serves as an aid to subsequent location and correction of errors.

15) ABORT

Pressed to terminate an observing session.

All actions were considered to be instantaneous acts, which the program recorded along with the elapsed time, in seconds from the start of the observing session, that the relevant key was pressed. The observer also kept a notebook, in which was entered summary information identifying the subject, date, time and filename for each observation session. This information was also stored in each of the data files, but the notebook proved useful in planning each observing day and for recording short notes and reminders.

RESULTS

Prior to the analysis the HANDY data files were processed into information about individual animals' percentage left and right preferences for each category of behaviour. A binomial z-score was calculated for each subject on each category of behaviour. This is used to evaluate the strength and direction of lateral preferences and is based on the formula: $z = (X - M) / \sqrt{(N * p * q)}$, where X = number of left responses, N = total of left and right responses combined, M = one-half of N, and both p and $q = .5$. This formula (Edwards, 1963) has been used in many of the studies of prosimian laterality by Jeannette Ward and her associates, which have been discussed above. Thus these results can be compared directly with the most methodologically consistent body of data available for any primate group. Their criterion for judging an animal to be lateralized for a given behaviour was also adopted. A subject was considered to be left- or right-preferent when the z-score exceeded, respectively a value of + or - 1.96 ($P<.05$). The processed data were presented in a format acceptable to most statistical software packages. The bulk of the analysis was performed using MINITAB Version 8.0 (1991, Minitab Inc.) running on a Research Machines NIMBUS PC-386 microcomputer.

Picking.

Among the 21 subjects a total of 519 instances of single-handed prehension of objects were observed (Mean = 24.1 acts/subject, SD = 16.28, range 4 - 64). These data are summarized in Table 1. Subjects ranged between 8.7% and 100% left-preferent (Mean = 45%). On the basis of the z-scores 4 subjects were classified as left-preferent, 6 as right-preferent and 11 ambipreferent. A binomial test on L vs R (n=10) indicates no evidence for population-level laterality (*P*=0.754).

TABLE 1. Percentage Left (%L) Preference For Unimanual Picking. Pick Preference (PP) Evaluated by z-score as Left (L), Right (R) or Ambipreferent (A)

Subject	Species	Sex	N	%L	z-score	PP
1	L.r	F	05	60	0.45	A
2	L.r	M	04	50	0.00	A
3	L.r	M	46	70	2.65*	L
4	L.r	F	52	40	-1.39	A
5	C.a	F	22	77	2.56*	L
6	C.a	M	24	50	0.00	A
7	L.r	F	33	12	-4.35*	R
8	L.r	M	38	82	3.89*	L
9	L.r	F	13	100	3.61*	L
10	L.r.c	M	06	50	0.00	A
11	S.i	M	16	31	-1.50	A
12	S.i	F	64	50	0.00	A
13	C.g	M	21	14	-3.27*	R
14	S.o	F	23	09	-3.96*	R
15	C.g	M	21	33	-1.53	A
16	C.g	F	14	71	1.60	A
17	C.p	M	45	56	0.75	A
18	C.p	F	16	13	-3.00*	R
19	C.p	M	19	26	-2.06*	R
20	L.r	F	09	11	-2.33*	R
21	L.r.c	M	28	46	-0.38	A

* Statistically significant z-scores (*P*<=.05, 2-tailed).

Scores were compared for males versus females (11M:10F) and also for the 10 *L. rosalia* (including the 2 of the *chrysomelas* subspecies) versus the 11 of other species. No significant diferences were found between sexes for direction of lateralization or for frequency of occurrence of picking behaviour. In terms of absolute strength of preference, measured by comparing z-score magnitude irrespective of sign, females were found to be somewhat more strongly lateralized (t =1.39, *P* = 0.18 2-tailed) but not significantly so. In comparing the two species groups, no differences of note were found in respect of picking behaviour.

Whole-Body Turning.

In all, 2139 whole-body turns were recorded (Mean = 101.86 act/subject, SD = 41.06, range 53 - 191). These data are given in Table 2. Subjects ranged between 32% and 69% left-preferent (Mean = 52% left). Sign test of z-score positive or negative *P*>.05.

TABLE 2. Percentage Left (%L) Preference For Whole-body turning. Turn Preference (TP) Evaluated by z-score as Left (L), Right (R) or Ambipreferent (A)

Subject	Species	Sex	N	%L	z-score	TP
1	L.r	F	170	66	4.14*	L
2	L.r	M	75	49	0.12	A
3	L.r	M	138	33	-3.92*	R
4	L.r	F	191	55	1.37	A
5	C.a	F	74	69	3.25*	L
6	C.a	M	123	67	3.70*	L
7	L.r	F	70	56	0.96	A
8	L.r	M	80	62	2.24*	L
9	L.r	F	129	57	1.50	A
10	L.r.c	M	80	57	1.34	A
11	S.i	M	176	66	4.22*	L
12	S.i	F	74	58	1.39	A
13	C.g	M	70	37	-2.15*	R
14	S.o	F	93	49	-0.10	A
15	C.g	M	151	46	-1.06	A
16	C.g	F	53	60	1.51	A
17	C.p	M	76	42	-1.38	A
18	C.p	F	72	32	-3.06*	R
19	C.p	M	75	39	-1.96*	R
20	L.r	F	80	55	0.89	A
21	L.r.c	M	89	46	-0.74	A

* Statistically significant z-scores (*P*<=.05, 2-tailed).

There were 5 left-, 4 right- and 13 ambipreferent animals. No significant differences were found either between sex or species groups in the direction or strength of lateralization, or in the observed frequency of turning activity.

Self-Grooming.

A total of 406 acts of self-grooming were observed (Mean = 19.33 acts/subject, SD = 15.03, range 3 - 50). Data are given in Table 3. Subjects varied between 0% and 75% left-preferent (Mean = 46.6%). There was just one significantly left-preferent animal, two right-preferent and 18 were classed as showing no preference. Sign test of z-score positive or negative *P*>.05.

TABLE 3. Percentage Left (%L) Preference For Self-Grooming. Preferences (S-GP) Evaluated by z-score as Left (L), Right (R) or Ambipreferent (A)

Subject	Species	Sex	N	%L	z-score	S-GP
1	L.r	F	12	50	0.00	L
2	L.r	M	08	75	1.41	A
3	L.r	M	45	73	3.13*	R
4	L.r	F	19	63	1.15	A
5	C.a	F	13	46	-0.28	L
6	C.a	M	15	33	-1.29	L
7	L.r	F	03	0	-1.73	A
8	L.r	M	23	22	-2.71*	L
9	L.r	F	04	25	-1.00	A
10	L.r.c	M	10	70	1.26	A
11	S.i	M	19	63	1.15	L
12	S.i	F	18	33	-1.41	A
13	C.g	M	07	57	0.38	R
14	S.o	F	27	48	-0.19	A
15	C.g	M	50	34	-2.26*	A
16	C.g	F	49	47	-0.43	A
17	C.p	M	04	50	0.00	A
18	C.p	F	04	50	0.00	R
19	C.p	M	09	33	-1.00	R
20	L.r	F	32	56	0.71	A
21	L.r.c	M	35	49	-0.17	A

* Statistically significant z-scores ($P<=.05$, 2-tailed).

