

Hand preference predicts behavioral responses to threats in Barbary macaques

Eva S. J. van Dijk¹ | Debottam Bhattacharjee¹  | Elena Belli²  | Jorg J. M. Massen¹

¹Department of Biology, Animal Behavior and Cognition, Utrecht University, CH Utrecht, The Netherlands

²Department of Physics, Chemistry and Biology, IFM Biology, Linköping University, Linköping, Sweden

Correspondence

Debottam Bhattacharjee
Email: bhattacharjee.debottam@gmail.com

Funding information

HORIZON EUROPE Marie Skłodowska-Curie Actions, Grant/Award Number: 893016

Abstract

The structure and functioning of the brain are lateralized—the right hemisphere processes unexpected stimuli and controls spontaneous behavior, while the left deals with familiar stimuli and routine responses. Hemispheric dominance, the predisposition of an individual using one hemisphere over the other, may lead to behavioral differences; particularly, an individual may be programmed to act in a certain way concerning hemispheric dominance. Hand preference is a robust estimator of hemispheric dominance in primates, as each hemisphere controls the opposing side of the body. Studies have found links between hand preference and the exhibition of behaviors in contexts such as exploring and manipulating objects. However, little is known whether hand preference predicts behavioral variations in other ecologically relevant contexts like predation. We investigated the relationship between hand preference and behavioral responses to two types of predator models in captive Barbary macaques (*Macaca sylvanus*) ($n = 22$). Besides, a nonpredator novel object was included as control. We found 91% of the macaques to be lateralized with no group-level bias. A higher rate of tension and focus (behavioral response) behavior was found in predator contexts than in the novel object condition. Unlike their right-hand counterparts, individuals with a strong left-hand preference elicited frequent focus and tension behavior toward the predator models. Additionally, the behavioral response varied with predator type. We also found an interaction effect between hand preference and predator type. Our study suggests that hand preference can reliably predict behavioral variations in the context of potential predation. While these results are consistent with lateralized brain function, indicating lateralization a neural mechanism of behavioral variation, the interaction effect between hand preference and predator type elucidates the importance of context-specificity when investigating laterality noninvasively. Future research on other nonhuman primates using the current framework may provide insights into the evolution of laterality and underlying behavioral predispositions.

Abbreviations: AIC, Akaike information criterion; CI, confidence interval; HI, handedness index; LMM, linear mixed effect model; MSCA-IF, Marie Skłodowska-Curie Actions Individual Fellowship; SD, standard deviation.

Eva S. J. van Dijk and Debottam Bhattacharjee contributed equally to this study.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2023 The Authors. *American Journal of Primatology* published by Wiley Periodicals LLC.

KEYWORDS

brain lateralization, handedness, individual variation, nonhuman primates, predator response

1 | INTRODUCTION

The left and right hemispheres control opposing sides of the body, process information differently, and control contrasting behaviors. Such asymmetries in the structure and/or function of the two hemispheres are called cerebral lateralization (Bisazza et al., 1998). The contrasting behavioral responses linked to cerebral lateralization follow the same basic pattern among vertebrates (Rogers, 2002; Rogers & Andrew, 2002). Roughly, the left hemisphere controls routine behavior and functions, while the right one detects and responds to novel and unexpected stimuli like responses to potential predators. Overall, the left hemisphere is said to be involved when controlling responses that first require weighing different options, while the right hemisphere is involved in spontaneous and intense reactions to various stimuli (Rogers, 2002, 2010).

