

Hand and paw preferences in relation to the lateralized brain

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Hand preferences of primates are discussed as part of the broad perspective of brain lateralization in animals, and compared with paw preferences in non-primates. Previously, it has been suggested that primates are more likely to express a species-typical hand preference on complex tasks, especially in the case of coordinated hand use in using tools. I suggest that population-level hand preferences are manifested when the task demands the obligate use of the processing specialization of one hemisphere, and that this depends on the nature of the task rather than its complexity *per se*. Depending on the species, simple reaching tasks may not demand the obligate use of a specialized hemisphere and so do not constrain limb/hand use. In such cases, individuals may show hand preferences that are associated with consistent differences in behaviour. The individual's hand preference is associated with the expression of behaviour controlled by the hemisphere contralateral to the preferred hand (fear and reactivity in left-handed individuals versus proactivity in right-handed individuals). Recent findings of differences in brain structure between left- and right-handed primates (e.g. somatosensory cortex in marmosets) have been discussed and related to potential evolutionary advances.

Keywords: hand preference; hemispheric specialization; coping style; cortisol; cortical structure; common marmoset

1. INTRODUCTION

A few years ago, I engaged in a somewhat acerbic debate with Crow on the existence of lateralization in non-human animals (Crow 2004; Rogers 2004; see comments by Corballis 2007). Crow firmly adhered to the earlier, widely held notion that directional asymmetry is unique to modern *Homo sapiens* and saw it, in association with right-handedness, as the pivotal event in hominid evolution that determined the emergence of language. I, on the other hand, pointed out the now extensive literature on lateralization in a wide range of vertebrate species and argued that there was no such discontinuity in the evolution of lateralization that coincided with the appearance of human language and so placed humans apart from other species on this particular characteristic. As far as I know, we still hold these differences of opinion, although others, such as Corballis (2005, 2007, 2008), who once also defined humans as the lopsided ape (Corballis 1991) and unique in terms of their asymmetrical brains, have now embraced the evidence for lateralization in other vertebrate species and reached the conclusion that it is very unlikely that Crow is correct.

Handedness has been important in this continuity/discontinuity debate, largely because right-handedness in humans is associated with the left hemisphere's specialization for language and speech production. Not surprisingly, the first attempts to see whether animals other than humans might be lateralized focused on

measuring hand preferences in primates. The first conclusion drawn from these investigations was that non-human primates lacked any species-typical, directional bias for using a preferred hand, although individuals of some species often had hand preferences, left and right in approximately equal numbers, which were seen to be the result of learning through practice (see Warren 1977, 1980). Furthermore, it was concluded that non-human primates preferred to use different hands for different tasks. Later, MacNeilage *et al.* (1987) re-examined the research on hand preferences in primates and concluded that there was evidence of preferences at the species level and, moreover, that this bias was for use of the right hand and arm to support the body while employing the left hand for snatching at and grasping insects, as seen in the early primates, prosimians (Ward *et al.* 1993). This specialization of the left hand to grab moving targets has been retained in higher primates, including humans (MacNeilage *et al.* 1987). As adoption of an upright body posture freed the right hand from its role of supporting the body, the right hand was used to perform fine manipulation of objects and, as evolution proceeded, this hand was adopted for tool using. Recent studies of hand preferences in chimpanzees have supported this hypothesis; chimpanzees show consistent and significant right-hand preferences in tool using (captive chimpanzees: Hopkins *et al.* 2004; wild chimpanzees: Lonsdorf & Hopkins 2005) and in throwing (Hopkins *et al.* 2005).

The theory of MacNeilage and colleagues has become known as the Postural Origins Theory, meaning that postural changes were instrumental in the origin

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of the hemispheric asymmetries present in humans (MacNeilage 1998, 2007). Hence, the emphasis is on motor functions, rather than sensory functions.

Meanwhile, during the 1970s and 1980s, evidence of lateralization in non-primate species was coming to light, and in these cases, it had nothing to do with manifested hand or limb preferences but rather with hemispheric differences in sensory processing and/or motor control. Nottebohm (1971) showed that, in the male chaffinch, the motor control of song production is lateralized to the left syringeal nerve and, as he showed later, in the canary, it is lateralized to the vocal centre in the left hemisphere (Nottebohm *et al.* 1976). By injecting cycloheximide into the left or right hemisphere of the domestic chick, I showed that the left and right hemispheres control different patterns of behaviour (Rogers & Anson 1979). Using ablation of one or other hemisphere, Denenberg (1981) demonstrated differential functioning of the left and right hemispheres of the rat. Since the time of these initial discoveries of lateralization in non-human species, a growing number of examples have accumulated (summarized by Rogers 2002a; Rogers & Andrew 2002; Vallortigara & Rogers 2005).