No significant differences between sex or species grouping differences were found in respect of direction of lateralization, or in frequency of occurence of the behaviour. However, it was noted that males showed slightly stronger preferences than females ($t = -1.81$, $P = 0.089$ 2-tailed), however this finding falls a little short of significance.

Dropping.

Dropping of an object held in one hand was observed 193 times (Mean = 9.19 acs/subject, SD = 5.27, range 0-21). One animal was not seen to drop objects at all. Values between 12.5% and 100% left-hand preference were seen (Mean = 47.6% left).

TABLE 4. Percentage Left (%L) Preference For Dropping. Preferences (DP) Evaluated by z-score as Left (L), Right (R) or Ambipreferent (A)

Subject	Species	Sex	N	%L	z-score	DP
1	L.r	F	03	33	-0.58	A
2	L.r	M	03	33	-0.58	A
3	L.r	M	15	73	1.81	A
4	L.r	F	11	63	0.90	A
5	C.a	F	12	58	0.58	A
6	C.a	M	14	50	0.00	A
7	L.r	F	08	25	-1.41	A
8	L.r	M	12	75	1.73	A
9	L.r	F	07	100	2.65*	L
10	L.r.c	M	NIL			
11	S.i	M	02	50	0.00	A
12	S.i	F	21	43	-0.65	A
13	C.g	M	08	12	-2.12*	R
14	S.o	F	09	22	-1.67	A
15	C.g	M	12	58	0.58	A
16	C.g	F	09	89	2.33*	L
17	C.p	M	18	33	-1.41	A
18	C.p	F	08	25	-1.41	A
19	C.p	M	10	40	-0.63	A
20	L.r	F	04	25	-1.00	A
21	L.r.c	M	07	43	-0.38	A

* Statistically significant z-scores (*P*<=.05, 2-tailed).

Two subjects were classed as left-preferent, one right and the remaining 17 for which data were available were ambipreferent. No differences were observed between the sex and species subgroups for direction or strength of preference. The sign test of z-score positive or negative was not significant (*P*>.05). The *L. rosalia* group were seen to drop items somewhat less frequently than the multi-species grouping, though, once again this finding fell short of the alpha value (t = -1.94, *P* = 0.067 2-tailed). Data are given in Table 4.

TABLE 5. Percentage Left (%L) Preference For Bimanual Manipulation. Preferences (MP) Evaluated by z-score as Left (L), Right (R) or Ambipreferent (A)

Subject	Species	Sex	N	%L	z-score	MP
1	L.r	F	NIL			
2	L.r	M	NIL			
3	L.r	M	01	00	-1.00	A
4	L.r	F	10	30	-1.26	A
5	C.a	F	03	67	0.58	A
6	C.a	M	04	75	1.00	A
7	L.r	F	01	00	-1.00	A
8	L.r	M	NIL			
9	L.r	F	01	100	1.00	A
10	L.r.c	M	NIL			
11	S.i	M	05	40	-0.45	A
12	S.i	F	05	80	1.34	A
13	C.g	M	03	00	-1.73	A
14	S.o	F	01	100	1.00	A
15	C.g	M	01	00	-1.00	A
16	C.g	F	03	33	-0.58	A
17	C.p	M	11	64	-0.90	A
18	C.p	F	03	33	-0.58	A
19	C.p	M	NIL			
20	L.r	F	NIL			
21	L.r.c	M	05	40	-0.45	A

Bimanual Manipulation.

Two-handed object manipulation was recorded 57 times (Mean = 2.71 acts/ subject, SD = 3.15, range 0 to 11). Only fifteen subjects were seen engaging in this behaviour. The laterality of the action was defined by the hand which acted upon the object while the other grasped it. Laterality ranged between 0% and 100% left preferent (Mean = 44.13%). No subjects could be classed as lateralized for this activity by z-score, and the sign test of z-score positive or negative was not significant (*P*>.05) No differences were found between the sex and species groupings for direction or strength of preferences, or for frequency of occurence.

Intermanual Object Tranfer (Swapping).

Passing an object from one hand to the other was observed 67 times (Mean = 3.33 acts/subject, SD = 4.4, range 0 to 15). Six animals were not seen to perform this action. The laterality of the action was denoted according to the hand towards which the object was passed. For example a transfer from the right hand to the left is counted as a "left-handed swap". The full range of 0% to 100% left preference was seen (Mean = 63.81% left). Though all animals were declared ambipreferent according to the z-score criterion it was notable that only one individual made more right-handed swaps than left, while 11 preferred left-handed swaps and 3 made equal numbers of right and left transfers (Sign Test *P* = 0.0063). No noteworthy differences were found between sex or species groups in respect of direction or strength of preference or in frequency of swapping behaviour. Summary data are presented in Table 6.

TABLE 6. Percentage Left (%L) Preference For Intermanual Object Tranfer (Swapping). Preferences (SP) Evaluated by z-score as Left (L), Right (R) or Ambipreferent (A)

Subject	Species	Sex	N	%L	z-score	SP
1	L.r	F	NIL			
2	L.r	M	NIL			
3	L.r	M	02	100	1.41	A
4	L.r	F	10	70	1.26	A
5	C.a	F	02	00	-1.41	A
6	C.a	M	NIL			
7	L.r	F	03	67	0.58	A
8	L.r	M	03	67	0.58	A
9	L.r	F	NIL			
10	L.r.c	M	NIL			
11	S.i	M	03	67	0.58	A
12	S.i	F	15	60	0.77	A
13	C.g	M	NIL			
14	S.o	F	02	50	0.00	A
15	C.g	M	14	57	0.53	A
16	C.g	F	02	50	0.00	A
17	C.p	M	01	100	1.00	A
18	C.p	F	01	100	1.00	A
19	C.p	M	05	60	0.45	A
20	L.r	F	02	50	0.00	A
21	L.r.c	M	05	60	0.45	A

Hand to Mouth Actions.

Food items were brought to the mouth using a single hand in 1208 recorded instances (Mean = 57.52 acts/subject, SD = 36.58, range 7 - 135). Subjects were between 2.86% and 100% left-hand preferent for this activity (Mean = 51.93%). As expected, on most occasions the hand bringing food to the mouth was the same as that initially used to pick it up, as suggested by the relatively low incidence of swapping. Since most food items required 2-3 bites to consume, z-scores were relatively high. According to the z-score criterion there were 7 left-, 7 right- and 7 ambipreferent individuals (See Table 7.). No differences between sex or species groupings were noted.

