Research report

A new tool for measuring hand preference in non-human primates: Adaptation of Bishop's Quantifying Hand Preference task for Olive baboons

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ABSTRACT

As non-human primates are phylogenetically close to humans, they are ideal models to investigate the precursors of human brain hemispheric specialisation. However, in spite of hundreds of reports investigating hand preference, empirically based theories generating valuable predictions are still lacking, mainly because of a disappointing deficiency in comparability between studies and even more so between species. Therefore, we propose here to adapt, for the first time, the Quantifying Hand Preference (QHP) task, devised for humans, to non-human primates. This test could be a very useful standard measure of hand preference for simple reaching in non-human primates because of its simplicity to set up and of the parameters (e.g., subject's posture; position of the item) it can control. Our test subjects were 42 baboons of various ages and both sexes. Our results highlight the crucial influence of item position on hand preference for simple reaching, even when the item is positioned close to the subjects' body midline. Both sex and age influence baboons' handedness index but this effect varies according to the position of the item to be grasped. We discuss our results within the theoretical framework concerning hemispheric specialisation for object manipulation and with the perspective of replicating this experiment with other non-human primate species and genera.

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1. Introduction

Because hand preference is an indirect index of cerebral lateralisation and can be easily observed in several daily contexts of manipulation and gestural communication, the study of manual preferences became, few decades ago, a privileged topic of investigation in several of the fields of cognitive neurosciences. Historically, human behavioural and brain asymmetries at a population level have been considered as unique to evolution and associated exclusively with the emergence of speech (e.g., [9,11,35]). However, one of the main results of these recent investigations is that in many vertebrate species present similar asymmetries (see [31,32] for reviews). These findings obviously open new debates concerning the precursors of brain hemispheric specialisation in humans, including lateralisation for language (see [16,27,32] for reviews).

As non-human primates are phylogenetically close to humans, they are ideal models to investigate these precursors and have therefore been chosen for several dozens of stud-ies (see [6,13,21,22,25] for reviews). Several authors (e.g., [7,19,23,26,28,33,37]) have recently decided to present the same experimental coordinated bimanual task, the tube task initially proposed by Hopkins [15], to various non-human primate species.

In this task, subjects held a PVC tube with one hand and simultaneously removed peanut butter smeared on the inside of the tube with the opposite hand. This task has yielded reliable data for comparisons demonstrating hand preference at the population level (apes [15], old world monkeys [33,37] and new world monkeys [28]).

However, no comparable effort has aimed at standardising unimanual reaching tasks for non-human primates. Recently, Papademetriou et al.'s [25] meta-analysis of primate hand preference for reaching underlined the impossibility of proposing empirically based theories generating valuable predictions concerning the evolution of human brain–behaviour relations. Indeed, lack of consistency clearly appears between studies and the high variability between findings could be due mainly to the variability of the tasks used to assess hand preference for simple reaching. Not only the assessed reaching patterns but also the subjects' postures (e.g., sitting or moving) vary between tasks. McGrew and Marchant [22] noted that tasks testing primate handedness often involved reaching from an upright posture, which is a highly unusual posture for non-human primates. The current literature clearly indicates

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that more handedness data must be collected using similar, or at least comparable, tasks presented to relatively large samples of species in the field and in captivity. Of course the biology of the species must be taken into account before defining the degree of difficulty or complexity of a given task. For example, a hanging task is easier for arboreal species than for terrestrial species [2,3]. Bishop et al. [1] were the first to propose a standard method for quantifying laterality in humans to ensure uniformity in a field where failure to replicate is a major problem. They proposed a behavioural measure for Quantifying consistency of Hand Preference (QHP task). This task encourages the use of both hands by varying the spatial position of the object to be reached in relation to the body midline with the idea to determine where in the preferred hand's contralateral space the subject shifts to using his/her non-preferred ipsilateral hand. The stronger a subject preference for his/her right hand, the further in the contralateral space from his/her body midline he/she is likely to switch to using his/her left hand and *vice versa*.