The finding of hemispheric specialization in the rat was important for the main point that I am discussing here, because it was not associated with the paw preferences of the rats. Although the rats that Denenberg tested exhibited individual paw preferences to use either the left or right paw to reach into a tube to obtain food, there was no population bias for a preferred paw, whereas the lateralization of hemispheric function was present at a population level, as confirmed many times subsequently (Cowell *et al.* 1997; summarized by Bradshaw & Rogers (1993)). In other words, a brain can be lateralized without that lateralization being manifested as a paw or hand preference.

This lack of concordance between hand preference and hemispheric lateralization might have alerted those seeking to find evidence of lateralization in primates by measuring hand preferences, but it did not, probably because the hands of primates are considered to be special and of no comparison with hand/paw use by non-primates. Although I recognize the complexity of some primate hands and their ability to perform fine manipulations, I am not sure whether an absolute distinction between primate hands and non-primate paws is correct. The complexity of hand use, and hand structure, along with the presence or absence of claws, varies enormously across primate species and the whole-hand snatch-grab use of the hands by prosimians may not be qualitatively very different from the rat's use of its paws to grasp small objects (Whishaw & Gorny 1994; Whishaw *et al.* 1998a,b) or the cockatoo's use of its foot to hold food objects and manipulate them by coordinated use of the foot and beak (Rogers 2007). Internal control of the hand, which enables processing of food, evolved only in some primates. Hence, I am suggesting that hand/paw preferences in non-primate species might be compared with those of primate species to gain a broader picture of the relationship, or lack thereof, of hand preference with hemispheric specialization.

Directional bias to use a preferred paw has now been found in some species: toads use the right paw preferentially to wipe objects from their head and to push against a substrate in order to right their body posture (Bisazza *et al.* 1996), and parrots show preferred use of a foot, the left foot in most species, to hold food (Rogers 1980; Harris 1989). In fact, it has now been found that some strains of laboratory rats express directional biases to use a preferred paw (Tang & Verstynen 2002; Güven *et al.* 2003).

These examples demonstrate that species-typical hand/paw preferences are present in some primates and non-primates. Even right-hand preference is not exclusive to humans and did not evolve solely in the hominid line in association with language, as postulated by McManus (1999), Annett (2002) and Crow (2002). This does not mean that the right-handedness of humans is unrelated to specialization of the left hemisphere for language, but rather that we cannot consider language as the sole reason for adopting preferred use of a particular hand or limb, or vice versa. In other words, there was no single genetic mutation, no 'speciation event' as Crow (2002) hypothesized, that caused hemispheric asymmetry and handedness, and in so doing, brought about the evolution of *H. sapiens*.

The question to be addressed now is what does determine the preferred use of a hand/paw in different species and to what extent is it related to other aspects of brain lateralization?

2. SENSORY AND MOTOR LATERALIZATION

(a) *Sensory lateralization before hand/paw preferences*

To address the above question, I will consider that specialization of the left and right sides of the brain to perform different functions and process sensory information differently evolved before preferred use of limbs. There is evidence to support this. First, animals without limbs are lateralized (e.g. teleost fishes: Bisazza *et al.* 2000): fishes show eye preferences to view certain scenes (Bisazza *et al.* 1997) and conspecifics (Bisazza *et al.* 1998; Sovrano *et al.* 1999; Sovrano & Andrew 2006) and they have a preference to capture prey to their right side (Miklosi & Andrew 1999; Takeuchi & Hori 2008). Tadpoles also prefer to view conspecifics with a preferred (left) eye (Bisazza *et al.* 2002) and show lateralized escape responses (Rogers 2002b) that could depend on both perceptual and motor side biases. Andrew (2002) has developed a plausible hypothesis that lateralization had its origins in the earliest vertebrates, now represented by the *Amphioxus* larva, which had the mouth positioned on the side of the head and, as a consequence, feeding was under the control of the left side of the anterior central nervous system. This, Andrew argues, may have led to lateralized sensory processing first associated with feeding and then extending to other sensory processing and, presumably, motor control.

Recently, however, evidence of lateralization in invertebrates has become apparent. Spiders display lateralized attack behaviour (Ades & Ramires 2002); fruitflies with an asymmetrical structure in the central

nervous system have superior ability to form long-term memory compared with fruitflies lacking this structure (Pascual *et al.* 2004) and bees use the right antenna to learn associations between an odour and a food reward (Letzkus *et al.* 2006), and the left antenna to recall the long-term memory of this association (Rogers & Vallortigara 2008). All of these are examples of directional bias at the species or population level and all involve sensory processing. Considered against the earlier belief, discussed above, that lateralization was a unique feature of the human brain, these examples of lateralization in the invertebrate brain are quite revolutionary: even relatively simple nervous systems are functionally differentiated on the left and right sides. However, this does not mean that lateralization of the invertebrate nervous system is homologous to lateralization of the vertebrate brain.

Returning to the question of limb and hand preferences, it seems definite that these motor biases did not evolve prior to brain lateralization for sensory processing, as MacNeilage *et al.* (1987) implied, although did not discuss in detail. Instead, I suggest, limb/hand preference is determined by which hemisphere's sensory processing specializations are being used to perform a particular task.

