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FACTORS ASSOCIATED WITH EXPLORATION IN MARMOSETS: AGE, GENDER AND HAND PREFERENCE

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ABSTRACT: Age, hand preference and gender are shown to be associated with exploration behaviour performed by *Callithrix jacchus*, depending on the context in which the marmosets are tested. When each marmoset was tested alone in a novel environment, hand preference had a significant effect on exploration: right-handed marmosets explored more actively than left-handed ones. This difference is probably related to hemispheric specialisation for processing novel stimuli and controlling emotional responses. Age and gender were found to have no significant effect on exploration in this context. When the marmosets were tested in the social groups and by placing novel objects in their home cages, both hand preference and age influenced approach and interaction with the stimuli, but again gender had no significant effect. Solving a novel problem in the home cage was influenced only by age, or related social dominance, and not by gender or hand preference. The implications of these results to behaviour of wild marmosets and other species are discussed.

This paper will discuss the influences of age, gender and hand preference on responses to novelty in the common marmoset, *Callithrix jacchus*. It will show that the relative contribution of each of these factors varies with the context in which the exploration is taking place, specifically whether the marmosets are in social groups in a familiar setting or in isolation in a novel setting.

Age has been shown to affect exploration in primates in many taxa (e.g. Menzel and Menzel, 1979). Typically juveniles are more likely to approach novel stimuli than are adults and they are more active than adults when placed in a novel setting. Menzel and Menzel (1979) found that juvenile saddle-backed tamarins (*Sanguinus fuscicollis*) approach a novel stimulus in the home cage sooner than do adults, and they spend

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more time attending to it than adults. Attention to a novel stimulus may involve active approach and interaction, but it may also involve visual investigation from a distance, and this form of visual exploration might be achieved by head cocking, rotation of the head around the longitudinal axis of the body while orienting toward a stimulus. Head cocking in primates appears to be a form of visual exploration because it occurs more frequently when novel stimuli are presented (Rogers, Stafford & Ward, 1993). Since head cocking is more common in juveniles than adults, as Menzel (1980) found in squirrel monkeys, we may use this specific behaviour as another indication that juveniles pay more attention to novel stimuli than do adults.

Gender is also known to influence some aspects of exploration in primates, as well as other species. Typically females show more exploration than males, although this is not the case for vigilance (Box, 1999). Female primates, across widely different taxa, also acquire new behaviour patterns more readily than males (Kappeler, 1987; Bachevalier, Hagger & Bercu, 1989), suggesting that females may be more attentive to novel situations than males. In galagos, females head cock more frequently than males when presented with a novel stimulus (Rogers et al., 1993), indicating that they pay more attention to novel stimuli than males.

Recently, hand preference has been shown to influence responses to novelty (Hopkins and Bennett, 1994). Left- and right-hand preferring chimpanzees were given the opportunity to explore novel toys. Hopkins and Bennett (1994) found that the right-hand preferring subjects approached the novel objects and interacted with them more than the left-hand preferring subjects. Hence approach and exploration may be related to greater control by the left hemisphere (which controls the right hand) than by the right hemisphere (which controls the left hand). Hand preference has also been shown to influence the responses of bushbabies (*Otolemur garnettii*) in a novel environment. Watson & Ward (1996) found that left-hand preferring subjects were more active (scored as jumping and sector crossing) than the right-hand preferring ones. This may indicate that left-hand preferring bushbabies explore the novel environment more than right-hand preferring ones, and this would be opposite to the result obtained with chimpanzees. If so, the difference between these two results may depend on the species tested or the conditions of the testing. The bushbabies were, for example, tested singly, whereas the chimpanzees were tested in their social group. It is known that social conditions influence the responses to novelty (Fragaszy & Mason, 1978). Age and sex differences between

subjects and studies need to be considered also, as well as species differences.

The relationship between hand-preference and exploration is likely to reflect differential use of the left and right hemispheres. A subject with a consistent preference to use the right hand may have a tendency towards greater use of the left hemisphere than the right in most situations. The converse may be the case for subjects with a preference to use the left hand. If so, hand preference may reflect more general aspects of cognitive function, since each of the hemispheres is specialised to carry out different kinds of information processing and to control different functions.