Next to the processing of stimuli and controlling behaviors, both hemispheres are involved in regulating short-term affective states, that is, emotions (Désiré et al., 2002). Like behavioral responses, emotional functioning seems lateralized across human and nonhuman primates (Leliveld et al., 2013). The left hemisphere is dominant for positive emotions, at least concerning responses to food rewards; on the contrary, the right hemisphere is specialized in expressing intense, often negative emotions, such as fear and disgust, which likely relates to the specialization for the control of aggressive interactions (Rogers, 2002). Similarly, the right hemisphere is associated with the stress response (Ocklenburg et al., 2016; Rogers, 2010). For example, in black-tufted marmosets (*Callithrix penicillata*), there is a stronger right hemisphere activation under acute stress as measured by tympanic temperature (Tomaz et al., 2003); and in rhesus macaques (*Macaca mulatta*), plasma cortisol levels positively correlate with activity levels in the right frontal cortex, associated with high levels of fear and defensive behavior (Kalin et al., 1998). As each hemisphere processes stimuli differently and controls distinct sets of behaviors and emotions, hemispheric specialization may be considered a neurobiological mechanism underlying intraspecific behavioral variation (Rogers, 2009, 2010). However, noninvasive measurements are incredibly difficult to implement while investigating the role of cerebral lateralization as a predictor of behavioral variation.

Across cultures, by far, most humans are right-handed for manipulative actions (Raymond & Pontier, 2004). Up until recently, right-handedness in humans was considered a “social norm” and “corrective” attempts had been made at early ontogeny if deviations were noticed (McManus, 2009). Yet there exists a considerable variation in hand preference both within and across primate species, including humans (Caspar et al., 2022; Meguerditchian et al., 2013; Soto et al., 2022). Each side of the body is controlled by the opposite brain hemisphere; that is, the right hand is controlled by the left hemisphere and vice versa (Bisazza et al., 1998). When there is a

group-level hand bias for a task, such as human right-hand bias for manual tasks, this could result from functional hemispheric specialization favoring the hemisphere best equipped for the task. However, when there is no group-level hand bias for a task and likely no functional hemispheric specialization, individual hand preference reflects an individual's tendency to use the related hemisphere more than the other, a feature called hemispheric dominance (Rogers, 2011; Hook & Rogers, 2000). Hemispheric dominance may thus program an individual to act in a certain way, leading to behavioral variation.

Although bimanual tasks are proposed to be more suitable when investigating hand preference on a group level (Nelson, 2022; Soto et al., 2022), an individual's hand preference for simple and cognitively less demanding tasks, such as unimanual reaching, also reflects one hemisphere's dominance over the other (Rogers, 2018; Gordon & Rogers, 2010, 2015). Individual hand preference for unimanual reaching or unimanual foraging is highly consistent within individuals across primates (e.g., *Callithrix jacchus*: Kuběnová et al., 2022; *Macaca silenus*: Rogers, 2009; *Rhinopithecus roxellana*: Fu et al., 2022). Moreover, research on nonhuman primates found differences among right- and left-handed individuals; the hand preference of common marmosets, for example, which is stable over adulthood and across tasks (Gordon & Rogers, 2015), also predicts the marmosets' reaction to novelty, with left-handed individuals taking longer to enter novel rooms and touching or exploring novel objects (Cameron & Rogers, 1999). A different study also showed that left-handed marmosets were less responsive to their social group and less proactive when investigating novel stimuli (Gordon & Rogers, 2010). On the other hand, right-handed marmosets are said to be more explorative, inquisitive, and proactive, and more influenced by and of influence to their social group (Rogers, 2018). A recent study, however, did not find a link between handedness and interindividual behavioral differences, aka personality, in common marmosets (Masilkova et al., 2022). In chimpanzees (*Pan troglodytes*), right-handed individuals appear more curious than left-handed individuals (Hopkins & Bennett, 1994). Similarly, in a comparative study on multiple primate species, left-handed individuals took longer before inspecting novel objects but were also less fearful and less inactive (Fernández-Lázaro et al., 2019). Overall, right-handed nonhuman primates are more likely to approach and interact with novel stimuli than their left-handed conspecifics, and studies in humans are consistent with this pattern (Rogers, 2018; Wright et al., 2013).