Because the QHP task could be a standard measure of hand preference for simple reaching by non-human primates and lack of comparability between studies on humans and studies on other primates (even for the tube task) still exists, we propose here, for the first time, to adapt the QHP task, classically presented to human participants, for non-human primates. We assessed 42 Olive baboons' (*Papio anubis*) hand preference for simple reaching. Our main goal was to collect data on manual laterality for a simple reaching task in a very controlled and replicable setup, where a subject's posture is restricted to being seated but both its hands are free. This adaptation of the QHP task should reveal precisely the crucial impact of the position of the object to grasp on the quantitative and qualitative expression of hand preference.

2. Materials and methods

All the experiments with these baboons were carried out following the principles of laboratory animal care in accordance with the CNRS guidelines.

2.1. Subjects

Data were collected between September and December 2009 at the Rousset Centre of Primatology, France. The subjects were 42 captive Olive baboons (*Papio anubis*) and included 13 adult males (7–12 years old, mean = 9, SE = 0.58), 23 adult females (6–20 years old, mean = 10, SE = 0.74), and 6 juveniles (2–4 years old, mean = 3, SE = 0.36). All the subjects lived in social groups, and were housed either in parks or large cages, both with free access to an indoor shelter. Baboons were fed commercial primate pellets twice a day, fresh fruits and vegetables once a day and seeds three times a week. Water was available *ad libitum*.

2.2. Experimental procedure

The experimental procedure was our adaptation of Bishop's QHP task, originally presented to human children by Bishop et al. [1] to evaluate their degree of hand preference. Bishop originally placed seven picture cards positioned 30 degrees apart one from the other and within the child's reach. Children stood in front of the template in the centre of the baseline. They were asked by the experimenter to pick up a specific, named card and to place it in a box located directly in front of them. The experimenter recorded the hand used to pick up each card. The card order was random but the sequence of positions was the same for all participants [1]. Our study is the first to present the QHP task to a non-human species. We adapted it to non-human primates by replacing cards by raisins. Monkeys sat in front of the setup. However, only one of the seven locations was baited at a time, when the subject grasped the food item the experimenter recorded which hand was used. The distance between raisins and subject was adjusted taking into account the subject arm's length: 20 cm for juveniles, 25 cm for females and subadult males and 30 cm for adult males. We retained the seven positions at successive 30-degree intervals (see Fig. 1). Positions 1, 2 and 3 were on the subject's right, position 4 was the central position and positions 5, 6 and 7 were on the subject's left (see Fig. 1).

As for children, position order of the raisins was random, but presentation order was the same for all subjects and the experimenter recorded the hand used to pick up each raisin. The experimenter used his/her left and right hand randomly to place each raisin on one of the seven positions on the experimental table.

The experimental setup was fixed outside the cage or park on the wire mesh. A 10 cm × 60 cm hole in the wire mesh allowed baboons to move their arms freely over the experimental table. To adjust the horizontal position of the subject, we placed, inside the cage, a concrete block perpendicularly to the mesh, 25 cm below

Fig. 1. A young baboon waiting to reach a raisin at one of the seven positions of the experimental setup.

the level of the table, in the medium plane of the table so that when the subject sat down on the concrete block, it faced the set up and as in line with the middle of the experimental table (see Fig. 1).

A trial was valid when a subject sat in front of the experimental table with its sagittal median plane in line with the middle axis of the setup and when both its hands were free and placed symmetrically on the table. Before the next trial could start, the experimenter waited for the subject to sit down again correctly, in the position described above.

We recorded 13,148 trials, taking into account all positions and all subjects. This number of trials corresponds to a number of trials per subject for each of the seven positions ranging from 20 to 60 (mean = 44.65; SE = 2.47). These data were recorded collected either in one or in several sessions. The number of sessions per subject ranged from 1 to 8 (mean = 3.74; SE = 0.23). Between 4 and 140 trials (mean = 83.62; SE = 3.85) were recorded per individual and per session.

2.3. Data analysis

z-scores were calculated for each baboon for each of the seven positions proposed in the QHP task, on the basis of the total number of reaches made with each hand using the following formula: $z\text{-score} = [R - (R+L)/2]/\sqrt{[(R+L)/4]}$ (where R represents the total number of reaches using the right hand and L the total number of reaches using the left hand). These scores allowed us to classify baboons as left-handed ($z < -1.96$), right-handed ($z > 1.96$) or ambidextrous ($-1.96 < z < 1.96$) for each of the seven positions. These data were completed using an individual Handedness Index (HI) calculated by the formula $(R - L)/(R + L)$ for each position. This index ranges from -1.0 to 1.0 and estimates the strength of hand preference along a continuum, with negative values indicating a left-hand preference and positive values indicating a right-hand bias. The absolute values of HI (ABS-HI) reflect the strength of lateralisation.