TABLE 7. Percentage Left (%L) Preference For Hand to Mouth Actions (Mouthing). Preferences (MP) Evaluated by z-score as Left (L), Right (R) or Ambipreferent (A)

Subject	Species	Sex	N	%L	z-score	MP
1	L.r	F	12	42	-0.58	A
2	L.r	M	07	71	1.13	A
3	L.r	M	80	85	6.26*	L
4	L.r	F	108	57	1.54	A
5	C.a	F	76	75	4.36*	L
6	C.a	M	49	76	3.86*	L
7	L.r	F	95	14	-7.08*	R
8	L.r	M	82	93	7.73*	L
9	L.r	F	36	100	6.00*	L
10	L.r.c	M	08	75	1.41	A
11	S.i	M	41	46	-0.47	A
12	S.i	F	115	58	1.77	A
13	C.g	M	35	03	-5.58*	R
14	S.o	F	42	05	-5.86*	R
15	C.g	M	87	24	-4.82*	R
16	C.g	F	39	85	4.32*	L
17	C.p	M	135	87	8.69*	L
18	C.p	F	49	06	-6.14*	R
19	C.p	M	23	35	-1.46	A
20	L.r	F	27	15	-3.66*	R
21	L.r.c	M	62	37	-2.03*	R

* Statistically significant z-scores ($P<=.05$, 2-tailed).

Allogrooming Behaviours.

Grooming between animals was seen rather infrequently, and when it did occur, it was often in locations where it was extremely difficult to be certain who was doing what to whom, and with which hand. Under such circumstances, events were not recorded when there was felt to be a possibility of error. As a result the data gathered are somewhat sparse. The "probing" behaviour was not clearly seen to occur at all during an observing run, so there are no data to be considered. The "release" action is a simple sequitur to "grip" and is not considered further.

TABLE 8. Percentage Left (%L) Preference For Gripping. Preferences (GP) Evaluated by z-score as Left (L), Right (R) or Ambipreferent (A)

Subject	Species	Sex	N	%L	z-score	GP
1	L.r	F	02	50	0.00	A
2	L.r	M	02	00	-1.41	A
3	L.r	M	05	80	1.34	A
4	L.r	F	01	00	-1.00	A
5	C.a	F	NIL			
6	C.a	M	NIL			
7	L.r	F	NIL			
8	L.r	M	03	33	-0.58	A
9	L.r	F	01	100	1.00	A
10	L.r.c	M	NIL			
11	S.i	M	02	50	-0.47	A
12	S.i	F	NIL			
13	C.g	M	NIL			
14	S.o	F	04	100	2.00*	L
15	C.g	M	NIL			
16	C.g	F	03	100	1.73	A
17	C.p	M	NIL			
18	C.p	F	NIL			
19	C.p	M	02	50	0.00	A
20	L.r	F	10	80	1.90	A
21	L.r.c	M	02	100	1.41	A

* Statistically significant z-score ($P<=.05$, 2-tailed).

Gripping.

Only 37 acts of gripping were recorded (Mean = 1.76 acts/subject, SD = 2.41, range 0 to 10). Nine animals were not seen to exhibit this behaviour. The remaining 12 subjects showed a preference range between 0% and 100% left-preferent (Mean = 61.9%). Only one animal could be classed as left-preferent by z-score, the remainder being ambipreferent. Sign test $P>.05$. There were no differences between sex or species groupings on the basis of this limited information, which is summarized in Table 8.

Raking.

The one-handed raking action was recorded 257 times (Mean = 12.24 acts/subject, SD = 22.09, range 0 to 97). Nine animals did not perform this action. These were not precisely the same nine which did not grip, since one subject raked without gripping and another gripped but did not rake. One subject (Number 8) accounted for more than 37% of all the instances seen.

TABLE 9. Percentage Left (%L) Preference For Raking. Preferences (RP) Evaluated by z-score as Left (L), Right (R) or Ambipreferent (A)

Subject	Species	Sex	N	%L	z-score	RP
1	L.r	F	07	29	-1.13	A
2	L.r	M	10	50	0.00	A
3	L.r	M	10	20	-1.90	A
4	L.r	F	02	100	1.41	A
5	C.a	F	NIL			
6	C.a	M	NIL			
7	L.r	F	NIL			
8	L.r	M	97	47	-0.51	A
9	L.r	F	03	33	-0.58	A
10	L.r.c	M	NIL			
11	S.i	M	NIL			
12	S.i	F	NIL			
13	C.g	M	NIL			
14	S.o	F	09	33	-1.00	A
15	C.g	M	16	44	-0.50	A
16	C.g	F	28	54	0.38	A
17	C.p	M	NIL			
18	C.p	F	NIL			
19	C.p	M	13	38	-0.83	A
20	L.r	F	34	47	-0.34	A
21	L.r.c	M	28	43	-0.76	A

Left-hand preference ranged from 20% to 100% (Mean = 44.86%). All animals were considered ambipreferent by z-score (See Table 9.). As a group they showed a tendency to slightly prefer the right hand for raking, with only 2 of 12 animals performing more raking actions with the left (Sign Test, *P* = 0.0654). No differences were found between sex or species groups in respect of direction or strength of preferences or in the frequency of occurrence of the behaviour.

Correlations.

In order to establish whether the lateral preferences of the subjects for each behaviour were concordant with, or complementary to their preferences on other behaviours, a series of correlation coefficients were computed. It should be obvious that preferences for picking, mouthing and dropping will be highly positively correlated with each other (as indeed was the case). Equally it is clear that gripping and raking preferences will correlate negatively. Such logically inescapeable relationships have been regarded as trivial and are not considered further. Since there was no reason to expect the same hand or direction to be preferred for all activities, and the purpose was simply to investigate what relationships, if any, exist, comparisons made between other behaviours were two-tailed.

z-Score Comparisons.

Among the whole population of 21 animals, z-scores for turning preference were found to be negatively correlated with direction of intermanual transfer ("swapping") (Pearson's r=-0.514, *P*=0.05). Thus anmals right-preferent for direction of turning tended to swap items from right to left hands, and vice versa. This was almost equally true for males as females, and also between the two species groupings, all showing similar values of r when considered separately. Among males there was a strong relationship between self-grooming and swapping preferences (r=0.720, *P*<0.02). This was not true of females, or of the population as a whole. Males also showed a significant negative relationship between raking and swapping preference (r=-0.926, *P*<0.05). For the whole sample there was a weak tendency for the hand preferred for fine manipulation to be that preferred for bringing food items to the mouth (r=.443 0.1>*P*>0.05). Comparisons made between the two taxonomic groupings revealed no specific relationships that were not true of the whole group.

Strength of Preferences.

Leaving aside the trivial relationships between picking, dropping and mouthing etc. there were other significant relationships between strength of preferences for some other behaviours. In the whole group, strength of turning preference was positively correlated with strength of raking (r=0.614, *P*<0.05) and swapping (r=0.577, *P*<0.05) preferences, and negatively with gripping preference (r=-0.692, *P*<0.05). Strength of raking and swapping preferences were also strongly related (r=0.815, *P*<0.01). For males considered separately, both the observed significant relationships were positive. These were: turn and rake (r=0.883, *P*<0.02) and rake and swap (r=0.926, *P*<0.05). For females there was a negative association between strength of turn and grip preference (r=-0.91, *P*<0.05) and positive correlations between self-groom and manipulate (r=0.728, *P*<0.05) and between turn and swap (r=0.717, *P*<0.05).

Frequency of Occurrence.