Nonhuman primate lateralization and hand preference in relation to behavior have been investigated in different contexts (Rogers, 2018). Yet, only a few studies looked at the effects of handedness on behavior in ecologically relevant contexts. Zonato et al. (2022) argue that ecological factors should be evaluated when assessing hand preference. They tested hand preference in ring-railed lemurs (*Lemur catta*) and found evidence of individual hand

preference for grasping static food items but not for food in motion, a dynamically complex condition. Examining ecological factors when evaluating hand preference is gaining importance but remains relatively understudied. Differences between left- and right-handed individuals have been investigated for context-specific behaviors such as exploration (Braccini & Caine, 2009; Fernández-Lázaro et al., 2019), social behavior (Westergaard et al., 2003), cognitive bias (Gordon & Rogers, 2015), fear and stress responses (Rogers, 2009), and learning (Cameron & Rogers, 1999) as well as performance in cognitive tasks (Wang et al., 2022). To validate and understand the implications of relationships between hand preference and behavioral measures, more ecologically valid measures are required. For example, little is known about whether hand preference predicts individual behavioral variation in contexts such as predation.

As predator avoidance is of high ecological relevance, it is interesting to investigate whether hemispheric specialization results in individual behavioral differences with regard to reactions to predators. Predation is considered a strong selective pressure driving primate evolution, including the evolution of sociality (Anderson, 1986; Kappeler & van Schaik, 2002). Encounters with both live and simulated predators can result in stress (Cheney & Seyfarth, 2009). To avoid being preyed on, primates display antipredator behavior (Barros et al., 2008; Stanford, 2002), including elevated vigilance and avoidance strategies, such as alarm calls and flight, but sometimes also confrontation (i.e., mobbing). The failure to avoid predation may have severe survival consequences, including death; thus, appropriate antipredator responses are vital, yet, there are clear interindividual differences when it comes to responding to potential predators (Carter et al., 2012). For example, in common marmosets, interindividual variation has been observed in response to potential predators, which is considered part of a nonsocial personality trait, "Boldness-Shyness in Predation" (Šlipogor et al., 2016). The right hemisphere may be especially important to the behavioral responses to predators as the right hemisphere detects unexpected stimuli such as potential predators and controls spontaneous behaviors such as flight. Moreover, it is specialized in expressing negative emotions such as fear and controls the stress response. Individuals with a left-hand bias and thus right-hemispheric dominance might, therefore, be more reactive to predators. One of the few studies to date that we know of, which investigated the link between predator responses and handedness, indeed found that left-handed Geoffrey marmosets (*Callithrix geoffroyi*), when confronted with a hawk call, freeze for longer than right-handed individuals (Braccini & Caine, 2009). Conversely, when common marmosets are confronted with a threat, right-handed individuals produce more mobbing calls and perform more head cocking and parallax movements than left-handed individuals (Gordon & Rogers, 2010). Interindividual differences in hemispheric dominance could thus play a major role in the observed interindividual behavioral responses to predators.

Due to the high variation in the social, behavioral, and ecological characteristics, macaques are considered highly relevant when investigating lateralization (Regaiolli et al., 2018). One species of interest for lateralization is the relatively socially tolerant Barbary macaque (*Macaca sylvanus*) (Thierry et al., 2000). To the best of our

knowledge, only three studies have so far investigated hand preference in Barbary macaques. These studies reported 7 out of 20 (35%), 7 out of 15 (47%), and 9 out of 12 (75%) individuals to be significantly lateralized (Baldachini et al., 2021; Regaiolli et al., 2018; Schmitt et al., 2008). However, these studies used different methods to collect data on hand use and to determine hand preference. Nevertheless, the results of these studies showed that for sequences of unimanual reaching, older individuals had an overall stronger hand preference (Schmitt et al., 2008). They did not find any effect of dominance rank on hand preference during bouts of unimanual interactions with inanimate targets using both food and nonfood (Baldachini et al., 2021). Finally, none of these studies reported group-level lateralization for unimanual reaching or manipulation of inanimate objects (Baldachini et al., 2021; Regaiolli et al., 2018; Schmitt et al., 2008). None of these studies, however, investigated the relationship between hand preference and response to predators in Barbary macaques.

