Behavioural Brain Research 248 (2013) 144–150

Contents lists available at SciVerse ScienceDirect

Behavioural Brain Research

journal homepage: www.elsevier.com/locate/bbr

Research report

Hand preference depends on posture in common marmosets

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HIGHLIGHTS

- We examined hand use in the common marmosets using three experimental conditions.
- Postures and size of apertures for reaching were manipulated in the conditions.
- No lateralization in hand use was observed in any conditions at the group level.
- Individual subjects changed their hand use depending on the conditions.
- Posture was more influential than size of apertures for reaching on their hand use.

ARTICLE INFO

Article history:
Received 25 January 2013
Received in revised form 28 March 2013
Accepted 2 April 2013
Available online 8 April 2013

Keywords:
Asymmetry
Bimanual response
Callithrix jacchus
Lateralization
Reaching

ABSTRACT

Postural conditions are known to affect hand use in many primate species. It remains to be examined how posture and task differences modulate, or interact with, hand use in common marmosets (*Callithrix jacchus*). Three experimental conditions were introduced to assess the occurrence of preferential hand use as a function of posture and size of aperture for the subjects to grasp and retrieve the food item bi- or unimanually: ground level condition for requiring quadrupedal posture with enough space for food reaching with both hands, large hole (4 cm in diameter) condition for requiring upright posture with available space for both hands, and small hole (2 cm in diameter) condition for requiring upright posture with available space for only one hand. While the distribution of hand preference did not significantly differ among the three conditions at the group level, eight out of twelve marmosets did not change hands when identical upright postures were required in large and small hole conditions. Some marmosets simultaneously used both hands when both hands were free to reach the food items; however, the number of left hand users increased when the marmosets were forced to use either hand to pass through the reduced hole size. Significant correlations in hand use between the upright posture conditions were observed, whereas no correlation was observed between the different posture conditions. These results suggest that, although preferential hand use was not found at group level, posture, but not size of aperture, has effects on hand use in individual common marmosets

1. Introduction

Preference in hand use is one of the many remarkable characteristics that emerged in the course of hominid evolution [1]. Humans are notably lateralized, and more than 90% of the population is considered right-handed [2]. Except for some reports from wild and captive chimpanzees [3–5], however, no other primate species have shown handedness, left or right, analogous to the handedness in humans [6].

In primates, the observed hand preference is affected by several variables such as task complexity (e.g., [7,8]), and postures (e.g., [9]). Especially for arboreal species, postures are important because primates are frequently forced to maintain postural stability with their limbs on tree branches. In accordance with the postural origins theory of asymmetries in primates [10], population level shifts toward a greater use of the right hand for upright versus quadrupedal reaching have been reported in chimpanzees, orangutans [11], gorillas [12], macaques [13], and capuchins [14]. However, shifts in the reverse direction (greater left hand use for upright versus quadrupedal postures) were observed in gibbons [12] and squirrel monkeys [15]. Bush babies were observed to have a left hand population bias when they reached for food from a upright posture, but the bias was diminished when they captured the food item in a quadrupedal posture [16]. Ruffed lemurs were

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0166-4328
http://dx.doi.org/10.1016/j.bbr.2013.04.001

tested in free-foraging and discrete food presentation conditions and showed a strong left hand bias in the latter conditions [17]; however, gray mouse lemurs showed no population-level hand bias depending on postural demands [18]. Milliken et al. [19] examined the feeding postures and hand preferences in three species of Sifakas in their normal group settings and observed that the majority of subjects used their mouths when retrieving the food item from a tray on a flat surface but tended to use one hand when engaged in arboreal feeding on foliage. These studies showed that bias in hand use is associated with foraging situations (e.g., hands-free, arboreal, or spatially restricted) and the original foraging habits of the given species.

One of the purposes of the present study is to examine the effects of posture on hand use in captive common marmosets (*Callithrix jacchus*). Common marmosets are arboreal in the wild and have claws on their fingers that are adaptive for upright postural stabilization on tree trunks [20]. An upright posture enables marmosets to use their forelimbs freely to feed on insects and tree exudates using vertical clinging postures [21]. However, both hands are used occasionally in spontaneous food-taking and holding behaviors [22]. Therefore, the hand use of marmosets in the standing posture, in which both hands are available, can reveal any tendencies for behavioral lateralization and hemispheric specialization [23–25]. In non-primate mammals (cats, tree shrews, and marsupials), there has been no study reporting the effects of posture on paw preference [26–28]. Therefore, the postural origin theories of laterality are worth examining in small arboreal primates like common marmosets.

A previous study on hand preference in common marmosets has shown that common marmosets begin to exhibit hand preference in daily food intake at 5–8 months of age and that the preference remains stable up to 70 months [29]. Several studies have also shown individual hand preferences when the marmosets were forced to only use one hand [30–32]. In four tasks requiring different levels of visual guidance and postural control for reaching, individual-level hand preference was observed in common marmosets, together with the effects of task demand on the strength of preference [32]. When performing a complex task, such as tool use, in which the marmosets had to use one hand to operate a rake on a table while ensuring postural stability with the other hand, one marmoset consistently used the left hand for the task, whereas the other four individuals showed no such preference; the hand that the four marmosets used depended on the location of the food item relative to the location of the rake [33].