Rank order correlation coefficients (Spearman) were computed for the frequency of occurrence of behaviours. It is recognised that the values obtained should be treated with caution due to the large numbers of tied ranks on some behaviours, particularly the less commonly occurring ones where numbers of subjects were tied on zero responses. For this reason the results will not be discussed in detail. However most of the correlations obtained were moderately to strongly positive, indicating that animals showed distinctive levels of general activity, rather than performing some activities to the neglect of others. The only persistently negative relationships were between bimanual manipulation and both gripping and raking behaviours, suggesting possibly that animals engaging in more bimanual manipulation may allogroom less and vice-versa. There seems no reason to expect this, and since all three behaviours were infrequent, with many zero ties, the relationship should be regarded as spurious.

Bouts of turning activity.

In locomotor activity within the enclosures, consecutive turns were frequently observed. An analysis of the frequency and composition of bouts was undertaken. For the purpose of the analysis a bout of turning activity was taken to be a period of time during which successive turns were observed, terminated by the occurrence of any other recordable activity, loss of visual contact with the subject or a period of 30 seconds during which no turns were seen. A bout could thus consist of a single turn or a sequence of several turns. A total of 884 turning bouts were recorded. The average duration of bouts was 23.08 seconds (single-act bouts effectively have zero duration. The mean number of turns/bout was 2.469 (SD = 0.88), and subjects performed on average 42.1 bouts each during the time under observation. There were no sex or species-group differences in the number or duration of bouts or in the number of acts/bout.

In an effort to gain information about lateral preferences, the subjects were assessed according to the numbers of their turns within bouts that occurred in runs of more than 1 turn in the same direction. More right turns occurred singly than in runs ($t=2.64$, $P<0.02$ 2-tailed). Somewhat more left turns than right turns happened in multiple runs ($t=1.72$, $P=0.096$ 2-tailed NS) and it was hypothesised that this was primarily due to the influence of the females who showed a slight preference for left turning (See Table 2.). In fact females were found to make more left turns in runs than right turns ($t=1.95$, $P<0.05$, 1-tailed).

DISCUSSION

Subjects.

The animals observed in this study were from a selection of closely related taxa of the family Callitrichidae. Since only ten members of a single species (*L.rosalia*) were available for study, a population felt to be rather small for the purpose, their numbers were supplemented with eleven other animals from five species. Similar measures have been adopted by other laterality researchers seeking to draw general conclusions about a taxonomic group. The extreme example perhaps was the work of Ward *et al* 1990 on 194 members of the genus *Lemur*. The animals selected for the present study ranged across generic boundaries as well, five different genera being involved. It was clearly important to establish whether these 21 animals can be regarded as a homogeneous sample as far as their lateral preferences are concerned. The comparisons made between the "*L. rosalia*" and "other species" subgroups give reason for confidence in this respect. Very few indications of differences in lateralization, and certainly none of significance, were observed between the two groups. It is probably justifiable to claim that the study population was representative of Callitrichid species in general, or at least those from which the sample was drawn.

Computer Data-Recording Technique.

The use of computers for recording observations in both laboratory and field settings has become more common with the increasing availability and reduced cost of computing power. Hardware developments such as laptop and pocket computers are becoming valuable tools to researchers who care to exploit their potential (See Barton & Whiten, 1988). Increasing interest in computer data-recording has been exploited by software designers and there are now several commercial programs available, the best known probably being Noldus's "The Observer".

In the present study commercial software was not used for two reasons; firstly, consideration of cost precluded the purchase of a suitable program, and secondly, previous experience with "The Observer" led me to conclude that it lacked the flexibility for the application I was considering. Since I was capable of developing suitable software for this specific application myself, I decided to do so.

This decision was vindicated by the flawless performance of the HANDY program throughout the observing period. Having been created for a very specific task, the program, in its current state of development is unsuitable for any other application. However, it could quite easily be modified with the addition of a routine to allow users to set it up for their own observations. If I have need for a similar program again, I may develop HANDY in this manner and release the program as "Shareware" to provide a free alternative to commercial software for some applications.

Population-level Laterality in Callitrichids.

The findings of this study do not provide support for the existence of any population-level lateral preference in Callitrichids comparable with those claimed, for example, to exist in lemurs (Ward, 1990; Masataka, 1989). Nor do these results accord with those of Box (1977) for common marmosets, who found six of eight animals to be left hand-preferent for grasping, though whether her findings amount to a population-level bias is unclear given the small sample size.

In general, the findings for most behaviours most closely resemble those of the majority of simple reaching studies in monkeys, subjects showing a range of individual preferences, but with rather few significantly lateralized one way or the other.

It may be true that population-level laterality does not exist among Callitrichids, but before this can be concluded, factors mitigating against the expression of lateral preferences must be taken into account. Much recent evidence has underlined the importance of posture in the expression of hand preference. Sanford *et al* (1984) and Forsythe *et al* (1988) have reported posturally related variations in hand-preference for prosimians, while Fagot *et al* (1991) form a similar conclusion about monkeys. It was not possible in this study to place any constraints upon posture which might have allowed lateral preferences to be more easily seen. Spontaneous behaviour only could be observed as this was not an experimental situation. In retrospect it would have been desirable to have noted the posture spontaneously adopted by the animals when engaged in manual behaviour, as it would have been useful to document posturally related variations if any existed. It should be expected that the subjects would not adopt extreme postures to grasp food when they are not required to. These animals fed primarily from dishes placed on the floor, or very quickly upset onto the floor if they were not. Thus there was no compelling reason to stand bipedally or hang from a branch in order to feed. Under these circumstances it seems that lateral preferences will not be shown to their greatest extent. It is interesting to note the significant finding that most animals passed food items more frequently from their right to their left hands. It may be that some individuals, while equally able to seize an item with either hand under posturally undemanding conditions, prefer to transfer the item to the left hand, leaving the right hand empty to support them in a tripedal locomotory posture. This hypothesis could have been tested if note was taken of the forelimb used in tripedal locomotion. An early version of the observation schedule incorporated this item, but it was discarded to reduce keyboard operating demands upon the observer, allowing more measures of grooming behaviours to be made. With hindsight this now appears unfortunate.

While there is no evidence *for* population-level laterality from these data, neither is there conclusive evidence for absence of laterality, while scope for refinement of the observation schedule exists. The question of the existence of a population bias in lateral preferences in Callitrichids remains an open one.

Individual Lateral Preferences.

The strongest lateral preferences were seen for the hand-to-mouth behaviour. Preferences were strongly correlated, as would be expected with picking preferences and occurred more frequently. This behaviour probably provides the best indication of lateral preference for the set of tasks involved in unimanual feeding. The subjects' preferences were distributed equally, with seven animals each in the left-handed, right-handed and ambidextrous categories. The distribution is strikingly similar to that found in Warren's early (1953) study of food-reaching in rhesus monkeys.