Both primates and non-primates might display population biases to use a preferred limb or paw/hand if a task demands the obligate use of a particular hemisphere. For example, since the right hemisphere is used to process geometrical and global spatial cues, known to be the case in a wide range of species (e.g. humans: Wendt & Risberg 1994; rats: Cowell *et al.* 1997; chicks: Tommasi & Vallortigara 2004), use of the left hand to snatch and grab a moving object might be expected. This might well explain the species-typical left-hand preferences displayed by primates that feed on insects using snatch and grab (i.e. ballistic) tactics, as in the case of prosimians (Forsythe & Ward 1988; Ward *et al.* 1990), as well as the superior ability of the left hand for ballistic aimed movement in humans (Guiard *et al.* 1983). The latter is also in keeping with the superior ability of the human right hemisphere for trajectory perception (Boulinguez *et al.* 2003). Use of the right hemisphere for spatial processing might also explain the use of the left paw by cats to reach for and attempt to grasp small moving targets (Fabre-Thorpe *et al.* 1993) and the directional bias of the left-hand preference found in squirrel monkeys when they capture live fish, also using a ballistic movement (King & Landau 1993).

Fagot & Vauclair (1991) proposed that population biases to use a preferred hand are more common when the task is complex in terms of postural, perceptual and cognitive demands, and some evidence supports this (e.g. Blois-Heulin *et al.* 2007). However, we must keep in mind the kind of tasks any particular species may find difficult rather than the assumed difficulty of the task itself, as perceived by the human experimenter. This might explain why some non-mammalian species show limb preferences at a population/species level to perform apparently simple tasks, such as the right-paw preference of toads and the left-footedness of many species of parrots. Postural constraints when performing apparently simple tasks could well be important in

lower vertebrates. Malashichev (2006) has argued that amphibians may show species-typical limb preferences depending on whether they move by jumping or crawling. These differences in locomotion are matched by differences in body structure that make it more or less difficult to balance on three or four limbs (Rogers 2007). A toad with its rigid body structure might, therefore, find the task of raising one limb to wipe an object from its head quite a balancing feat. This, I suggest, may demand the use of the right hemisphere to stabilize the body using coordinated visual, possibly spatial, and motor processing, and so lead to preferred use of the left limb and paw to support the body while the right paw is used to remove the offending object from the head or snout. For this species, even this task, apparently simple, requires the obligate use of a limb/paw.

It is difficult to give a possible reason for the opposite limb preference in the case of parrots (i.e. left-foot preference to hold food), but since balancing is a very different problem in a bird, other lateralized processes unrelated to postural constraints may be paramount (e.g. visual stabilization of the retinal image while balancing).

Now we should consider tasks that are less demanding. These may not demand the obligate use of a particular hemisphere and so leave the limb/hand use unconstrained. One such task, often used to test primates, is the use of the hand to pick up static pieces of food from the floor or a bowl and to hold the piece of food while eating it. In fact, the same squirrel monkeys that display a left-hand preference for capturing fish show no population bias for a preferred hand to pick up static pieces of food (King & Landau 1993). Non-primate species may also show non-obligate limb use depending on task difficulty: for example, paw use by dogs to steady a bone or a Kong, (a rubber cone-shaped container with food inside) against the ground is present for individuals but not as a population bias (Branson & Rogers 2006).

(b) *Stability of hand preferences for simple reaching across the lifespan*

Although non-obligate limb use might, in theory, vary from one time to another in the same individual, even within the performance of one task, evidence suggests that it does not. Individuals often exhibit a consistent hand preference. Measured on the simple reaching task to pick up pieces of food, common marmosets, *Callithrix jacchus*, establish a preferred hand by the time they are 8–12 months old and each individual uses the same preferred hand across its lifetime (Hook & Rogers 2000). Data for simple reaching by marmosets in our colony at the University of New England are presented in figure 1. This is the most extensive longitudinal study of hand preferences in a primate species: we have measured the hand preference of the same individuals (based on 100 scores per measure) at different times throughout their entire lifespan, some animals reaching the age of 13 years.

The results show that the individual's hand preference remains constant throughout its life. Minor injury can cause a temporary weakening or a reversal of the hand preference, as we have seen in a few cases, but