The Barbary or North African leopard (*Panthera pardus panthera*) is expected to have been a major predator of the Barbary macaque when the two species were still sympatric (Bautista, 2019; Fooden, 2007). Currently, the main predator of Barbary macaques is the domestic dog (*Canis lupus familiaris*), but jackals (*Canis aureus*), genets (*Genetta genetta*), and some species of birds of prey are also suggested as potential predators (Bautista, 2019; Majolo et al., 2013; Waterman et al., 2020). Besides, Barbary macaques are known to respond to snakes. While fear of snakes is common among primates and particularly catarrhines, Barbary macaques have also coexisted with venomous snakes throughout their evolutionary history (Isbell, 2006; Öhman & Mineka, 2003). The semifree-ranging populations of these macaques living in monkey parks in Europe are known to give alarm calls to snakes (Fischer & Hammerschmidt, 2002). There are also anecdotal observations of Barbary macaques standing bipedally, peeking in surrounding grass, approaching and even mobbing a snake upon detection (Fischer & Hammerschmidt, 2001). Moreover, even the nonnative population of Gibraltar responds to snakes, despite the present snake species posing no actual threat to infant macaques (Fooden, 2007; Roberts et al., 2008). Snakes are thus proposed to be an ecologically relevant stimulus for Barbary macaques in addition to felid predators.

While both felid predators and snakes may constitute a relevant threat to Barbary macaques, potentially eliciting antipredator behavior and stress, the response to each type of predator may differ. Antipredator behavior serves to avoid predation and can thus vary for different types of predators based on their hunting techniques, perceived threat, mode of detection, and habitat structure (Lemasson et al., 2009). For example, wild Campbell's monkeys (*Cercopithecus c. campbelli*) show predator-specific behavior when presented with auditory or visual cues related to their natural predators, which are leopards, eagles, and snakes (Lemasson et al., 2009); males behaved conspicuously toward both eagle and leopard models, whereas females behaved conspicuously toward the leopard but were cryptic to the eagle. Additionally, individuals were found to ascend upon hearing a leopard or after detecting a viper but descend in response

to eagle shrieks. Barbary macaques were shown to display some predator-specific behavior too, as they produced different alarm calls in response to dogs, humans, and snakes (Fischer & Hammerschmidt, 2001); and when these alarm calls were played back, their response varied too—startle and escape responses occurred more often after dog alarm calls than after calls in response to humans. In contrast, calls related to snakes did not elicit any specific antipredator behavior. Thus, while there may be inter-individual differences in the behavioral response to predators due to differences in individual hemispheric specialization, these responses can also vary between different predators.

The current study sets out to identify whether there is a link between lateralization and the behavioral response of Barbary macaques ($n = 22$) in the context of predation. We hypothesize that the macaques would show individual but not group-level hand preference for unimanual foraging. We furthermore expected that the varying degree of bias in hand preference would relate to differentiated behavioral responses during predator exposure, which we quantified by looking at focus and tension behaviors. In comparison to the response during the presentation of predator models, we expected the macaques to display lower frequencies of focus and tension behavior during a nonpredator novel object (i.e., control) condition. Therefore, we hypothesize a relationship between the direction of hand preference and the intensity of focus and tension behavior, particularly during the predator context. Left-handed individuals are expected to display a higher frequency of focus and tension behavior during predator exposure than right-handed individuals, as the right hemisphere is specialized for predator detection and spontaneous behavioral responses. Finally, we predict that this relationship would vary with regard to the two different predator models.