Few animals showed strong lateral preferences for self-grooming. Undoubtedly the scope for expression of a preference in this behaviour is limited. The hand used will be the one which can most conveniently be applied to the body part to be groomed. Few target areas (only those lying on the midline of the body) will be equally accesible to either hand. It is probable that those animals which did show preferences simply happened to have specific irritations in a particular place during the observation period. If autogrooming in any way serves a self-calming function in conditions of emotional arousal, or occurs as a stereotypy in a captive animal, this might possibly evoke a lateral preference. However, neither case appeared to apply in this study.

Unfortunately, few allogrooming sessions were observed so very little can be said about individual preferences for hand use in this activity. There is little or no information available about hand preferences in grooming from other studies either. A systematic investigation of hand use in manual grooming is long overdue and would be a very worthwhile project if tackled vigorously.

Intermanual transfer ("swapping") preferences were quite weak, but as mentioned above, objects tended to move in the same direction, from right to left. Only 67 instances of this behaviour were observed. It would have been desirable to have had many more swaps recorded to see whether a weak but definitely directional trend persisted, or whether individual preferences became polarised, and if so, in which direction.

No subject showed a significant preference for one hand for the "fine control" side in bimanual manipulation. However, most subjects tended to prefer the right hand, as would be predicted by the MacNeilage et al (1987) model. The number of instances seen was small, so this might have amounted to a significant population characteristic given more data. Callitrichids do not have particularly dextrous hands, the digits being equipped with long, curved claws (Seth & Seth, 1986) and it may be that fine manipulation is a skill they generally manage without. The most common activity classed as bimanual in these observations was brushing detritus from a food item before eating it. This probably requires little in the way of finely controlled motor skill.

Whole-body turning was the most frequent activity recorded. Dodson et al (1992), employing precisely the same statistical criterion as was used in this study, found a very significant left-turning bias in mouse lemurs and galagos. Results in this study were not at all similar. Only 9 animals showed significant preferences, 5 left and 4 right. The observations were made under rather different conditions though. They were able to test turn preferences under controlled conditions which were the same for each animal. It is not possible to say whether the same preferences would have been shown by the subjects from the present study without duplicating the testing situation used by Dodson et al. Any inherent turning biases were no doubt weakened to some extent by the individual topography of the

11 different enclosures, and by continual interactions with cagemates. It is fair to say that there would be few occasions when subjects would have a truly free choice about which way to turn. Under these circumstances it is not very surprising that no population-level, and few strong individual preferences were seen.

Distribution of Individual Preferences.

Given that the animals studied showed a high degree of variability in both strength and direction of preferences, are these haphazardly distributed, or do individuals divide skills between hands and hemispheres in a systematic way? Dodson et al (1992) found no relationship between reaching and turning preferences in their study of prosimians. The present study however has found individual turning preferences to be related at least to one manual behaviour, swapping. Turn and swap preferences correlated negatively. Thus animals who prefer to turn right, prefer to pass items from right to left hand. If the primary purpose of intermanual transfer is to free a preferred forelimb for support in locomotion, one might link this with a general right forelimb preference for support, and variable turning preferences that tend slightly towards a left bias. The suggestion may then be made that there is a general preference for the use of the "outside" limb for support while turning. Thus animals can make "forehand" or "backhand" turns. Like many tennis players they prefer to play the forehand but choice is often constrained by the state of play. If this scenario bears at all on reality one could predict that free-ranging or spontaneous captive behaviour would be characterised by weakly-left turning biases, and in free-choice testing situations stronger-left turning biases would be seen. Clearly this hypothesis could be tested by observation. The present study however is the only one the author is aware of which has assessed *spontaneous* whole-body turning preferences in nonhuman primates. More are required.

Sex differences in laterality have not figured prominently in research findings to date. Nor do they here, though a few instances may be worth noting. For unimanual picking, females were found to be more lateralized than males, but not significantly so. More interesting is the fact that 5 of the six animals classed as significantly right-hand preferent were female. Associations between strength of right-reach bias with female gender have been reported in ring-tailed lemurs (Milliken et al, 1989), small-eared bushbabies (Milliken et al 1990), gibbons (Stafford et al 1990), a large multispecies population of *Lemur* (Ward et al, 1990) and also in humans (Annett, 1980; Seltzer et al, 1990). A strongly positive association was found in males only between swapping and self-grooming preference. For males there was also a significant negative correlation between swapping and raking preference. This suggests perhaps there ought to be a negative association between self-grooming and raking preference (Only weakly supported by the data). I cannot imagine why males would prefer one hand for self-grooming and another for allogrooming (except reduced transmission of parasites perhaps). The data on allogrooming behaviours were rather sparse unfortunately so too much should not be made of this relationship.

The importance of turning preferences as an indicator of the strength of an animal's general lateral organization is underlined by a number of findings. Strength of turning preference was positively correlated with both raking and swapping preferences, and interestingly, was negatively correlated with gripping preference. The implication is that some individuals are less able, or inclined, to adapt their lateral choices to fit the circumstances than others are. An animal does not have to be gripping the body of a cagemate in order to groom it. It may be that animals with strong lateral preferences are more insistent upon adjusting their position in such a way that the preferred grooming hand may be easily applied without the need to support themselves by holding onto the cagemate.

In strength of preferences, once again some gender specific relationships were noted. Females showed a negative association between strength of turn and grip preferences, and a positive correlation between self-groom and manipulating preferences that were not true of males nor of the population as a whole. Since gripping seems primarily to be a postural support activity this relationship between turn and grip strength preference might have been predicted for the population as a whole, as strongly preferent turners should be expected to move more often into positions where postural demands while grooming were minimal. The most common bimanual activity seen was brushing detritus from food items. It is possible that a strong lateral preference for this activity might be generalized to "brushing" of the animal's own body also. If true, this might be expected in either sex. The data on bimanual manipulation were rather few however, so caution precludes claiming this as a specifically female attribute.

The finding that females make more consecutive left turns than right turns within bouts is worth noting. The fact that the right-sided preferences of females are stronger than those of males, as previously discussed may help to explain this. If, as I have argued, the preferred hand for postural support influences the preferred direction of turning, it may be the case that females are more likely to orient themselves towards a particular direction by successive left turns rather than a single right turn, in order to place more of the turning load upon the preferred supporting limb, regardless of whether they are holding an object or not. Females may effectively make more "forehand" turns.

Most authorities are agreed that there should be some relationship between neuroanatomical and behavioural asymmetries. However the nature of the hypothesised relationship is not clear. MacNeilage *et al* (1987) have argued that cerebral asymmetries should not be found in species which do not show a right-hand preference for fine manipulation. In particular they predicted no asymmetry in the brains of prosimians. Since they wrote, manual lateralization in prosimians has been more or less proven to exist, not for right-hand fine manipulation, but for left-hand grasping, for which they do not expect to find an anatomical correlate. To discover such a correlate in prosimians would be extremely interesting, though doubtless difficult to demonstrate. Unfortunately there is no evidence available to indicate structural asymmetry in prosimians or in Callitrichids, between which groups a comparison might have been made as to the region and extent of the asymmetry in lateralized and non-lateralized primates *without* fine manipulation skills.

Conclusions.