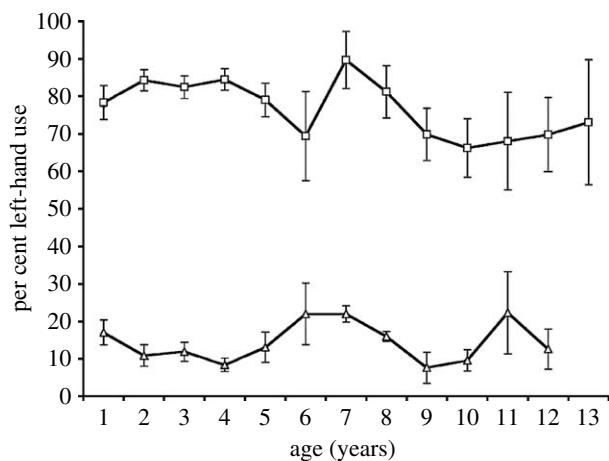


Figure 1. Mean per cent preferences for the preferred hand with standard errors are plotted against age in years for left- and right-handed common marmosets separately. These marmosets comprise my colony at the University of New England. A total of 21 left-handed and 17 right-handed were scored for hand preference to pick up pieces of food and take it to the mouth. For each point on the graph, a total of 100 scores were obtained per individual. As no more than 10 scores per marmoset were collected per day, the data for each point was collected over at least 10 days for each individual. A score for each of the 39 marmosets was obtained once per year for the first 4 years of life. From 4 years of age onwards, standard errors are larger because fewer individuals were tested in each year (scores were obtained for 7–12 individuals in any given year) since some members of the colony are currently not older than 4 years, others had missing scores for some years and some had died before the others (two had died before reaching 7 years and eight by 11 years of age). Note that above 7 years is considered to be old for common marmosets (Geula *et al.* 2002) and the reported lifespan is 10–15 years (Clarke 1994). Most of the marmosets in our colony have survived past this age. A number of different experimenters collected these results and each was blind to the previously scored hand preferences of the marmosets. The variation in years 6 and 7 was not significant, but there is no obvious explanation for these slight discrepancies, apart from possible scorer reliability or temporary injury of a hand in one or more subjects. The testing situation was always the same: the scores were always collected between 12.00 and 13.00 hours during the daily feeding time.

the original preference returns after recovery. No directional bias is present in the group (in our colony 21 prefer the left hand, 17 the right hand and only 2 have shown no consistent hand preference). The studies of colonies of common marmosets by Matoba *et al.* (1991) and de Sousa *et al.* (2001) show a similar absence of group bias in the marmosets when reaching for food, although slightly more marmosets appear to prefer the left than the number preferring the right hand, as seen in our colony and noted first by Box (1977).

Some of the marmosets ($n=21$) in our colony were tested on a range of tasks requiring them to reach for food, including reaching into a bowl through a small hole, taking food from a rotating disc, reaching while suspended on the cage wire to take the food presented on a plate held outside the cage and reaching for a piece of food suspended on a string (Hook & Rogers 2008). On all of the tasks, apart from reaching into the bowl through a hole in the lid ('bowl test'), individual

marmosets exhibited the same hand preference across tasks. Although the strength of hand preference varied somewhat according to the task (close to 100% when reaching for the food suspended on the string), the direction of an individual's hand preference remained constant. The bowl test was an exception: half of the marmosets (9 out of 17) changed over to use the opposite hand on the bowl task, and some of the subjects shifted from the left to right and others from the right to left. No obvious explanation for this shift is apparent since this was not the only task requiring visuospatial reaching, but it could depend on the body posture adopted during this task, one hand being placed on the edge of the bowl to support the body while the other was used to reach for the food (see fig. 1 of Hook & Rogers 2008). For the majority of tasks, however, each marmoset expressed the same hand preference. Hence, each individual has a consistent hand preference across age and a number of tasks, contrary to the original claims that Warren (1977, 1980) made about hand preferences in primates.

If we had used any one of these reaching tasks as a measure to determine whether the common marmoset has a lateralization of the brain, we would have concluded that this species has a non-lateralized brain. This would be incorrect, however, since the same group of common marmosets has been shown to display a strong group bias to use the left eye to view pieces of food through a peephole: all but one of the 21 marmosets tested had a significant left-eye preference (Hook-Costigan & Rogers 1998). It seems, therefore, that the common marmoset is no exception to the pattern of hemispheric specialization shown in other vertebrate species and that the hand used for simple reaching is non-obligate, not determined by the functional differences between the hemispheres.

We may now ask what determines an individual's preference to use the same hand consistently throughout its adult life. It could be argued that a random choice is made initially and that the individual retains this preference through practice. However, as elaborated below, left- and right-handed individuals differ in a number of more general characteristics outside hand use *per se* and it might be differential activation of the hemispheres associated with these aspects of behaviour that leads to the preferred use of one hand. Of course, one cannot exclude causal connection in the opposite direction (from hand preference to the expression of general differences in behaviour) but, in my opinion, this is unlikely, given that sensory lateralization preceded the evolution of limb preferences, and I am considering non-obligate hand use here. Nevertheless, at present, we are merely engaged in documenting the differences in behaviour and physiology between left- and right-handed individuals.

3. HAND PREFERENCE ASSOCIATED WITH GENERAL BEHAVIOUR

(a) *Response to novelty related to hand preference*

The first assessment of differences in general patterns of behaviour between left- and right-handed individuals was conducted on chimpanzees by Hopkins & Bennett (1994). This study found greater interaction

with toy objects by right- than left-handed chimpanzees. Following on from this, Cameron & Rogers (1999) tested the responses of left- and right-handed common marmosets when they were placed into a novel room containing a number of novel climbing structures and objects. They found that the right-handed marmosets came out of the carrying cage in which they had been transported to the room and began to explore the new environment sooner than did the left-handed marmosets. The right-handed marmosets also performed more parallax movements, which are used for depth perception, performed more leaps and touched more of the novel objects. All of these scores show that the right-handed marmosets explored the new environment by interacting with it directly.