Davidson (1992) has suggested that approach behaviour may be associated with greater activation of the left hemisphere and avoidance by greater activation of the right hemisphere. In humans, the right hemisphere is considered to be specialised for processing negative emotional stimuli and the left hemisphere for processing positive emotional stimuli (Bogen, 1985). The same may be true in nonhuman primates since there is evidence that the right hemisphere is involved in fear and aggressive responses. Specialisation of the left hemisphere for positive emotions (and approach) and the right hemisphere for negative emotions (and avoidance) may be the reason why right-hand preferring chimpanzees were more likely to approach the novel objects and interact with them. However, more species of primates will need to be tested to confirm this hypothesis.

Casperd and Dunbar (1996) have found that gelada baboons are more likely to direct agonistic responses to a conspecific on their left side than on their right side, indicating right hemispheric control. Hauser (1993) has shown that, in rhesus monkeys, fear responses are expressed more strongly on the left side of the face, also indicating control by the right hemisphere. In the common marmoset also, fear expressions involve greater movement of the muscles on the left side of the face (Hook-Costigan & Rogers, 1998a). In fact, when marmosets make a mobbing call, they open the left side of their mouth more widely than the right and the reverse occurs when they make a contact twitter call. These data indicate that the right hemisphere is specialised for aggressive and fear responses. It may, therefore, process negative emotions. The left hemisphere, by contrast, may be specialised for contact and approach, a more positive emotional state. That is why hand preference was taken into account in the analyses of exploration by the common marmoset to follow.

Common marmosets are excellent subjects to test the potential

influence of hand preference on responses to novelty because approximately half of the subjects in a group are right-hand preferring and the other half left-hand preferring (Box, 1977; Hook-Costigan & Rogers, 1997). Although their hand-preferences vary with the task to which they are applied (Hook-Costigan & Rogers, 1995), individuals use the same hand consistently over time to pick up pieces of food from the ground and take them to their mouth to feed (Hook-Costigan & Rogers, 1997). Hence, if hand preference reflects differential activity of the hemispheres, half of the individuals may have greater activity of the left hemisphere (the right-handed subjects) and the other half may have greater activity of the right hemisphere (the left-handed subjects). These biases may reflect different ways of processing information and reacting to stimuli. In fact, it is known that marmosets have differential specialisation of the left and right hemispheres, as shown by a group bias to view neutral stimuli with the right eye (Hook-Costigan & Rogers, 1998b; Hook-Costigan, 1999) and by group bias in asymmetry of facial expressions (Hook-Costigan & Rogers, 1998a). Therefore it was predicted that right-hand preferring marmosets might show more exploration behaviour in a novel environment and they might approach novel stimuli more readily than left-hand preferring marmosets.

Three contexts were used to test exploration in the marmosets in captivity: 1) exploration of a novel environment in isolation, 2) exploration of novel objects in the home-cage together with the familiar social group, and 3) approach and attention to solving an unfamiliar problem in isolation but still in a section of the home-cage. Although it is recognised that numerous factors may influence the responses of the marmosets in these contexts, including early experience (as described by Kaplan & Rogers, 1999), only age, gender and hand preference were considered here.

1. EXPLORATION ALONE IN A NOVEL ENVIRONMENT

METHODS

Subjects and Housing

Twenty, adult (21 to 68 months) common marmosets (12 females and 8 males) of the colony at the University of New England were tested by placing them singly into an unfamiliar room (approximately 3m square). The room contained a variety of novel objects on which

they could climb or which they could manipulate. The objects included branches, ropes, wire-mesh and bamboo structures for climbing, a variety of toys and strips of hanging cloth. Some of the objects were freshly scented with banana or blueberry odour before each test. A basket of straw from the home cage was also suspended in the room to provide a familiar odour.

Procedure

Each marmoset was taken into the room in its nesting box and then the door of this box was opened and the experimenter left the room. For the next hour the behaviour of the marmosets was recorded by videotaping through two one-way mirrors. The mirrors themselves were an aspect of the novelty of the room. Playback of the videotapes provided scores of latency to leave the nesting box to enter the unfamiliar environment, number of leaps (feet and hands off the substrate together), parallax movements of the head from side to side (used in perceiving depth), touches of the objects, head cocking movements and number of objects touched. The marmosets could return to the nesting box if they wanted to, and total time spent in the box was also recorded.