We evaluated whether mean HI values for each position indicated a right- or left-bias and differed significantly from 0 (no bias) using one sample t-tests. Non-parametric Wilcoxon matched-pairs signed-ranks tests assessed effect of position on HI and on ABS-HI. Non-parametric Mann–Whitney U-tests assessed sex effects on z-scores and ABS-z-scores and non-parametric Kruskal–Wallis tests assessed age effects on z-scores and ABS-z-scores. Corresponding post hoc analyses used Dunn's multiple comparisons tests. Results were considered significant when $p < 0.05$. All tests were two-tailed.

3. Results

3.1. Hand preference at the central position

When the item to be reached was placed in the central position (position 4), 12 subjects were right-handed, 20 were ambidextrous and 10 subjects were left-handed. No group-level bias in hand use could be evidenced for this central position ($t(42) = 0.764$; $p = 0.449$, see Fig. 2).

3.2. Influence of item position on hand preference

Eleven individuals presented hand preferences for all of the seven positions, 25 for 6, 2 for 5 and 4 for 4 of 7 positions.
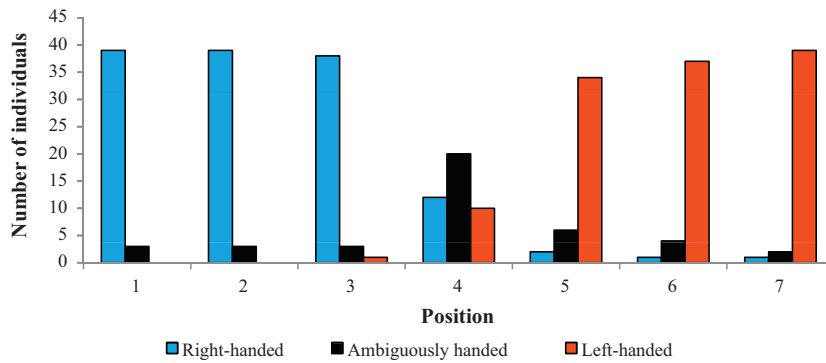
Fig. 2. Handedness in relation to object position. Numbers of right-handed, ambidextrous and left-handed baboons for each of the seven positions tested in the QHP task.

At the group level, right biases appeared for positions 1 ($t(42) = 20.974$, $p < 0.0001$), position 2 ($t(42) = 23.409$, $p < 0.0001$) and position 3 ($t(42) = 13.940$, $p < 0.0001$) and left-biases appeared for position 5 ($t(42) = -8.892$, $p < 0.0001$), position 6 ($t(42) = -11.980$, $p < 0.0001$) and position 7 ($t(42) = -17.267$, $p < 0.0001$).

The number of right-handed baboons was negatively correlated ($r = -0.982$; $p = 0.0004$, see Fig. 2) with position number (from 1, the position the furthest to the subject's right, to 7, the position the furthest to the left) of the item to be reached; conversely, the number of left-handed baboons was positively correlated ($r = 0.991$; $p = 0.004$, see Fig. 2) with the number of the position of the item to be reached.

The position of the raisin influenced HI significantly (see Fig. 3a). HI for position 2 were significantly higher than HI for position 3 ($W = 576$; $p < 0.0001$), which, in turn, were significantly higher than HI for position 4 ($W = 845$; $p = 0.0047$). HI for position 4 were significantly higher than HI for position 5 ($W = 861$; $p < 0.0001$), which, in turn, were significantly higher than HI for position 6 ($W = 410$; $p = 0.0047$). No significant differences could be evidenced between both pairs of extreme positions 1 and 2, and 6 and 7. Differences concerning ABS-HI were also significant (see Fig. 3b). ABS-HI for position 2 were significantly higher than ABS-HI for position 3 ($W = 466$; $p = 0.0001$), which, in turn, were significantly higher than ABS-HI for position 4 ($W = 783$; $p < 0.0001$). ABS-HI obtained for position 4 were significantly lower than ABS-HI for position 5 ($W = -616$; $p < 0.0001$), which, in turn, were significantly lower than ABS-HI for position 6 ($W = -432$; $p < 0.0001$). Finally, ABS-HI for symmetrical positions in relation to the body's midline (1–7, 2–6 and 3–5) did not differ significantly between ABS-HI pairs.