The left- and right-handed marmosets performed the same amount of head-cocking movements, which are used in visual exploration (Rogers *et al.* 1993; Kaplan & Rogers 2006), which suggests that the left-handed marmosets were as interested in exploring the new environment as were the right-handed marmosets, but they preferred to do so visually at some distance rather than actively engage with the novel objects and structures. Their response can be described as reactive, compared with the proactive response of the right-handed marmosets. The difference in behaviour between these two groups may depend on emotional state, *viz.* the level of fear.

Braccini & Caine (2006, *in press*) have found similar differences in reactivity and proactivity between left- and right-handed Geoffroy's marmosets (*Callithrix geoffroyi*). They found that left-handed marmosets were slower than right-handed marmosets to approach and sniff novel foods and that they froze for longer after hearing the vocalizations of hawks, the latter being predators of marmosets in their natural habitat. Again, the left-handed animals were more fearful.

Recently, we (Gordon & Rogers *in preparation*) have extended the comparison of left- and right-handed common marmosets (10 left compared with 10 right and matched for sex and age) by testing them with stimuli that elicited mobbing behaviour. We found that the right-handed marmosets approached the novel stimuli twice as often as did left-handed marmosets. When they were presented with the stimulus that elicited the most powerful mobbing response, the right-handed marmosets emitted more 'tsik' (mobbing) calls than the left-handed marmosets. In another task, the marmosets, tested with their social companions, were presented with crickets, a relatively unfamiliar food to the marmosets of our colony. The right-handed marmosets captured their first cricket after a shorter latency than the left-handed marmosets. They also made more tsik calls when they were observing and capturing the crickets.

All of these results indicate less fear and more proactive interaction in the right-handed marmosets compared with the left-handed marmosets, and this matches the known differences between the hemispheres. A large number of studies show that the activity of the right hemisphere is associated with the expression of intense emotions, especially negative emotions, including fear, and with withdrawal (summarized by Rogers & Andrew 2002). Hence, the

left-handed marmosets, with the activation of right hemispheric functions, perform as expected. The converse association between preferred use of the right hand and approach to novel stimuli is also expected since the activation of the left hemisphere suppresses fear and, as proposed by Davidson (1995), enhances approach behaviour.

(b) *Hand preference and temperament or 'personality'*

Although it is a topic under debate, there is a notable amount of evidence that populations comprise individual animals with consistent differences in temperament or coping style (Dall *et al.* 2004; Bell 2007; Wolf *et al.* 2007), and that these differences fit with the general categorization as proactive versus reactive (Koolhaas *et al.* 1997, 1999). The individual may retain its coping style throughout its life, although, of course, the expression of the particular behavioural characteristic varies according to the context. In addition to reactivity, such consistencies in individuals have been reported for aggression (Reichert & Hedrick 1993), activity (Sih *et al.* 2004), exploration behaviour (Dingemanse *et al.* 2002), fearfulness (Boissy 1995) and risk taking (Fraser *et al.* 2001). In fact, there is some evidence that some or many of these types of behaviour are associated or clustered so that individuals have consistent personality types or coping styles (e.g. Øverli *et al.* 2004). Such differences may have implications for adaptation to change and, in fact, some researchers have argued that maintaining both types within the population may facilitate adaptive change and speciation (Wilson 1998).

Consistent differences in behavioural style or type, it seems, may depend on the predominance of the left or right hemisphere in control of processing and behaviour. Hand preference for simple reaching may therefore be a reflection of consistent behavioural types, as we have seen in marmosets. More research comparing the left- and right-handed animals is required to test whether suites of behaviour are consistently associated with one or the other hand preference for simple reaching. Furthermore, it is now possible to make testable predictions about associations between hand preference and social behaviour, including aggressive behaviour, which has been shown to be primarily a function of the regions of the right hemisphere in humans and other species (summarized by Rogers 2002a). Here, it is interesting to note the research showing, in human populations, that the proportion of left-handed individuals correlates positively with homicide rate (Faurie & Raymond 2005), although there are many possible explanations for this association. In fact, Westergaard *et al.* (2003) have reported that left-handed, male rhesus macaques receive more aggressive interactions and lower levels of grooming from conspecifics and they are more likely to be submissive than right-handed males (summarized in Howell *et al.* 2007). However, the opposite is the case for females (Westergaard *et al.* 2004). Research on more species and in more contexts is needed in order to clarify the reasons for these interesting associations between hand preference and social aggression.