Analysis

The data were analysed for the effects of gender, age and hand preference, and these results have been reported in detail in Cameron and Rogers (1999). The hand preference of each subject had been determined 1 month prior to testing. It was calculated from 100 scores of picking up food and taking it to the mouth. The subject was in a relatively relaxed state in the home cage. No more than 15 scores were recorded on any day and runs or bouts were avoided by not scoring repeated taking of the same piece of food to the mouth. The hand preference was considered to be significant on the basis of z -score analysis (Cameron & Rogers, 1999). There were no subjects without a significant hand preference. As an additional check of the hand preference scored, the preferences scored one month prior to testing were correlated with data collected for the same individuals and in the same manner 10 months prior to that time. There was a strong positive correlation (Pearson correlation, $r = .91$, $p < .0005$), showing the consistency of hand preference for each individual. In the group tested there were 5 right-handed males, 3 left-handed males, 3 right-handed

females and 9 left-handed females. The statistical analyses took into account the variation in group sizes.

RESULTS AND DISCUSSION

The latency scores differed significantly in the left- and right-handed subjects (for details of statistical results see Cameron & Rogers, 1999). All but one of the right-handed subjects left the nesting box to enter the unfamiliar room in less than 100 seconds. This was true also of half the left-handed subjects, but the remaining left-handed subjects formed a second cluster with latencies in excess of 100 seconds (range of 110 to 250 secs).

It will be noted that none of the latencies were long enough to have a significant effect on behaviour in the room because 1 hour was allowed to collect those scores. Hand preference had a separate and significant effect on behaviour in the room. The right-handed marmosets performed twice as much leaping and twice as many parallax movements and touches of objects as did the left-handed marmosets (Fig. 1; for details of statistics see Cameron & Rogers, 1999). In addition, they touched more than twice the number of different objects than did the left-handed ones. These results are consistent with the prediction outlined above. Age at testing and gender had no significant effects on these particular behaviours and, furthermore, gender had no significant effect on any of the behaviours scored.

Head cocking, however, occurred at the same levels in the right- and left-handed subjects. Although it was not influenced by hand preference, head cocking was affected by age. Older marmosets had lower scores of head cocking than younger ones ($r = -.66$, $p = .01$, Pearson correlation). Time spent in the nesting box also had no relationship to hand preference but correlated negatively with age ($r = -.55$, $p = .01$). Therefore age affected some of the behaviours that can be termed exploratory but not the same behaviours as hand preference.

The fact that right-handed subjects perform more visual exploration by parallax movements than left-handed subjects but both groups perform the same amount of head cocking deserves further mention. It was considered possible that the extra parallax movements of the right-handers stems from the fact that they explore the novel environment more actively by leaping than do the left handers. Leaping requires accurate assessment of distance and parallax movements would provide

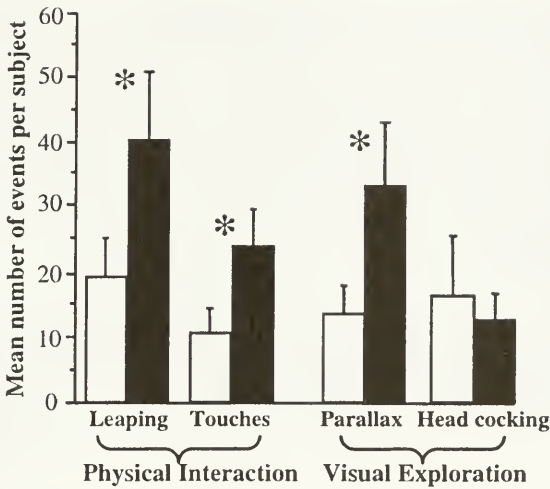


Figure 1. Exploration alone in a novel environment. The mean number of events of each behaviour has been plotted with standard errors indicated. The white and black bars are for left-handed and right-handed subjects respectively. The asterisks indicate significant differences between the scores for left- and right-handed subjects. This figure has been adapted from Cameron & Rogers (1999). Note that right-handed subjects perform more active exploration of the novel environment than left-handed subjects. They also perform more visual exploration by parallax movements than the left-handers but both groups perform similar amounts of head cocking.

information for this. Head cocking, by contrast, might be seen as a way of visually exploring the new environment without physically interacting with the novel stimuli. It might be ‘exploration at a distance’ and, if so, could explain why left-handed subjects engage in it as much as right-handed subjects.