Investigation of lateral preferences in the spontaneous motor activity of 21 Callitrichid primates found no evidence to support the existence of population-level lateral biases in this group. Observations of spontaneous behaviour in captive animals are thought to be unlikely to elicit the best information about the underlying preferences of individuals or populations due to the constraints upon lateral choices imposed by the environment and interactions between individuals. Given the difficulty of observing Callitrichids in the wild, laboratory based testing is the method of choice for investigating lateral preferences in these animals. For these reasons it is not safe to refute the possibility that population-level preferences may exist. Further investigation will be required before the question can be settled.

Individual preferences were noted in a number of manual behaviours as well as whole-body turning activity. Relationships observed between strength and direction of preferences for several directional behaviours suggest very compellingly that "handedness" is far from being a simple attribute and it may well be more appropriate to talk about manual specialization for specific tasks as Fagot & Vauclair (1988a) have argued.

The "Postural Origins" model of primate laterality, proposed by MacNeilage et al (1987) is certainly not contradicted by any findings from this study. In fact postural specialization has been invoked as a possible determining factor in the direction of turning and intermanual object-transfer preferences, suggesting a course for further research.

The use of a multispecies population of subjects as representative of the Callitrichid family as a whole was considered valid as there were no significant differences in lateral preferences between two taxonomically divided subgroups. The study may well have benefited if information about posture while performing manual activities had been obtained. Also information about stance in locomotion and whole-body turning may have helped to clarify some of the relationships which can only be speculated about at present, on the basis of these results. Data gathered on laterality in allogrooming behaviour were disappointingly few. Grooming occurred infrequently, and when it did occur was often difficult to observe.

The use of a laptop personal computer for recording data was found to be a very satisfactory technique. Application-specific software was created for the study. This approach was advantageous in terms of both cost and performance.

APPENDIX 1

Development of Data-recording program "HANDY".

Design of User Interface.

Real-time behavioural data-recording is an application which imposes several important constraints upon upon user interface design. The various functions of the program should, ideally, be completely transparent to the user. It is desirable that the sequence of steps required to record data be logical and self-explanatory, with on-screen prompts where necessary, obviating the need for an instruction manual. In order to minimise errors and maximise the rate at which data can be recorded, the style of interaction with the program required by the user should be as simple as possible. The program should be forgiving. Where the user makes errors while observing they should be correctable, and the user should not be able to lose data by crashing the program inadvertently.

In this instance demands were less stringent than usual since the programmer and user were the same person. However for maximum utility and to furnish a sound basis for future program development, the above principles were followed as far as practicable.

The HANDY program is menu-driven, offering the user five straightforward options:

(1) Enter Subject Details
(2) Start Observing Run
(3) View and Correct Errors
(4) Send Data File to Hard Disk
(0) Return to DOS

The order in which menu options are presented suggests the sequence of actions required to collect and store a file of data. Selection is made by a single keypress. Keys pressed other than those offered are ignored by the program.

Menu Options

(1) Enter Subject Details

The user is prompted to enter the date, subject number, species, age and sex of the animal to be observed. Confirmation is requested that the details entered are correct and they may be re-entered if they are not. Null entries are acceptable if one or more pieces of information are not available. In the present observations, for example, precise ages of the animals were not available at the time of observation, so this entry was usually left blank. The subject details form part of the header to the data file created for each observing session. Blank lines may, if desired be filled subsequently using a text editor or by manually amending a hard copy.

(2) Start Observing Run

Selection of this option invokes the observation display which provides feedback and information during the observing session. Subject details are displayed and the user is prompted to press the space key to begin the session when ready. The user then places his hands over the keys, and when positive identification of the subject is made he may commence observing. When the space key is pressed the session start time is indicated on the screen. A reminder also appears that the session may be terminated by pressing "6". The observer continues with the session, pressing marked keys every time the various behaviours of interest are seen. Every time a key is pressed the behaviour it represents is indicated on screen along with the session-elapsed time. Error-trapping may occur in two ways. Where the user presses a key that has no function for the program this is indicated on screen. It would have been perfectly possible for the program to have simply ignored such inputs, but it was felt that this might have led to repeated wrong inputs at times of intense activity, and a resultant loss of data. An audible warning was considered, but it was thought that this might have startled the animals and thus influenced their activity. The on-screen indication of an invalid keypress was therefore something of a compromise. Where the user presses a valid key, but realises that it was not the one which was intended, he can press "0" to tag the error for later correction. Once again the program confirms that this action has been taken. When the session is complete, the user terminates it by pressing "6" as prompted on screen. It would have been possible for the program to have control of session termination after a preset interval. However this responsibility was left to the user, who may wish, for various reasons, to abandon, shorten or extend the session. Once the session has been terminated the program displays information about the duration, number of actions and number of errors recorded. The user is then invited to return to the menu.

(3) View and Correct Errors.

If an observing session contains detectable errors, this has been indicated at the end of the session. If no errors were noted the user can ignore this stage and proceed directly to the next menu item. This routine makes use of straightforward on-screen prompts to allow the user to view the data and correct known errors. User-detected errors, tagged by the program occured rather infrequently. Most sessions contained none at all. When they did occur, they were usually not more than one or two to a session so the user could rescue the situation from memory in most cases. Program-detected errors (i.e. invalid keypresses) were also infrequent and generally isolated due to the effectiveness of the on-screen feedback. In most cases it was possible to be quite certain what the entry ought to have been by reference to the context in which the error occurred and also by looking at which actions were represented by keys adjacent to the mistakenly pressed one. Where reasonable doubt existed as to which action should have been recorded, these errors were left uncorrected and were thus meaningless in the analysis, rather than misleading. When error correction is complete, the user is prompted to return to the menu.

(4) Send Data File to Hard Disk.

When an observing session has been completed and rendered error-free as far as possible, the user selects this option to secure the information on the computer's internal hard disk. When the option is invoked, subject details and summary information about the session are displayed on the screen. The user is invited to assign a filename to the session. A standard filename protocol was devised which encoded the subject number, species and date. This protocol is displayed as a prompt to the user. The program might have been allowed to assign the filename by itself, using the standard protocol, from subject information already entered. However, since some flexibility had been allowed to the user in the entering of subject details, this might have resulted in the program attempting to create DOS-illegal or non-unique filenames. Therefore this responsibility was left to the user. When the filename is entered and the data file created, this is confirmed to the user who is prompted to press a key to return to the menu.

(0) Return to DOS.

This menu option causes execution of the program to stop and returns the user to the DOS environment. Before this can happen the user is required to confirm that this is desired.

Keyboard Layout.

The layout of keys for data recording was designed to minimise the amount of time spent looking down at the keyboard. The sets of functions duplicated either side to indicate laterality of an action were laid out as mirror images of each other, as far as the topography of the keyboard would allow. Thus the same finger on either hand may be used for a given action. Side-independent functions were presented in the middle of the keyboard. The "END" function was positioned well away from others to reduce the likelihood of being pressed inadvertently. The keys were marked with small printed labels affixed with clear adhesive tape. This arrangement was found to be very satisfactory in use and quite easy to memorise with a little practice.

Choice of Programming Language.

