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Research report

Cognitive bias, hand preference and welfare of common marmosets

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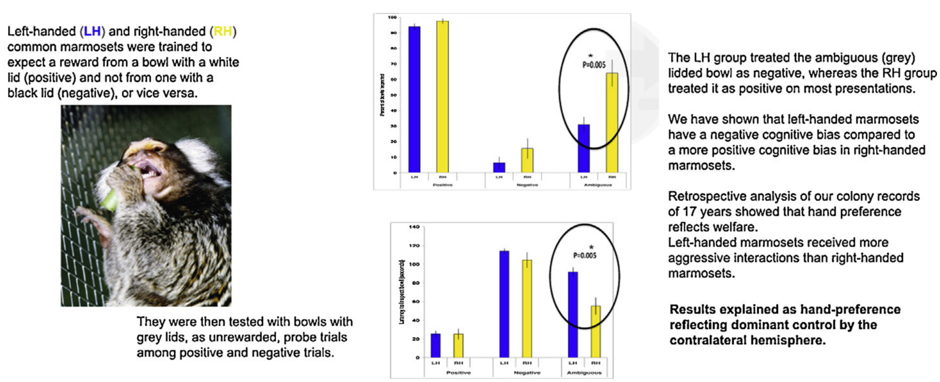
HIGHLIGHTS

- First evidence of an association between hand preference and cognitive bias.
- First evidence of hand preference being linked to long-term welfare.
- More aggression directed by colony members at left-handed than right-handed marmosets.

GRAPHICAL ABSTRACT



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ABSTRACT

Common marmosets (*Callithrix jacchus*) have hand preferences for grasping pieces of food and holding them while eating and these are stable throughout adult life. We report here that left-handed marmosets have negative cognitive bias compared to right-handed marmosets. Twelve marmosets were trained to expect a food reward from a bowl with a black lid and not from one with a white lid, or vice versa. In probe tests with ambiguous, grey-lidded bowls a left-handed group ($N = 7$) were less likely to remove the lid to inspect the bowl than a right-handed group ($N = 5$). This difference between left- and right-handed marmosets was not dependent on rate of learning, sex or age. In fact, hand-preference was not associated with rate of learning the task. Furthermore, retrospective examination of colony records of 39 marmosets revealed that more aggression was directed towards left- than right-handed marmosets. Hence, hand preference, which can be measured easily, could serve as an indicator of cognitive bias and may signal a need for particular care in laboratory environments. We explain the results by arguing that hand preference reflects more frequent (or dominant) use of the opposite hemisphere and this predisposes individuals to behave differently.

1. Introduction

Common marmosets (*Callithrix jacchus*) have hand preferences that, once established during the first 8 months of life [1], remain unchanged throughout their life span [2]. Each individual's hand preference is also consistent across a range of tasks involving picking up food from the floor (called simple reaching), a bowl, a moving disc or the end of a string, all tasks requiring roughly the same body posture [3]. Approximately, half of common marmosets are left-handed and the remainder are right-handed [2,4,5].

Previously we have shown a significant association between hand preference and both exploratory and social behaviour. Right-handed marmosets are more likely than left-handed marmosets

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to interact with and explore novel objects, as found when they were tested alone in an unfamiliar setting [6]. When tested with social companions, social facilitation of capturing unfamiliar live insects (crickets) was found to be more marked in right-handed than left-handed marmosets [7]. These results are largely consistent with the discovery by Braccini and Caine [8] that right-handed Geoffroy's marmosets are more likely than left-handed ones to approach and sniff novel foods. Also, right-handed marmosets mob a fear-inducing stimulus more than left-handed ones, as indicated by production of more tsik calls as well as more head-cocking and parallax movements [7]. Hence, in general, evidence indicates that right-handed primates are less fearful than are left-handed ones. There is some evidence of this in humans also [9].

Since each hand is controlled by its opposite hemisphere, we have explained these differences as manifestations of functioning of the hemisphere opposite the preferred hand [7]. Hand preference when the animal is relaxed may reflect a bias to use the hemisphere controlling that hand in a range of contexts.

As known for a number of vertebrate species, there is a consistent pattern of specialisation of behaviour expressed by each hemisphere (summarised in [10]). The right hemisphere is specialised to detect novel stimuli and respond to them by expressing fear and escape responses, whereas the left hemisphere controls categorisation of stimuli especially food items, approach behaviour and sustained pursuit of prey [10,11].