3.3. Sex effect on hand preference

Z-scores for adult males differed significantly from z-scores for adult females for all except the extreme positions (1 and 7) (see Fig. 4a). The direction of the difference changed in relation to position. Males' z-scores were higher than females' z-scores for positions 2 and 3, (position 2: $U = 47$; $N_{Male} = 13$; $N_{Female} = 23$; $p = 0.0008$; position 3: $U = 24.5$; $N_{Male} = 13$; $N_{Female} = 23$; $p < 0.0001$). This indicates that males use their right hand to reach these positions more than do females. On the contrary, females' z-scores were higher than males' z-scores for the central position 4 and for positions 5 and 6 (position 4: $U = 80$; $N_{Male} = 13$; $N_{Female} = 23$; $p = 0.0231$; position 5: $U = 43$; $N_{Male} = 13$; $N_{Female} = 23$; $p = 0.0005$; position 6: $U = 50$; $N_{Male} = 13$; $N_{Female} = 23$; $p = 0.0011$). This indicates that females use their right hand to reach these positions more than males do.

When ABS-z-scores are taken into account the difference for position 4 disappeared (see Fig. 4b), but differences in the other positions were still present and significant, as ABS-z-scores for males were higher than those for females (position 2: $U = 47$; $N_{Male} = 13$; $N_{Female} = 23$; $p = 0.0008$; position 3: $U = 24.5$; $N_{Male} = 13$; $N_{Female} = 23$; $p < 0.0001$; position 5: $U = 43$; $N_{Male} = 13$; $N_{Female} = 23$; $p = 0.0005$; position 6: $U = 50$; $N_{Male} = 13$; $N_{Female} = 23$; $p = 0.0011$).

3.4. Age effect on hand preference

Because sex had an effect on hand preference, we compared juveniles to adult males and to adult females separately. An effect of the age of the subject on its z-scores appeared for position 2 ($\chi^2 = 14.686$; $N_{Adul\ Males} = 13$; $N_{Adult\ Females} = 23$; $N_{Juveniles} = 6$, $p = 0.0008$), for position 3 ($\chi^2 = 16.917$; $N_{Adul\ Males} = 13$; $N_{Adult\ Females} = 23$; $N_{Juveniles} = 6$, $p = 0.0002$), for position 5 ($\chi^2 = 21.085$; $N_{Adul\ Males} = 13$; $N_{Adult\ Females} = 23$; $N_{Juveniles} = 6$, $p < 0.0001$), for position 6 ($\chi^2 = 20.858$; $N_{Adul\ Males} = 13$; $N_{Adult\ Females} = 23$; $N_{Juveniles} = 6$, $p < 0.0001$) and for position 7 ($\chi^2 = 9.291$; $N_{Adul\ Males} = 13$; $N_{Adult\ Females} = 23$; $N_{Juveniles} = 6$, $p = 0.0096$). Post hoc analyses revealed that z-scores for positions 2 and 3 were lower for juveniles than for adult males ($p < 0.05$, see Fig. 4a). This indicates that males use their right hand more than do juveniles to reach these positions. Z-scores for positions 5, 6 and 7 were higher for juveniles than for adults males ($p < 0.05$, see Fig. 4a) and their z-scores for position 6 were also higher than those of adult females ($p < 0.05$, see Fig. 4a). This again indicates that juveniles use their right hand more.

ABS-z-scores also revealed differences between adult males and juveniles for the same positions (see Fig. 4b), but their direction differences were always the same: ABS-z-scores for juveniles were lower than those of adult males.

4. Discussion

This study is the first of its kind to adapt the QHP task to non-human primates. This experimental setup allowed us to confirm that Olive baboons do not exhibit hand preference for simple reaching task when the object to be reached is placed in their median plane (our central position 4). Our results bring new elements concerning (1) the crucial influence of the position of the object to be reached on hand preference, as well as (2) age and sex effects on hand preference in this species.