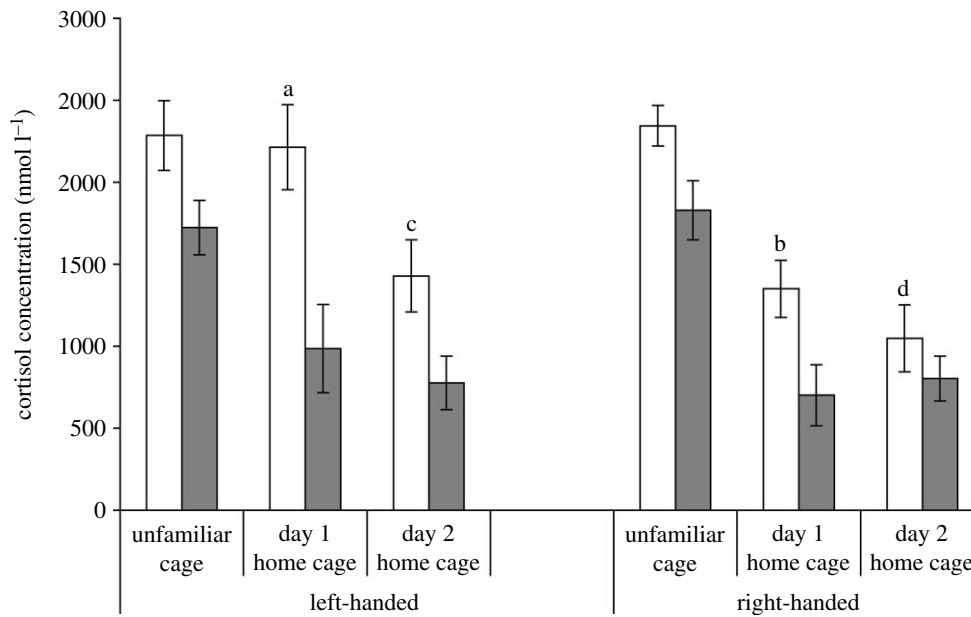


Figure 2. Cortisol concentrations in samples of saliva collected at 09.30 hours (white bars) and 16.30 hours (grey bars) from nine left-handed and eight right-handed common marmosets for the third day after being housed in an unfamiliar cage and for the first 2 days following return to the home cage. Note the diurnal cycle on all days, especially on the days in the home cage: cortisol levels are typically higher in the morning than in the afternoon (Cross & Rogers 2004). Also, note the decline in cortisol levels once the marmosets had been returned to their home cage, but morning cortisol levels of the left-handed compared with the right-handed marmosets are higher on both days in the home cage (the bars marked with a and b differ significantly, two-tailed t -test, $t=2.76$, $p=0.015$, and so do the bars marked c and d, $p=0.04$). Values are presented as means and standard errors.

Populations or species comprising roughly equal numbers of left- and right-handed individuals can be considered to be poised for adaptation in response to environmental change (favouring one or the other type through individual selection and depending on which type has the advantage). Does this mean that populations with a directional bias for the use of a preferred hand also have a directional bias for a particular coping style and that those with a left-hand bias are less likely to exploit new resources than those with a right-hand bias? This should be possible to test in natural populations.

4. HAND PREFERENCE ASSOCIATED WITH PHYSIOLOGY AND NEUROANATOMY

(a) *Stress hormone levels associated with hand preference*

If left-hand preference is associated with greater fear than is right-hand preference, stress hormone (glucocorticoid) levels should be higher in left-handed animals either chronically or at least in some situations. In fact, as shown in humans, activity of the right hemisphere is associated with higher levels of cortisol secretion (Wittling & Pflüger 1990; see also Sullivan & Gratton 2002) and greater sympathetic nervous system activity (Wittling 1995, 1997). Also, activity of the right hemisphere is related to both cortisol and fear levels in rhesus macaques (Kalin *et al.* 1998). Two studies show that this right hemispheric control of the stress response may well be associated with hand preference: Westergaard *et al.* (2001, 2003) reported an association between hand preference and plasma cortisol levels in rhesus macaques, and Nevue & Moya (1997) found that left-pawed mice have higher corticosterone levels than right-pawed mice.

Here, I report that salivary cortisol levels tend to be higher in left-handed common marmosets compared with right-handed marmosets in certain circumstances. As part of a study concerned with welfare and housing of primates (Pines *et al.* 2007), salivary samples were collected from the marmosets in the University of New England colony and assayed for cortisol using a technique that we have developed (Cross *et al.* 2004).

Twice a day, at 09.30 hours and 16.30 hours, saliva samples were collected by an experimenter blind to the hand preferences of the marmosets. These two times were selected because marmosets show the typical cycle of cortisol secretion seen in diurnal animals, cortisol levels being the highest in the morning and decreasing throughout the day (Cross & Rogers 2004). Each marmoset was moved with its cage mate from its home cage to temporary housing into an unfamiliar cage of approximately the same size as the home cage, but with different climbing structures and unfamiliar odours (Pines 2005), where it remained for 3 days before being returned to its home cage after 17.00 hours on that third day. The results of the saliva samples collected on the third day in the novel cage and for the next 2 days back in the home cage are reported here, since they showed significant differences between left- and right-handed marmosets (figure 2).