The number of parallax movements performed does, in fact, correlate with the number of leaps (Spearman correlation, $r = .42$, $p = .023$) but there is a tendency for the same relationship to hold between head cocking and leaping ($r = .42$, $p = .063$). In fact, head cocking and parallax correlated strongly in the left-handed subjects ($r = .82$, $p = .002$) but not in the right-handed subjects ($r = .31$, $p = .42$). This disassociation between head cocking and parallax movements in the right handers indicates that they are separate ways of actively exploring the novel environment. However, parallax did not correlate

significantly with leaping in the right handers ($r = .33, p = .38$), whereas it did in the left handers $r = .63, p = .039$). The extra leaping performed by the right-handed subjects, therefore, is not associated with extra parallax movements. This examination of the data fails to provide strong support for the hypothesis about head cocking being exploration at a distance and parallax being an aspect of interactive exploration, but it does show that the two types of visual exploration are separate to at least some degree.

2. EXPLORATION OF NOVEL OBJECTS IN THE HOME CAGE AND WITH THE SUBJECT'S SOCIAL GROUP

METHODS

Subjects and Procedure

Nineteen of the same subjects were also tested by presenting novel stimuli to them in their home-cage groups (tests conducted 1 year prior to the above). The marmosets were tested in familiar, unisex groups of 2 to 4 subjects. A platform on which novel objects were presented was placed in the home cage. The novel stimuli presented on the platform were either potential food items, presented inside 4 glass Petrie dishes (live cockroaches, plastic models of insects or a small mirror inside each dish, in which the marmosets could see their own image), or they were potential predators, simply placed on the table (a coiled, model snake or a model resembling two rearing snakes inside a jar). The stimuli were presented for one hour on each of four consecutive days separated by intervals of 7 days, but only the data for the first day of presentation will be considered here because only then were the stimuli entirely novel. Only one stimulus type was presented at a time and the order of presentation was randomised. A video camera directed at the platform was used to record the responses of the marmosets to the novel stimuli. The number of periods spent by each subject on the platform was determined and also the total time spent on the platform.

Analysis

As these data have not yet been submitted for publication elsewhere (Rogers, Hook-Costigan & Johnston, in preparation), they will be presented in somewhat more detail here than the data for the

other experiments. However, as total time spent on the platform correlated with the number of periods on the platform, only the latter will be presented. The scores of number of periods on the platform were analysed first for any effects of gender. As no significant effect of gender was found, the data for males and females together was examined using the log-transformed data in a 3-way ANOVA, with stimulus type as a repeated measure together with the factors age (subadult versus adult) and hand preference (left or right). The age dividing subadults from adults was 20 months, and there were 8 subadults (4 left-handed and 4 right-handed) and 10 adults (6 left-handed and 4 right-handed). One subject was eliminated from the analysis because it was ambipreferent for picking up food at this time, although later it did develop a hand preference.

RESULTS AND DISCUSSION

There were significant main effects of stimulus ($F_{4,70} = 13.9, p < 0.0001$), age ($F_{1,70} = 14.2, p = 0.0003$) and hand preference ($F_{1,70} = 5.9, p = 0.018$). The only significant interaction was between age and stimulus ($F_{4,70} = 3.6, p = 0.0097$). Subadults scored almost twice as many periods on the platform as did adults. This was true for all stimuli except the rearing snakes, which elicited the highest levels of fear. Hand preference for food holding was significantly associated with the number of periods on the platform: right-hand preferring individuals had higher scores than the left-hand preferring individuals.