4.1. Item position and hand preference

The position of the object to be reached influences hand preference in baboons: our subjects reached spatial positions located to the right of their body's midline (positions 1, 2 and 3) predominantly with their right hand and positions situated to the left (positions 5, 6 and 7) predominately with their left hand. Inter-
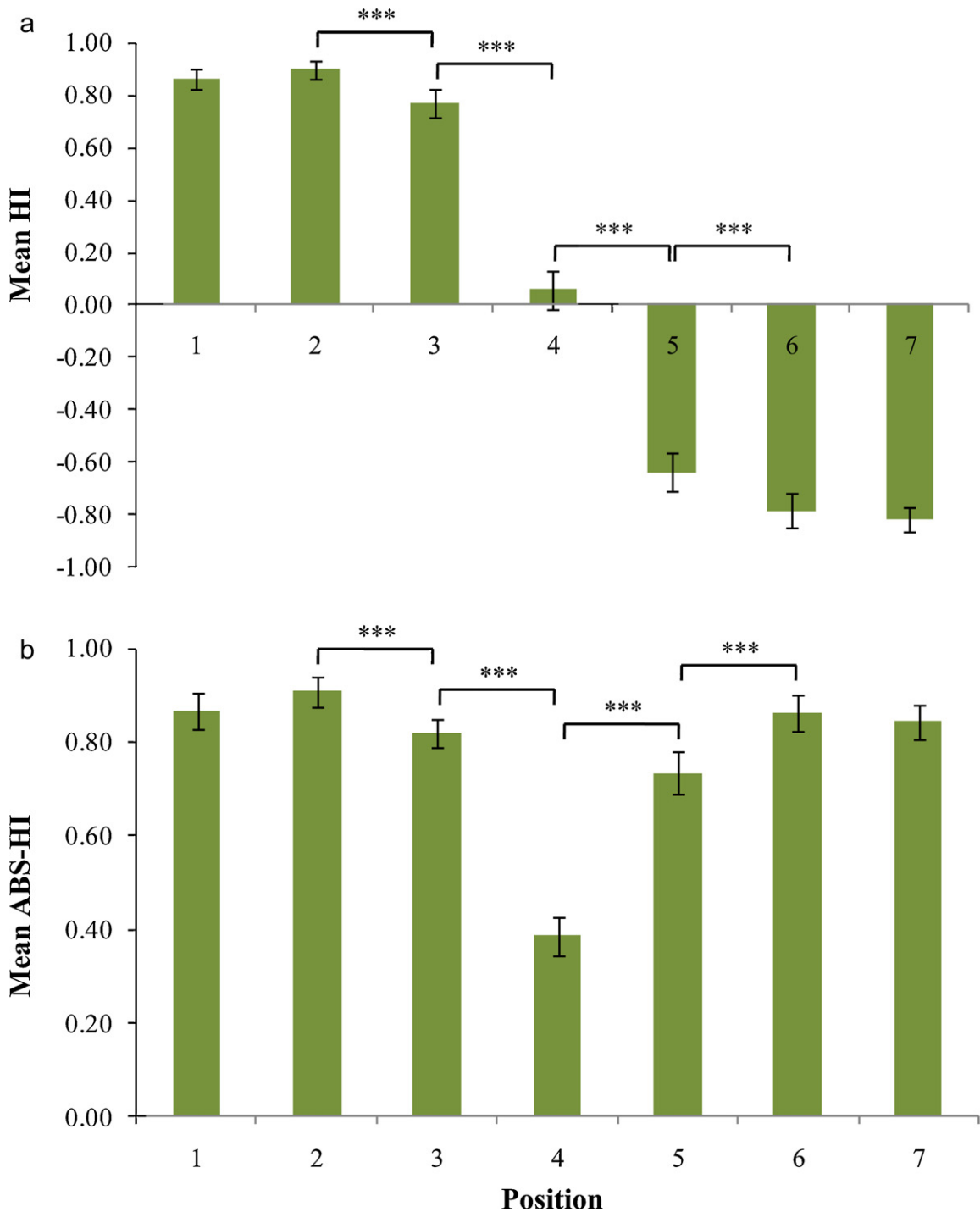
Fig. 3. Influence of the position of the item to be reached on HI (a) and ABS-HI (b) (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