The typical diurnal pattern of cortisol levels was present on all days sampled. Cortisol levels at both times of the day sampled were higher when the marmosets were in the unfamiliar cages than when they were in the home cage. The levels of left-handed marmosets did not differ from those of right-handed marmosets when the marmosets were in the unfamiliar cage but a difference between the left- and right-handed groups occurred after the marmosets were returned to their home cages. On day 1 in the home

cage, the morning cortisol levels of the left-handed marmosets were significantly higher than those of the right-handed marmosets (U -test, $0.01 < p < 0.025$, one-tailed since the direction of the difference had been predicted). On this day, the morning cortisol levels of the left-handed group had remained elevated, whereas they had declined in the right-handed group. The decline in cortisol levels in the left-handed group was delayed until day 2 in the home cage, but on this day too the levels were significantly higher than those of the right-handed marmosets ($p = 0.04$). Therefore, the stressful effects of being in the unfamiliar cage lasted for longer in the left- compared with the right-handed marmosets.

Therefore, there is some evidence that hand preference is associated with differing cortisol levels in a manner consistent with the behavioural differences between left- and right-handed individuals. Left-handed, reactive animals have higher cortisol secretions in certain contexts than do right-handed, proactive animals. In common marmosets, we have other evidence that proactive behaviour lowers cortisol levels: the act of mobbing lowers cortisol levels (Cross & Rogers 2006), and marmosets that consistently perform mobbing more than others have lower cortisol levels (Clara *et al.* 2007). Hence, it would seem to be a fruitful line of investigation to explore these associations between stress physiology, behaviour and hand preference more fully. Furthermore, it would be interesting to investigate the effects of experience in early life on the stress response, proactive/reactive behaviour and hand preference, since early separation from littermates (mostly studied in rats) is known to have a long-lasting influence on the stress hormone response (e.g. Rees *et al.* 2006, 2008) and on other behaviour (e.g. Lovic *et al.* 2001).

(b) Brain structure and hand preference

Movement of a limb and hand is largely controlled by the motor cortex of the contralateral hemisphere. Entirely consistent with this, predominant use of one hand is matched by enlargement of the cortical representation of that hand in the contralateral motor cortex (Nudo *et al.* 1992). Also concerning the motor cortex, Hopkins & Cantalupo (2004) found, in chimpanzees, a correlation between structural asymmetry of the precentral gyrus and hand preference on a task requiring coordination of both hands, and Dadda *et al.* (2006) showed that this asymmetry is restricted to the area of the motor cortex controlling the hands. A similar relationship between asymmetry of the precentral gyrus and hand preference in capuchins has also been reported (Phillips & Sherwood 2005).

The question of interest now is whether the use of a preferred hand is associated with structural enlargements or increased connectivity in other cortical regions of the contralateral hemisphere, such as the sensorimotor cortex, the regions used for integrating somatosensory and visual information relating to eye-hand coordination and even the prefrontal cortex.

Some evidence indicates that hand preference is associated with asymmetries in the regions of the cortex outside the motor cortex. For example, Hopkins *et al.* (2007) found that asymmetry of the fronto-orbital

sulcus and planum temporale region of the cortex of the chimpanzee correlates with hand preference for tool using. Moreover, the cerebral torque, characterized by broader right frontal and left occipital lobes, is present in the great apes (Pilcher *et al.* 2001).

Recent collaborative research with my colleagues, P. Waite and C. Gorrie, at the University of New South Wales, has revealed, in the common marmoset, that length of the right lateral sulcus, adjusted for brain weight, correlates positively and strongly with per cent right-hand preference ($n = 11$, $r = 0.86$, $p = 0.001$; Gorrie *et al.* 2008). Thickness of a region of the cortex next to the lateral sulcus, most likely the SII cortex, as far as can be determined from the current brain maps, also correlates positively and strongly with per cent right-hand preference. The latter relationship was found to be significant for the right cortex and there was a close to significant ($p = 0.052$) trend for the left cortex. In other words, marmosets with right-hand preferences have thicker SII cortices than left-handed marmosets. Since this region of the cortex is involved in integrating light-touch, somatosensory responses from several digits and the palm of the hand (Krubitzer & Kaas 1990; Kaas 2004) and it is known to have a role in discriminating textures (Murray & Mishkin 1984; Pruett *et al.* 2000), we have hypothesized that right-handed marmosets might be better than left-handed marmosets in discriminating textures using tactile cues. The SII region of the cortex also has neurons that receive inputs from the frontal visual fields (Krubitzer & Kaas 1990; Kaas 2004), which means SII has a role in visually guided reaching behaviour. The latter might also be superior in right-handed marmosets. These predictions based on the neuroanatomical findings can now be tested empirically. It is plausible that the earlier finding (Cameron & Rogers 1999), that right-handed marmosets touch more novel objects than left-handed marmosets, might depend on superior tactile discrimination ability by right-handed marmosets.