Figure 2 illustrates the effect of age on investigation of the novel stimuli. It shows that subadults had higher scores for the number of periods spent on the platform than adults. This was the case for all of the stimuli, except the model of rearing snakes and there was only a trend towards this difference for the coiled snake. The rearing-snakes model elicited a distinctly different set of responses from the marmosets than did any of the other stimuli. First, as can be seen in Figure 2, the marmosets were much less likely to approach this stimulus than any of the other stimuli. Second, only this stimulus evoked the mobbing (tsik) calls. In other words, the marmosets showed fear responses to this stimulus, whereas this was not the case for any of the other stimuli. None of the other stimuli evoked the types of vocalisations characteristic of a state of fear (tsik, egg or ock calls). The rearing-snakes model has been referred to by Kaplan and Rogers (1999a, 1999b) and approach to this stimulus was found to depend on

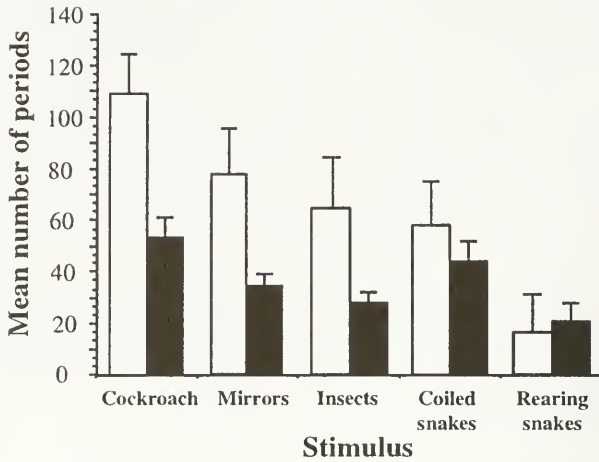


Figure 2. Exploration of novel objects in the home cage: the influence of age. The number of periods spent on the platform exploring each set of novel stimuli is plotted as means and standard errors for the subadults (white bars) and adults (black bars). Note that subadults investigate all of the stimuli, apart from the rearing snake model, more than the adults.

the amount of anogenital licking received by the marmoset during the first 2 months of life. Age did not have any influence on the responses to this particular stimulus.

The influence of hand preference on the number of periods spent on the platform is shown in Figure 3. Overall the marmosets with a right-hand preference investigated the novel stimuli more than the left-hand preferring marmosets. This result is consistent with the fact that right-handed marmosets explored the novel room more actively than the left-handed ones (see above). The only stimulus for which this relationship was not true was the coiled snake (Fig. 3), although this result was caused by the lumping of scores for adults and subadults. The relationship between increased exploration and hand preference was stronger for subadults than adults: hence the significant interaction between age and hand preference mentioned above. As shown in Figure 4, right-handed subadults investigated all of the novel stimuli to a greater extent than left-handed subadults.

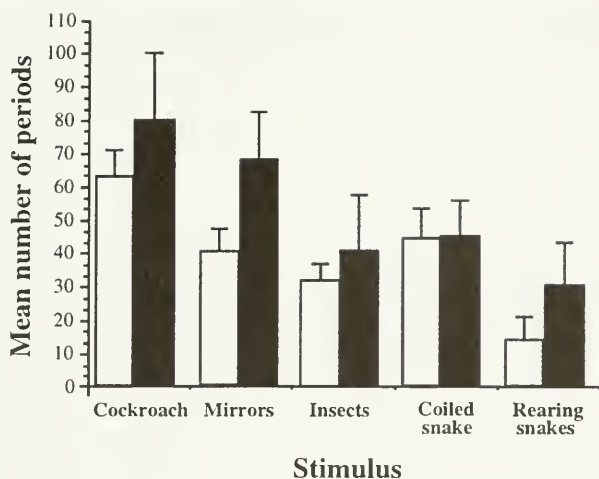


Figure 3. Exploration of novel objects in the home cage: the influence of hand preference. The data for subadults and adults combined are plotted as in Figure 2. The white bars indicate the scores for marmosets preferring to use the left hand during feeding and the black bars represent those preferring to use the right-hand.