For all practical purposes, choice of language was restricted to BASIC or Pascal, since these were the two with which the author was most familiar. Both are high level computer languages, relatively easy to learn and well supported in academic institutions. Pascal was chosen (in this case Borland Turbo Pascal, a popular and powerful implementation for Personal Computers) for several reasons. Pascal employs a compiler which converts the programmer's source code into compact machine code which occupies little memory and executes extremely quickly. Speed of execution is of critical importance when accurate timing of events is required. Timing accuracy in this instance was limited by the inherent innacuracy of the system clock, rather than the slowness of the program, to about +/- 0.1 seconds. Pascal has been well developed as a vehicle for teaching programming skills. It is designed to encourage parsimonious, top-down programming. As a result, Pascal source code tends to be shorter and more comprehensible than comparable BASIC, which facilitates the process of refinement and debugging.

The Program.

The HANDY.EXE file is approximately 18 Kilobytes long and typically generates data files of between 1 and 3 Kilobytes from each twenty minute observing session. Thus the program imposes only modest demands upon memory and disk storage. HANDY uses the system CRT device to control screen output and obtains timing information by accessing the DOS system clock. Since the program is quite short, for ease of programming and comprehension of the listing, all program parameters are global.

Program Listing

```
PROGRAM handy (input, output);
USES Crt, Dos;
LABEL 1, 2;
TYPE times = array [1..1000] of real;
     keys = array [1..1000] of char;
VAR ch:char;
    starttime, nowtime, elapsed : real;
    n, line, changeno, count, errors, events : integer;
    subject, species, age, sex, activity, filename : string;
    y, m, d, dow,
    hr, min, sec, hund : word;
    clock : times;
    action : keys;
    f : text;
{***********************************************************
*}
PROCEDURE details;
BEGIN
     clrscr;
     gotoXY (18,3); write
     ('*** Enter Subject Details ***');
     gotoXY (22,6); write
     ('Subject Number : '); readln                (subject);
     gotoXY (22,9); write
     ('Species        : '); readln                (species);
     gotoXY (22,12); write
     ('Age (Yrs,Mths) : '); readln                (age);
     gotoXY (22,15); write
     ('Sex  (M/F)     : '); readln                (sex);
     gotoXY (18,21); write
     ('*** All correct? (Y/N) ***');
     while ch <> 'y' do
     begin
          ch := readkey;
               if ch = 'n' then
          details;
     end;
END; {Details}
{**********************************************************}
PROCEDURE getact;
begin
               case action[n] of
               'p' : activity := 'R-Pick ';
               'l' : activity := 'R-Drop ';
               ',' : activity := 'R-Turn ';
               'o' : activity := 'R-Rake ';
               'k' : activity := 'R-Probe';
               'm' : activity := 'R-Manip';
               'i' : activity := 'R-SelfG';
               'j' : activity := 'R-Grip ';
               'q' : activity := 'L-Pick ';
               'a' : activity := 'L-Drop ';
               'z' : activity := 'L-Turn ';
               'w' : activity := 'L-Rake ';
               's' : activity := 'L-Probe';
               'x' : activity := 'L-Manip';
               'e' : activity := 'L-SelfG';
```

```
               'd' : activity := 'L-Grip ';
               ' ' : activity := 'Mouth  ';
               'b' : activity := 'Swap   ';
               'g' : activity := 'Release';
               'f' : activity := 'Unseen ';
               'h' : activity := 'Seen   ';
               '0' : activity := 'ERROR! ';
               else
                   activity := 'INVALID';
               end;
end; {getact}
{*********************************************************}
 PROCEDURE observe;
 BEGIN
     clrscr;
     for count := 1 to 1000 do
     begin
          clock [count] := 0;
          action [count] := '#';
     end;
     count := 1;
     getdate (y,m,d,dow);
     gotoXY (25,3); write
     ('*** OBSERVATION ***');
     gotoXY (1,6); writeln
     ('Date           :                 ',d,'/',m,'/',y);
     writeln ('Subject Number : ',subject);
     writeln ('Species        : ',species);
     writeln ('Age            : ',age);
     writeln ('Sex            : ',sex);
     gotoXY (40,6); write
     ('Press Space Key to Start                   Session');
          repeat
               ch := readkey;
          until
               ch = ' ';
     gettime (hr,min,sec,hund);
     starttime := (hr*3600) + (min*60) + sec + (hund/100);
     gotoXY(35,6); write
     ('Press "6" to Abort Session  "0" to Mark Error');
     gotoXY(40,9); write
     ('Session Started at ',hr,':',min,':',sec,'.',hund);
     gotoXY(19,12); write
     ('*** Last Action Recorded ***');
     gotoXY(19,14); write
     ('Time    Left   Centre   Right');
     while ch <> '6' do
     Begin
          ch := readkey;
          gettime (hr,min,sec,hund);
          nowtime := (hr*3600) + (min*60) + sec +
(hund/100);
          elapsed := nowtime - starttime;
          if ch <> '6' then
          begin
               clock [count] := elapsed;
               action [count] := ch;
          end;
          gotoXY(16,16); write (elapsed:7:2);
```

```
          case ch of
          'p' : write ('                    Pick    ');
          'l' : write ('                    Drop    ');
          ',' : write ('                    Turn    ');
          'o' : write ('                    Rake    ');
          'k' : write ('                    Probe   ');
          'm' : write ('                    Manip   ');
          'i' : write ('                    Self G  ');
          'j' : write ('                    Grip    ');
          'q' : write ('    Pick                    ');
          'a' : write ('    Drop                    ');
          'z' : write ('    Turn                    ');
          'w' : write ('    Rake                    ');
          's' : write ('    Probe                   ');
          'x' : write ('    Manip                   ');
          'e' : write ('    Self G                  ');
          'd' : write ('    Grip                    ');
          ' ' : write ('           Mouth            ');
          'b' : write ('           Swap             ');
          'g' : write ('           Release          ');
          'f' : write ('   Subject Not Visible      ');
          'h' : write ('     Subject Visible        ');
          '0' : write ('   Error Noted in Last Entry');
          '6' : write ('     SESSION ENDED          ');
          else
                write ('  Invalid character "',ch,'"     ');
          end;
             count := count + 1;
    end;
    count := count -2;
    gettime (hr,min,sec,hund);
    nowtime := (hr*3600) + (min*60) + sec + (hund/100);
    elapsed := nowtime - starttime;
    events := 0; errors := 0;
    for n := 1 to count do
    begin
         case action[n] of
         'p','l',',','o','k','m','q','a','z','w','s','x','
          ','b','e','i','j','d','g','f','h' : events :=
events         + 1;
         '0'  : errors := errors + 1;
         end;
    end;
    gotoXY(10,19); write
('*******************************************************');
    gotoXY(10,20); write
     ('  Session Ended after ',elapsed:7:2,' Seconds');
    gotoXY(10,22);
     write ('  Actions = ',events,',  Errors = ',errors,',
     Invalid keypresses = ',count-events-errors,'       ');
    gotoXY(10,23); write
('*******************************************************');
    gotoXY(20,24); write ('Press "SPACE" to Return to
MENU');
    repeat
          ch := readkey
    until ch = ' ';
end;
{**********************************************************}
```

```
PROCEDURE correct;
BEGIN
     clrscr;
     gotoXY(20,3); writeln
     ('*** VIEW and CORRECT ERRORS ***');
     writeln
('_____________________________________________________________
______________________');
     writeln;
     writeln ('* Subject Info *');
     writeln;
     writeln ('Subject Number : ',subject);
     writeln ('Species        : ',species);
     writeln ('Age (yrs/mths) : ',age);
     writeln ('Sex            : ',sex);
     gotoXY(55,6);  write ('* Session Info *');
     gotoXY(55,8);  write (elapsed:7:2,' Seconds Duration');
     gotoXY(55,9);  write ('Actions         : ',events);
     gotoXY(55,10); write ('Errors          : ',errors);
     gotoXY(55,11); writeln
     ('Invalid Keys   : ',count-events-     errors);
     writeln
('_____________________________________________________________
______________________');
     n := 1; line := 1; changeno := 1;
     gotoXY(1,13); write ('Event     Time     Action
Key');
     gotoXY(1,14);
     while n <= count do
           begin
               getact;
               writeln (n:4,'    ',clock[n]:7:2,'
               ',activity:7,'   ',action[n]);
               n := n+1; line := line +1;
               if (n>count) and (line<11) then
               repeat
                     writeln
    ('                                                        ');
                     line := line + 1;
               until line = 11;
               if (line = 11) or (n>count)  then
               begin
                    line := 1;
                    gotoXY(45,13); write
               ('* Changes? (Y/N)                             *');
                    ch := readkey;
                    if ch = 'y' then
                    begin
                         gotoXY(45,15); write
                         ('ENTER "0" when finished');
                         repeat
                         gotoXY(72,17); write ('    ');
                         gotoXY(72,19); write ('    ');
                         gotoXY(45,17); write
                         ('ENTER EVENT No TO CHANGE : ');
                         readln (changeno);
                         gotoXY(45,19); write
                         ('ENTER CORRECT ACTION     : ');
                         readln (ch);
```

```
                         if changeno <> 0 then
                         action[changeno] := ch;
                         until changeno = 0;
                    end;
                    gotoXY(1,14);
              end;
      end;
END;
{*******************************************************}
PROCEDURE diskops;
BEGIN
     clrscr;
     gotoXY(35,3); write ('*** DISK OPERATIONS ***');
     gotoXY(1,6); write ('* Session Info *');
     writeln;
     writeln ('Date              : ',d,'/',m,'/',y);
     writeln ('Subject No        : ',subject);
     writeln ('Species           : ',species);
     writeln ('Age (yrs,mths)    : ',age);
     writeln ('Sex               : ',sex);
     writeln ('________________________________');
     writeln (elapsed:7:2,' Seconds Duration');
     writeln (count,' Data Points Recorded');
     writeln ('________________________________');
     writeln ('     *** Filename Protocol ***');
     writeln (' "h" SubNo Genus Species Date');
     writeln ('         e.g.  "h1lso31"');
     writeln ('________________________________');
     writeln ('ENTER FILENAME'); readln (filename);
     assign (f,filename);
     rewrite (f);
     writeln
     (f,'*** HANDY DATA FILE *** (Filename :',filename,')');
     writeln (f);
     writeln (f,'Date              : ',d,'/',m,'/',y);
     writeln (f,'Subject No        : ',subject);
     writeln (f,'Species           : ',species);
     writeln (f,'Age (yrs,mths)    : ',age);
     writeln (f,'Sex               : ',sex);
     writeln (f,'___________________________');
     writeln (f,'Time Elapsed    Action');
     writeln (f);
     for n := 1 to count do
     begin
          getact;
          writeln (f,clock[n]:7:2,'         ',activity);
     end;
     writeln (f,'___________________________');
     writeln (f,elapsed:7:2,' Seconds Duration');
     writeln (f,count,' Data Points Recorded');
     writeln (f,'___________________________');
     close (f);
     gotoXY(1,21);
     writeln
     ('OK! File Written.   Press SPACE to Return to MENU');
     ch := 'q';
     repeat
           ch := readkey;
     until ch = ' ';
```

```
end;
{*************************************************************}
BEGIN  {HANDY - MAIN PROGRAM BLOCK.}
      clrscr;
      gotoXY (19,12);
      write ('*** "HANDY" data-logging program ***');
      gotoXY (30,15); write ('Jon Watts 1993');
      gotoXY (25,20); write ('(Press SPACE key to begin)');
      gotoXY (80,25);
      repeat
            ch:=readkey;
      until ch=' ';
1:    clrscr;
     gotoXY (29,3); write ('*** MENU ***');
     gotoXY (22,6); write ('(1)  Enter Subject Details');
     gotoXY (22,9); write ('(2)  Start Observing Run');
     gotoXY (22,12); write ('(3)  View and Correct Errors');
     gotoXY (22,15); write
     ('(4)  Send Data File to Hard Disk');
     gotoXY (22,18); write ('(0)  Return to DOS');
     gotoXY (80,25);
     while ch <> '0' do
           begin
                ch := readkey;
                case ch of
                '1' : details;
                '2' : observe;
                '3' : correct;
                '4' : diskops;
                end;
                goto 1;
           end;
     gotoXY (20,25);
     write ('Are you sure you want to Quit? (Y/N)');
     gotoXY (80,25);
     ch := readkey;
     if ch <> 'y' then
     goto 1;
     clrscr;
     gotoXY (28,13); write ('Have a nice day!!');
     gotoXY (80,25);
     delay (3000);
     clrscr;

END. { HANDY - MAIN PROGRAM BLOCK}
```