Strong emotions are expressed when the right hemisphere is active, especially so for negative emotions such as hostility and aggression [12–14] and social withdrawal [12]. This has been contrasted to expression of approach and positive emotions when the left hemisphere is more active [12]. Some evidence from study of animals supports the differential specialisation of the hemispheres for approach versus withdrawal: for example, dogs show a bias to wag their tail to the left side (controlled by the right hemisphere) when they see a stimulus eliciting withdrawal and to the right side (left hemisphere control) when they see a stimulus eliciting approach [15,16]. Based on these specialisations, we hypothesised that right-handed marmosets (left hemisphere biased) would be more likely to have a positive cognitive bias, compared to a negative cognitive bias in left-handed marmosets (right hemisphere biased).

The concept of cognitive bias was formulated originally to describe human behaviour [17]. Humans presented with an ambiguous stimulus that could be interpreted as either negative or positive are considered to have negative cognitive bias if they opt for the negative interpretation and to have positive cognitive bias if they opt for the positive interpretation. Similar tests are now applied to animals [18,19]. For example, if animals are trained to expect a white bowl to be associated with a reward and a black with either no reward or punishment, their responses to a grey bowl can be assessed. Other methods of testing cognitive bias are also available, such as presenting a bowl in a position half way between a previously learnt, rewarded location and a non-rewarded location.

Over recent years measurement of cognitive bias has emerged as a way of assessing animal welfare. Cognitive bias becomes more negative as a result of poor housing conditions or other stress-inducing paradigms. This cognitive state is regarded as "pessimistic", to borrow a term from the literature on humans and introduced into the research on animals by, for example, Bateson and Matheson [20]. European starlings, for example, housed in barren cages have negative cognitive bias compared to those in enriched conditions [20,21]. Also enrichment of housing enhances positive cognitive bias in rats [22], rhesus macaques [23] and sheep [24]. Indeed, negative cognitive bias is associated with expression of stress behaviour, including performance of stereotypies, as shown for head twirling in capuchins [25]. From the opposite perspective, as shown in lambs, pharmacological reduction of fear enhances positive cognitive bias [26].

Not only does cognitive bias change in response to housing conditions but also individuals may be predisposed to judge ambiguous stimuli as negative or positive and so be more or less prone to stress in captive or experimental conditions, as shown in rats [27]. We, therefore, decided to compare the cognitive biases of left- versus right-handed common marmosets since hand preference would be a simple measure that might predict ability, or inability, to cope with stress. In fact, any association between hand preference, hemispheric bias and cognitive bias would be enlightening in understanding the neural aspects of expression of emotions in animals [28].

We also examined retrospectively how left- and right-handed marmosets in our entire colony had fared in terms of aggression and injuries. We decided to do this because we hypothesised that negative cognitive bias might have been associated with negative (aggressive) treatment by other marmosets in the colony. Furthermore, right hemisphere use (left hand control) has been associated with stress responses and the expression of strong emotions [10,11].

2. Materials and methods

2.1. Subjects and housing

A total of 12 marmosets from the colony at the University of New England were tested (for details of care see [29,30]). All marmosets were housed in same-sex, family groups of two to four individuals and were in visual and auditory contact with other members of the colony. Home cages (mean cage space 3.85 m^3 per marmoset) were connected via runways to larger indoor rooms (4 m × 4 m × 3.5 m) and to outdoor cages (1.7 m × 1.7 m × 2.6 m). All of these enclosures were furnished liberally with branches, wooden perches, suspended pipes in which the marmosets could hide and ropes for climbing.

Temperature of the rooms containing the home cages and in the indoor rooms was maintained between 18 °C and 30 °C. In these rooms lights were turned on at 7.00 h and off at 19.00 h. Access to sunlight was available in the outdoor cages and via UV lights turned on in the home-cage rooms for 30 min per day. Food was replenished once daily between 12.00 h and 14.00 h. The diet was changed daily and included banana and polenta cake, meatloaf, dog pellets, various fruits and vegetables, yoghurt, cereal, peanuts, sultanas and vitamin supplements. Water was available ad libitum. Feeding was carried out by the same person who tested the marmosets (DJG). Training and testing was carried out blind to hand preference, which was determined only after completion of the experiment.

2.2. Training

Using a modified version of the test of cognitive bias used by Matheson et al., 2008 [21], each marmoset was trained by presenting a bowl with either a black or a white lid. The bowls and the lids were oval in shape, 12.2 cm × 8.5 cm. The bowls were 5 cm deep. By removing the lid from the positive bowl the marmoset could obtain a small piece of its favourite food, a mealworm in all cases except two. One of the remaining two marmosets was rewarded with a piece of blueberry and the other a piece of marshmallow (these preferences had been determined in an earlier experiment). No food was available in the negative bowl. Nine marmosets were trained with black positive/white negative and three were trained with the opposite. [Note that the number trained with white positive was fewer than with black positive because the