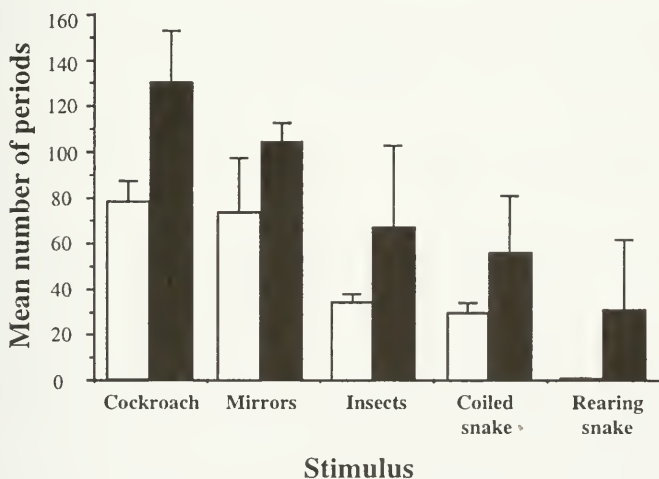


Figure 4. Exploration of novel objects in the home cage: the influence of hand preference for subadults only. The white bars represent the left handers and the black bars the right handers.

3. AN UNFAMILIAR PROBLEM IN THE HOME CAGE

METHODS

Procedure

Problem solving in the home cage was also scored for the same 20 subjects, approximately 3 months after they had been tested in the unfamiliar room (see Section 1 above). In this case, the marmoset being tested was partitioned off from the other members of its social group in a section of the home cage. There it was allowed 30 minutes to solve a novel problem. The problem was to slide a horizontal sheet on which a meal worm had been placed so that the worm fell through a hole in the middle of the sheet and so dropped to the bottom of a transparent cylinder from which it could be retrieved by the marmoset (Cameron & Rogers, 1999). Retrieval required the marmoset to reach through a small opening at the bottom of the cylinder. Once the meal worm had been retrieved and eaten, another worm was placed on the sliding sheet and a new trial could begin. The following were scored: the latency to approach the apparatus, total time spent on the platform interacting with the apparatus and the number of times the sliding sheet was successfully manipulated so that the marmoset could obtain the meal worm.

RESULTS AND DISCUSSION

The results have been published in detail by Cameron and Rogers (1999) and so will be summarised briefly here. There were no significant main effects of gender or hand preference on any of the behaviours measured, and there were no significant interactions with either of these factors. Age, however, did influence the time spent on the platform attending to the apparatus and the number of successful manipulations of the sliding sheet. Both of these behaviours correlated positively with age: the older marmosets were more successful than the younger ones in solving the problem. This result is inconsistent with the fact that younger marmosets pay more attention to novel stimuli presented in the home cage (see above). In the study reported here, there was no effect of age on the latency to approach the apparatus but older marmosets paid more attention to solving the problem.

The role of age in problem solving was further investigated. It was considered possible that the older marmosets may be more successful in solving the problem because they were more motivated to feed or because they were in a superior social position and less distracted by the nearby presence of other members of their group. Therefore competition for obtaining a favoured food was scored. A small piece of banana was placed on the wire wall of the home cage and the marmoset that obtained it was recorded. This was repeated for 100 scores per cage. Each individual was assigned as being 'dominant' or 'subordinate' depending on its relative success in obtaining the banana, although it is recognised that these labels are rather superficial and may have little to do with any broad assessment of social position. The accuracy of this categorisation was also limited by the fact that the marmosets were tested only with their own social group and only one individual per group was assigned as dominant, the rest being considered as subordinate. It was not possible to test each subject against every other subject because this would have disrupted the social groups and may have caused fighting and injury. In fact, even if it had been possible to test each individual against all others, the scores obtained would not have been particularly relevant because marmosets do not form simple hierarchies (Ferrari & Lopes Ferrari, 1989; Rothe & Keonig, 1991).

There was no significant effect of dominance on latency to approach the apparatus but dominant subjects spent more time attending to the apparatus and were more successful in solving the problem than the subordinate subjects. However, as dominant subjects tended to be older than subordinate ones (by some 10 months), the influences of age and dominance on problem solving could not be separated.