estingly, biases at the population level appeared as soon as the object to be reached was positioned at least 30° from the body's midline, independently of side (left or right). Our results highlight some discontinuity between human and non-human primate laterality. Thus, although manual laterality in humans has been clearly established at the population level, non-human primate laterality for reaching is less clear and appears to depend on the type of behaviour observed [25]. However humans and chimpanzees are right-handed whereas macaques and lemurs are left-handed [25]. This kind of discontinuity was not observed in previous studies on monkeys, apes, and humans that examined the effects of situa-

tional factors on hand preference for simple reaches (our study, [5,8,10,12,20]). All these studies agree that reaching is strongly influenced by situational factors. Thus the hand used for grasping depends on presentation side: the right hand is generally used when the object is presented on their right and the left hand when the object is presented on their left. In other words, human infants, children and human adults as well as non-human primates strongly prefer to use their hand closer to the item to be reached.

As in humans [1,4], the number of right-handed baboons increased with the position of the item to be reached, from the left to the right and *vice versa* for the number of left-handed individuals.
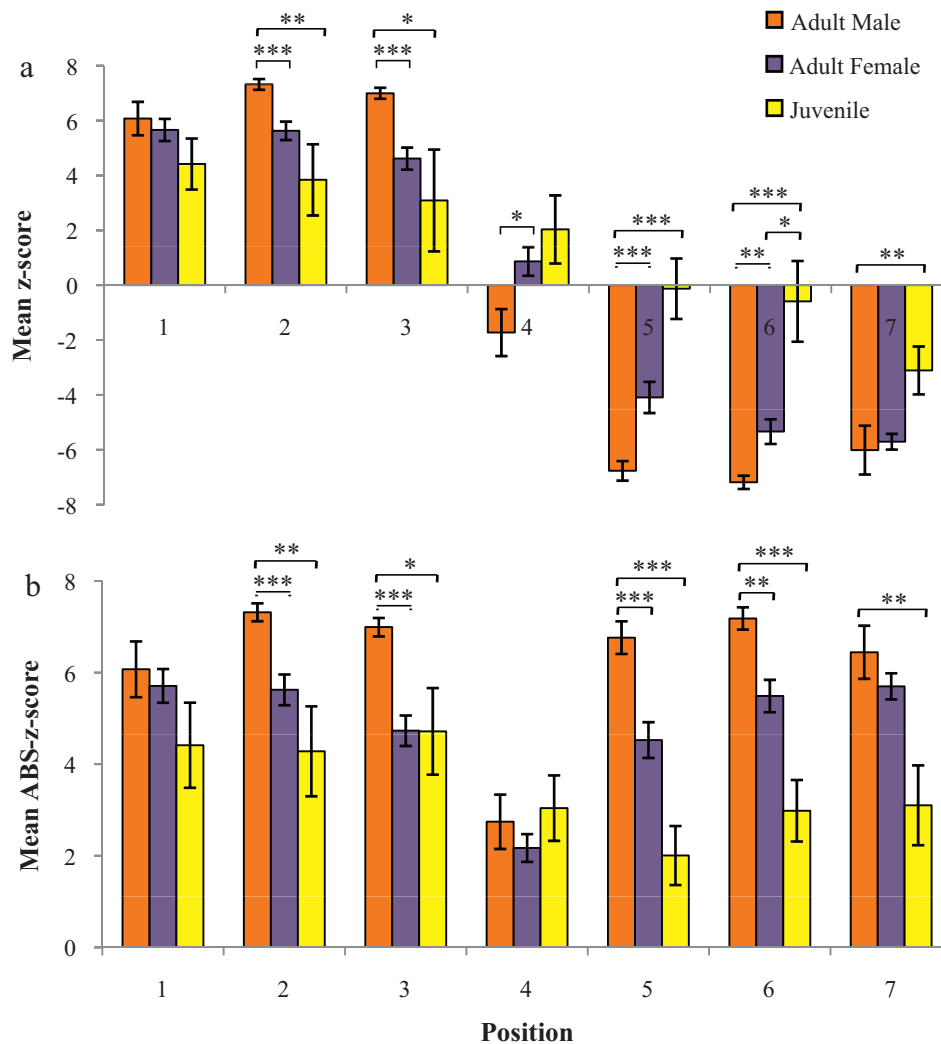
Fig. 4. Sex and age effects on z-scores (a) and ABS-z-scores (b) (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

However, even though the proportion of right-handed reaches was lower for left positions than for right positions, none of the human participants classified as strong-exclusive right-handers ever used the right hand less than the left [1]. By contrast, the majority of our subjects, even the baboons classified as right-handers for the central position, used the left hand preferentially to reach food on their left and *vice versa*. This behaviour is more comparable to that of humans classified as predominant right- or left-handers who shift more easily from their preferred hand to the other when crossing the midline [1,4].