2 | MATERIALS AND METHODS

2.1 | Subjects and study sites

We tested 22 adult Barbary macaques (female = 16, male = 8) in this study (see Supporting Information: Table S1). The age of the macaques ranged from 4 to 20 years (11.1 ± 4.9 years) at the start of data collection. Nine individuals (female = 8, male = 1) were socially housed in a single group along with four infants under a year old at Apenheul Primate Park in Apeldoorn, the Netherlands. Thirteen individuals (female = 8, male = 5) were housed in a social group at Gaia Zoo in Kerkrade, the Netherlands. At Apenheul Primate Park, the Barbary macaques were housed in an outdoor enclosure with a creek, boulders, wooden climbing structures, and synthetic rock-like plateaus. The macaques at Gaia Zoo had access to an indoor enclosure and an outdoor one with several trees and climbing structures on a hill-like terrain. At both zoos, the diet consisted of monkey pellets and vegetables and was supplemented with smaller food items such as grains, nuts, and seeds. Food was provisioned multiple times a day, and water was available ad libitum.

2.2 | Data collection and experimental design

2.2.1 | Hand use

Data on hand use were collected during regular feeding sessions, with each session typically lasting for 12–15 min. A session started after the macaques were given small food items such as monkey pellets. Within such feeding sessions, ad-libitum sampling of foraging behavior was carried out. The observations were conducted 2–3 days a week and data were collected from September to October 2022 at Gaia Zoo. To achieve an efficient sampling distribution of all individuals, a total of eight feeding sessions were video-recorded. Due to a different feeding schedule and layout of the enclosure at Apenheul Primate Park, it was not possible to restrict observations to feeding sessions as few individuals could be captured within the frame of the camera during a session. Instead, at Apenheul Primate Park, ad-libitum sampling of foraging behavior was done by recording individuals opportunistically when seen foraging. To keep consistency in sampling between the two groups, recordings were made at the Apenheul Primate Park only when the macaques were foraging on small food items, that is, monkey pellets. Data were collected from March to May 2022 at Apenheul Primate Park. Similar to Gaia Zoo, each foraging individual was observed eight times apart from one, who was filmed seven times. Altogether, we obtained data on each individual for 77.9 ± 7.1 min (mean \pm standard deviation), that is, a total observation duration of 1714 min. The use of specific hands by the macaques was noted during feeding from the ground (Figure 1b,c) while assessing hand preference (see Section 2.3.1 for details).

Additionally, data on the dominance rank relationships of the groups were obtained from an ongoing long-term study. We conducted focal observations (238.66 ± 29.26 min/individual) independent of the current study, and dominance-submissive matrices were calculated with individuals as actors and recipients (behaviors included displace, fear grimace, lip smack, avoid, leave, mock leave, social present; see Kluiver et al., 2022, for details).

2.2.2 | Behavioral response to predators and novel objects

We conducted experiments to quantify the behavioral responses of the macaques toward potential predator models. A plush large cat/tiger (~100 cm, Supporting Information: Figure S1c) and a rubber snake (~150 cm, Supporting Information: Figure S1b) with markings similar to that of a reticulated python were used (cf. Kluiver et al., 2022). Although the tiger is not a natural predator of Barbary macaques, the cat model might have resembled a leopard to the Barbary macaques (Stein & Haysen, 2013); besides, the model might also have resembled a large genet, a small predator with a cat-like body, pale fur, black spots, and a ringed tail (Larivière & Calzada, 2001; Majolo et al., 2013). The other predator model resembled a reticulated python. Snakes elicit fear in primates, and Barbary macaques are known to respond to numerous species of snakes, even those that pose no serious threat (Isbell, 2006;