To clarify their preferential hand use depending on the task differences, we examined the effects of two variables, posture and size of aperture, on hand use in common marmosets. In our tasks, the marmosets were required to reach for the food items using different postures (upright or quadrupedal) and different size of apertures of hand use (passing through a small or large hole). In the ground condition (Gr), the marmosets reached for the food item on a table that was level to the floor of the experimental chamber, thus requiring a quadrupedal posture. In the small hole (SH) and large hole (LH) conditions, the marmosets had to reach through small or large holes to retrieve the food item. The holes were placed at a height that required them to be in an upright posture. The size of the hole in the SH condition was established at 2.0 cm so the marmosets could only insert one hand at a time because of their palm size (approximately 1.5–2.0 cm). Similarly, the diameter of the LH was established at 4.0 cm so one or two hands could be passed through the hole simultaneously. Therefore, we manipulated the space of hand use for the subjects under these conditions.

Because we conducted the experiments in the different room from the housing one, there was possibility that additional variable such as novelty of the experimental situation would affect on the individual performance of hand use, because individual disposition was found to be correlated with the hand preference in a novel setting [34], Thus, we examined this possibility by conducting the same experiments in the housing cages using additional subjects.

2. Methods

2.1. Experiment 1: hand preference tests in an experimental room

2.1.1. Subjects

Twelve adult common marmosets, five males and seven females, ranging from 20 to 61 months old (mean = 33, *SD* = 11), were used in the experiment. The mean body weight of the marmosets was 343 g (*SD* = 60). All marmosets were laboratory-born. The marmosets were housed individually in a housing room on a 12:12 h (8:00/20:00) light/dark cycle. The temperature in the housing room were maintained at 27 °C and the relative humidity averaged 50%, respectively. The marmosets had ad libitum access to food and water in their home cages. All experimental procedures and handling methods were performed in accordance with the Guide for the Care and Use of Laboratory Animals of the National Research Council and the Guidelines for Animal Experimentation at RIKEN. The experiments were approved by the Animal Experiment Committee at RIKEN. This study complies with the current laws of Japan (the Act on the Welfare and Management of Animals).

2.1.2. Apparatus

The experimental chamber was 42.0 cm × 34.0 cm × 35.0 cm and constructed of stainless steel. The chamber was located in a sound-attenuated room. Three different front panels were used depending on the conditions of the task. For the Gr condition, the front panel (26.0 cm × 20.0 cm) had an aperture (3.0 or 1.5 cm × 16.0 cm, shaped like a comb with 2.0 cm × 1.5 cm teeth) at the bottom, through which the subjects could extend their forearms and hands to retrieve the food items (Fig. 1A). The food items were placed on a black acrylic table (9.5 cm × 35.0 cm × 24.0 cm), 2.0 cm above the floor, which was connected to the experimental chamber through the aperture. The front panel used in the LH upright condition contained a hole (4.0 cm in diameter) through which the subjects could put both hands simultaneously through the center of the panel (18.5 cm from the bottom; Fig. 1B). The hole in the SH upright condition was 2.0 cm in diameter, through which the subjects could only put one of their hands (Fig. 1C).

The animal placed in the experimental chamber was not isolated, but rather were in sight of another marmoset in a nearby cage. During the experimental sessions, the subjects' behaviors were videotaped with video cameras (HDR-HC9; Sony, Tokyo, Japan) that captured the side (from the left) and top views of the chamber. The videotapes were used for the observations of the subjects' behaviors and scoring. Marshmallows, which were used as rewards for the marmosets, were cut into tiny portions (approximately 0.3 cm × 0.3 cm × 0.3 cm) and served as the food item. The rewards were presented to the marmosets on the tip of a silver spoon (15 cm).

2.1.3. Procedures

The subjects were transferred from the housing room to the experimental room before the daily session. We placed another marmoset in a waiting cage behind the experimenter in the view of the waiting animal during the testing trials. The experimenters used their right hands to hold and transport the spoon to the desired position in front of the subjects. The food item was presented when the animal entered the posterior half of the chamber to prevent any positional bias. The experimenter tried not to look at the subjects' faces when they came to the front panel until they finished their responses, to prevent any social or emotional effects from the experimenter on their choice. When a marmoset was distracted, the experimenters attempted to capture their attention by making sounds and moving the spoon with the food item. The food item was presented at the fixed position (varied in the conditions, described below) when the animal started to approach it. When the marmoset grasped and pulled the spoon, the experimenter left it until the animal finished the food. The food item was withdrawn if the marmoset tried to reach it with its mouth. Marmosets always ate the marshmallow while remaining at the front of the chamber without changing their position. The day before the initial experimental day, the marmosets were individually carried to the experimental settings and apparatus without any scoring recorded. Shaping was defined as reaching for the reward within 30 s after the food presentation.

The criterion for preferred hand use was scored as the hand that was used to touch the food item or spoon on the initial attempt. The hand used to make initial contact was always the hand used in the retrieval. Bilateral hand use was scored when both hands touched the food item or spoon simultaneously or consecutively within 1 s. Only the trials with successful food retrievals were scored, although retrieval failures were rarely observed.

A session consisted of three conditions per day, and each condition consisted of twelve trials. The inter-trial interval was approximately 10 s. The order of the three conditions was counterbalanced between sessions, and seven sessions were conducted for each subject. An additional seven sessions were conducted for the marmosets (M20 and F28b) that did not reach for the food reward within 30 s after the food presentation on the initial trial of the last session in the small hole upright condition. These seven sessions (including all three conditions) were conducted