In the same study (Gorrie *et al.* 2008), we found no association between hand preference and the thickness of the ventral somatosensory area, the auditory cortex, the cortical region that may be Brodmann's area 1 or, surprisingly, the region of the motor cortex that is likely to be concerned with the hands. The association between per cent right-hand preference and thickness of the somatosensory cortex is, therefore, quite specific, although one cannot rule out the possibility that other regions of the cortex not yet measured have size differences associated with hand preference.

For certain, anatomical asymmetries outside the motor cortex are associated with hand preference in species other than humans. It is tempting to suggest that the enlarged somatosensory cortex associated with right-hand preference might have been an evolutionary precursor to tool using. Common marmosets have not been reported to use tools but they should be able to learn to do so in a laboratory setting, as shown possible for a rodent in a recent study (Okanoya *et al.* 2008). Based on right-handed marmosets having a larger SII somatosensory cortex than left-handed marmosets (Gorrie *et al.* 2008), one can predict that right-handed marmosets might acquire tool using behaviour more readily than left-handed marmosets.

5. IMPLICATIONS FOR BEHAVIOUR IN THE NATURAL ENVIRONMENT

The association between hand preference for simple reaching and temperament or coping style has been discussed, and the explanation for this association seems to be the predominant use of the left or right hemisphere by individuals. In other words, specialization of the left and right hemispheres (or sides of the brain) to process information in different ways and to control different patterns of behaviour may be the underlying mechanism of expressed behavioural type and hand preference. It seems that each individual has a tendency to use either its left or right hemisphere predominantly and so expresses a consistent coping style or temperament and consistent preference to use the same hand in simple reaching.

In some populations, or some species, there may be approximately equal numbers of left-handed, reactive individuals and right-handed, proactive individuals: that is, there is no population asymmetry, although each individual is asymmetrical. At another level, one or the other of these types may be in a majority and hence the population would be asymmetrical.

Presumably, as in the case of the common marmoset, having roughly equal numbers of each behavioural type, and its associated hand preference, would allow adaptive changes, both genetic and epigenetic, should the environment change, as others have argued (Dall *et al.* 2004), but what would it mean if a species shows a strong population bias to use a preferred hand? First, we would need to check that the directional bias has not been imposed by the task used to measure it: as argued above, certain tasks will necessarily demand the use of a particular hemisphere specialized for the processing required. Second, postural constraints may be important. Only simple reaching free from constraints to use the specializations of a hemisphere for processing, in primates at least, reflects behavioural type or coping style. If a strong directional bias to use a preferred hand still exists in the population once task constraints have been eliminated, we would have to conclude that most individuals in the population, or species, express a particular coping style or temperament. There is no reason why the individuals that comprise a species could not adapt to environments in this way. Populations and species may differ in relative dependence on the functions of the left or right hemisphere (as suggested by Vallortigara *et al.* 2008) and, in some species, this will be reflected in the relative numbers of left- and right-hand preferring individuals. I recognize the difficulties in making such behavioural comparisons across species, but it may not be impossible to assess and compare species along these lines and reliable comparisons of cortisol response could be made.

It has been recognized previously that populations and species may vary in behavioural type (e.g. referred to as behavioural syndromes by Sih *et al.* (2004)), and that this may affect the distribution of species and adaptability to environmental change. I am suggesting that hand preference for simple reaching could be added as a measure of the behavioural 'syndrome'. Of course, the hand preferences would need to be measured in wild populations. The adaptive flexibility potentially reflected in populations with equal numbers

of left- and right-handed individuals, as found in our marmoset colony, is not always advantageous and, in the case of captive animals, may result from the absence of natural selection or habitat demands.

Directional biases for hand and hemisphere preferences might also depend on social demands. Vallortigara & Rogers (2005) have drawn attention to the possibility that directional biases may be beneficial in terms of predictability of social interactions and a number of studies have shown that animals react differently to conspecifics on their left or right side (baboons: Casperd & Dunbar 1996; anurans: Robins *et al.* 1998; fishes: Sovrano *et al.* 1999; birds: Vallortigara *et al.* 2001; Zucca & Sovrano 2008). Such biases, however, can be expressed quite independently of limb preferences, but any consistent demand for a particular social behaviour, and hence hemisphere, to be expressed may be reflected in a directional bias of preferred limb use. Consistent and frequent agonistic interactions may, for example, mean that the right hemisphere assumes control of behaviour and, along with it, left-hand preference and a reactive coping style may also be expressed.

In summary, hand/limb preferences at the individual level are associated with general aspects of behaviour, particularly coping style and its associated approach and withdrawal behaviour. Recognition that hand preference may be a reflection of the dominant hemisphere (the hemisphere contralateral to the preferred hand) has led to the hypothesis that populations or species in which there is a majority of either left- or right-handed individuals have adapted in favour of one or other of the coping styles, or some other aspect of behaviour expressed by one of the hemispheres.

The experimental procedures were approved by the Animal Ethics Committee of the University of New England in adherence with the Australian Code of Practice for the Care and use of Animals for Scientific Purposes (Australian Government, 7th edn, 2004).

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