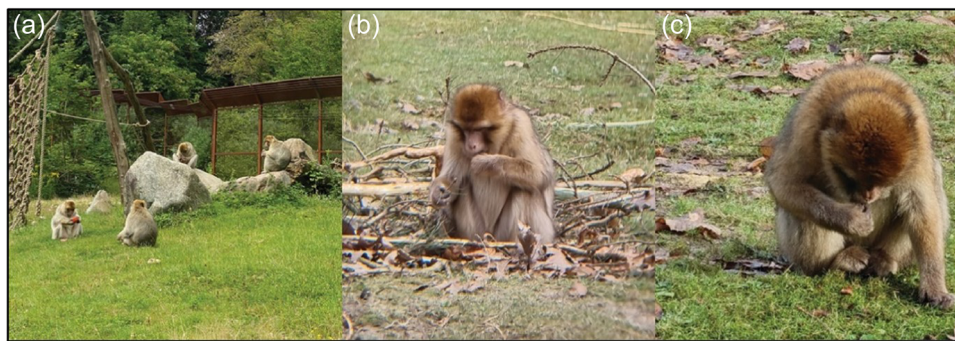


FIGURE 1 (a) Figure showing an example of the foraging behavior of multiple individuals within the group at Gaia Zoo; (b) example of left-hand unimanual foraging; (c) example of right-hand unimanual foraging.

Roberts et al., 2008). Even though the models used in this study might not completely match Barbary macaques' true natural predators, they still resemble those predators to some extent, thus, emphasizing the condition of predation. Besides, we used a nonpredator novel object (rubber ball, \varnothing 15 cm, Supporting Information: Figure S1a) to control for the potential effect of novelty associated with the predator models.

The predator models were placed on the ground, 1 m from the fence, but out of reach of the individuals. We placed the models in such a way that they were facing the macaques. The experiments commenced when a predator model became visible to the macaques either by lifting a blanket or moving it in sight. From uncovering or placing a model, we recorded the behavioral responses of the macaques for 30 min, after which the model was removed. The novel objects, on the other hand, were placed inside the enclosures of the macaques. The procedure did not differ from earlier. However, to avoid any potential monopolization, and to collect data efficiently from all individuals, we provided the macaques with three rubber balls, which were randomly placed in their outdoor enclosures. Therefore, the condition with novel objects differed to some extent in comparison to the predator models, as the macaques could interact physically with the objects. Nevertheless, the placement of the objects within the reach of the individuals ensured that they get adequate attention from the individuals. We recorded the behavioral responses of the individuals for 30 min in the novel object condition also. However, unlike predator models, the novel objects were only removed after an hour. All the experiments were recorded using a video camera mounted on a tripod.

We repeated each predator exposure and the novel object sessions once to obtain sufficient data on each individual. At Apenheul Primate Park, the first round of experiments was conducted in February 2022, when the park was closed to visitors. A second round occurred in May 2022, and experiments were conducted before visitors reached the enclosure. At Gaia Zoo, two rounds were carried out as well, but data from the first round on predator models could not be included due to the limited visibility of the macaques. The second round of experiments at Gaia Zoo was conducted at the end of September and beginning of October 2022. The order of the three conditions (i.e., novel object and the two predator models) was pseudorandomized, such that the two predator

sessions were not conducted consecutively. The tests were carried out in separate weeks in both zoos.

Not all individuals were visible during the different experimental conditions as they remained in parts of the enclosure out of sight of the camera. After removing the individuals observed for less than 5 min, on average, 22.1 ± 11.7 min of data were obtained per individual in sight ($n = 12$) during the tiger model. For the python model, it was 15.8 ± 7.7 min ($n = 15$). A total of 21 individuals were observed for at least 5 min in the nonpredator novel object condition. The average duration was found to be 16.13 ± 23.78 min per individual in the novel object condition. During all three conditions, we specifically looked at the focus and tension behavior of these individuals (see Section 2.3.2 for details).

2.3 | Data coding and preparation

The videos were coded in BORIS (v7.13.6) (Friard & Gamba, 2016) by two experimenters (E. S. J. D. and E. B.). To calculate the inter-rater reliability (IRR), both experimenters coded 160 min of data (translates to 8.6% of all collected data). IRR was found to be very high [ICC (3,k) = 1, $p < 0.001$].

2.3.1 | Hand preference

An extensive ethogram was followed, which consisted of foraging states, events of hand-use during foraging, and durational movements (Figure 1, Table 1).