The position of the item to be reached significantly influenced the HI, which increases progressively according to the position of the item, from negative values on the left to positive ones on the right. Moreover, the more the item to be reached was far from the body's midline of the subject, the more the ABS-HI. This increasing is symmetrical in that ABS-HI of symmetrical positions from the body's midline were not different.

4.2. Age and hand preference

We did not find an age effect for the central position. This result is in accordance with several studies on simple reaching by non-human primates (e.g., [13,30]). This lack of effect seems due mainly to the fact that adults were less lateralised for this position than for the other positions and thus their z-scores were more similar to those of juveniles. However, as soon as the item to be reached was moved away from the body's midline, to the left or to the right, we observed an age effect on hand use, with juveniles being still little-lateralised, whereas adult males and females exhibited higher z-scores.

As suggested by numerous authors (e.g., [17,34]), this lesser degree of lateralisation of juveniles may reflect their incompletely developed nervous system and most studies of the ontogeny of laterality in primates show lateralisation increasing with age, up to adulthood [18,20,29,34,36]. As described above, differences between adults and juveniles appear only when the item to be reached has been moved away from the midline. Bishop's QHP task could thus explain disagreements between studies that sometimes reach opposite conclusions concerning age effects on hand preference. Indeed, those differences may be due to differences in procedure, in that the authors who found no age effect, only took into account reaches when the object was in front of the subject, in its sagittal median plan, which corresponds to the central position in the Bishop's QHP task (e.g., [33]), whereas others, who found an age effect, took all the responses in consideration, whatever the position of the object to be reached (e.g., [29,34]). Thus Bishop's QHP task allows thus studying more precise investigations of age effect on hand use.

Another factor explaining age effects is the fact that juveniles are more mobile than adults and this moving behavioural tendency, observed in the present experiment, may have created circumstances that led to greater alternation of hand use.

4.3. Sex and hand preference

We found that females were more right-handed than males when the object was presented in the central position. Similar differences have been reported previously for other non-human primate species in the context of simple reaching (lemurs [24,34] and gibbons [29]). To our knowledge, the only theoretical explanation of these differences proposed in the literature is based on the relative rates of testosterone during the development of the cerebral hemispheres of humans. The higher rate of testosterone in males may act to delay left-hemisphere development selectively and thus favour right-hemisphere dominance and the use of the left hand (see [14] for details). However, our results for objects presented in peripheral positions showed that differences changed direction from one side to the other and thus that differences between sexes appear to be due to a difference in strength of hand preference and not to a difference in the direction of hand preference. Males reached a maximum strength of hand preference as soon as the object to be reached was placed 30° from the midline, whereas females reached this maximum strength of hand preference only when objects were placed 60° from their midline. Thus, the theory based on testosterone rates cannot explain our entire set of results so we suggest that, as for juveniles, the higher mobility of females and the fact that they moved more during the experiments than did males could have elicited circumstances that led to greater alternation in hand use. This difference in mobility could be explained by both sexual dimorphism (males are taller and broader than females) and potential differences in the subjects' emotional state. Indeed, because of their hierarchical rank, females, as juveniles, are used to receive more social pressure than adult males. This social pressure is still present during a test even more so as they may lose the access to the experimental setup and food.

To conclude, our results stress our successful adaptation, for the first time, of the Bishop's QHP task for non-human primates and highlight several advantages of its use to investigate hand preference of non-human primates. Positional effects appear here to be undisputable and this aspect stresses the crucial impact of methodological characteristics for studying hand preference on the conclusions that can be drawn, even and especially for the study of age and sex effects on hand preference. This procedure allows investigators to collect data on hand preference for simple reaching, as well as on the influence of positional factors on this preference. Because of all these characteristics, and also because this task will open better perspectives for comparisons between primate species, including humans, we suggest that the QHP task is the long-awaited standard measure of hand preference for simple reaching in non-human primates.

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