GENERAL DISCUSSION

In marmosets, the hand preference displayed by an individual while it is in a relaxed state feeding in the home cage and in its familiar social group may reflect the individual's baseline state of hemispheric control. In other words, a left-handed individual may have a baseline state in which the right hemisphere tends to be in charge of processing information and controlling behaviour, whereas the reverse may be the case for a right-handed individual. Therefore, although the hemisphere most active at any one time may change with context and state of arousal, there may be a tendency for some individuals to rely more strongly on activity of the right hemisphere and others on activity of the

left hemisphere. In turn, these differing dependencies on the left or right hemisphere may reflect differences in temperament and so determine the initial responses to novel stimuli (Table 1). For example, a left handed individual might begin a test in a more fearful state than a right-handed one and so be less likely to approach novel stimuli and interact with them. The hemisphere most active might well shift with time and experience in the testing situation but the resting or baseline state might set an initial bias of responding. Age and social position might override this effect of hand preference depending on context, as shown in the experiments reported here. It remains likely that gender would also have an effect on exploration in at least some contexts, although it had no significant influence on any responses scored in the tests used here.

Table 1. Summary of the results.

| Factors influencing approach and exploration | Hand Preference | Age | Gender |
|--|-----------------|-----|--------|
| Alone in a novel setting | + | - | - |
| Novel objects in familiar setting | + | + | - |
| Novel problem solving | - | + | - |

Although the association between hand preference and exploration is modified by age and social position, it is interesting to speculate on whether differences in migration and territoriality may, at least in some species, depend on the distribution of hand preferences within the population, or on the presence or absence of handedness within the population. For example, a species (or a population) comprised of a majority of right-handed individuals may be more mobile and exploratory than one comprised of a majority of left-handed individuals, or one without handedness. In fact, tamarins (*Saguinus oedipus*) have a population bias of right handedness (King, 1995) and they are known to move daily over distances two times greater than those moved by marmosets (Tardif, Harrison & Simek, 1993), which have no population bias for handedness. There may, of course, be other explanations for this species difference but the presence or absence of handedness is now worth considering. It might be noted that lemurs are nocturnal and 'shy' and they are also left-handed at the population level (Ward, Milliken, Dodson, Stafford & Wallace, 1990). However, against this hypothesised association, Watson and Ward (1996) have found that left-handed bushbabies are more active in a novel environment. Further

research is needed to test whether any associations between handedness and species-typical behaviour are more than just coincidence. Even if this is the case, it does not imply that either handedness or exploration levels must be largely genetically determined, since early experience might affect the development of both characteristics.

Although there may be species or population differences in the association of handedness and exploration, any population will be made up of individuals with a range of levels of interactive exploration. Age, social position, hand-preference, gender and early experience may all affect the level of exploration that characterises each individual, depending on the context. The role of hand-preference is a newcomer to the list of factors that are associated with exploration and whether an individual is 'bold' or 'shy'. It is a factor that might now be considered in other species and may have application to the reintroduction of rare, related species to the wild. Depending on the environment to which captive-bred individuals are to be introduced, it might be advantageous to release left- or right-hand preferring individuals. Right-handed subjects might fare better than left-handed ones in environments that are constantly varying, and left-handed subjects might survive better than right-handed ones in environments that are more stable and where fixed territories can be held.

Psychologists have referred to a continuum from shyness to boldness in human behaviour, and some researchers of animal behaviour have done the same (Wilson, Clark, Coleman & Dearstyne, 1994). In fact, the data from humans suggests that extremely shy and extremely bold individuals are more stable (or inflexible) in their respective characteristics than individuals in the middle of the continuum. The latter are said to exhibit shyness or boldness depending on the context. It is not known whether hand preferences are in any way related to the extremes of shyness and boldness in humans, but the data discussed here for marmosets suggests that it would be interesting to test for an influence of hand preference on shyness versus boldness in humans. In fact, Watson and Ward (1996) have suggested that hand preference is related to shyness and boldness in prosimians and the same terms might also be used to describe the differences that Hopkins and Bennett (1994) found between left- and right-handed chimpanzees. Whether there is a continuum from shyness to boldness or, instead, two discrete categories exist might vary from species to species. Also, any tendency for one factor (e.g. hand preference) to polarise individuals into either of these two categories may be modified by another factor (e.g. age) that obscures this trend, depending on the context in which testing occurs.

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