Structure of Data Files.

The HANDY program produces ASCII files in the following format:

```
*** HANDY DATA FILE *** (Filename : ha12se19)

Date              : 19/5/1993
Subject No        : 12
Species           : S.oedipus
Age (yrs,mths)    : 3,4
Sex               : f
______________________________
Time Elapsed     Action

   4.18          R-SelfG
   6.87          L-SelfG
   9.12          R-SelfG
   9.51          R-SelfG
  10.05          R-SelfG
  10.66          L-SelfG
  14.89          R-Pick
  18.68          Mouth
  20.55          R-Pick
  21.75          Mouth
  24.50          L-Pick
  29.33          Swap
  31.26          Mouth
  33.29          L-Pick
  33.89          Swap
  34.39          Mouth
  41.47          R-Grip
  49.55          L-Rake
  50.75          L-Rake
  51.25          R-Rake
  51.91          L-Rake
  52.51          Release
  53.56          L-Turn
  54.16          L-Turn
  55.20          R-Pick
  56.14          Swap
  56.69          L-Turn
  57.18          Mouth
  57.79          Mouth
  58.17          R-Drop
  58.66          L-Pick
  65.20          L-turn
  68.88          L-Manip
  70.03          Mouth
  71.57          Mouth
  73.66          Mouth
  74.21          Swap
  75.20          Mouth
______________________________
  78.44 Seconds Duration
38 Data Points Recorded
______________________________
```

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