For each individual, the total number of instances of feeding with the left hand and feeding with the right hand was calculated; handheld and bimanual feeding were excluded from our measure. In addition to this, the hand-use events were split up into foraging bouts. A new bout was said to start when either the durational movement changed between two instances of hand use or when there was a period (>10 s) without foraging between one event and the next (Regaiolli et al., 2018). We did not divide a continuous event into a series of events with a predetermined threshold. For each bout, the first occurrence of hand use was determined. The total number of

TABLE 1 Ethogram of foraging behaviors and their definitions.

Foraging (state event)	
Individual moves slowly while looking for food on the ground, or individual is sitting/standing while looking for food on the ground. Also includes individual consuming food.	
Symmetric	Individual is able to use either hand to feed, such as when standing on all fours or when sitting straight up.
Asymmetric	Individual is not able to use either hand to feed as the body posture limits the choice of hands, such as when lying on one side.
Hand-use (point event)	
Left hand	Individual uses the left hand to pick up a food item and put it in their mouth.
Right hand	Individual uses the right hand to pick up a food item and put it in their mouth.
Bimanual feed	Individual uses both hands to pick up a food item and transport it into the mouth.
Left handheld	Individual put a food item they were already holding in their mouth, using the left hand to transport it to the mouth.
Right handheld	Individual put a food item they were already holding in their mouth, using the right hand to transport it to the mouth.
Bimanual handheld	Individual put a food item they were already holding in their mouth, using both hands to transport it to the mouth.
Durational movement (state event)	
Travel; bipedal walk; stand; bipedal stand; climb up/down; hang; sit; lie down (see Kluiver et al., 2022, for details).	

TABLE 2 Ethogram of tension and focus behavior and their definitions.

Tension	
Avoid conflict	Individual focuses on a conflict without approaching it and moves away in the opposite direction.
Body shake	Individual rapidly turns their whole body in at least two different directions.
Head turn	While traveling or standing, the individual turns the head in a quick, jerky movement followed by a change of direction.
Scratch	Individual uses their finger, hand, or foot to rake across their own skin.
Vigilance	Individual has a tense body posture and looks around with hasty movements of head and/or eyes without an imminent reason.
Yawn	Individual opens their mouth wide and inhales intensely, which can be seen by the expansion of the chest.
Focus	
Attention	Individual looks toward a specific situation, individual or object with a clear focus without moving their head and eyes and with a frozen body posture.
Look around	Individual moves their head in at least three different directions without a clear focus.

bouts starting with a left-, or right-hand unimanual feeding was calculated for each individual, omitting bouts starting with handheld or bimanual feeding.

As a measure of hand preference, HI scores were calculated based on the instances and the bouts (Regaioli et al., 2018; Schmitt et al., 2008). The HI score ranged between -1 and 1, with negative scores relating to a left-side bias and positive scores to a right-side bias. We calculated the HI score for each individual in the following way:

$$HI = \frac{R - L}{R + L},$$

[*R* is the number of instances or bouts attributed to the right hand, and *L* is the number attributed to the left hand (Canteloup et al., 2013)].

2.3.2 | Behavioral responses to predators and novel objects

The response of individuals to the presence of a predator model was determined by the frequency or occurrence of tension and focus behavior (Table 2). It is important to note that we did not include vocalizations even though the presence of predators is known to elicit alarm calls by nonhuman primates in general. The observed frequency of vocalizations was very low and only restricted to a few individuals in one of the groups. Additionally, it was challenging to correctly identify the individuals who were vocalizing due to them being out of sight. Therefore, we avoided including a negligible and potentially skewed measure (of vocalization) in our ethogram. The tension and focus behavior displayed by an individual were combined to create a single measure of the behavioral response as both

categories of behavior can be classified as antipredator responses, and there were few occurrences per category, per individual, and per predator type. A total of 797 occurrences of focus and tension behavior were noted. As mentioned earlier, the macaques were not equally visible for the entire length of the experiments; therefore, we corrected them for the time out of sight. We calculated the frequency of these behaviors observed per minute per individual. The response to the tiger model was determined separately from that of the python model. Similar to the predator models, we calculated the frequency of tension and focused behavior during the novel object condition.

2.4 | Statistical analyses

2.4.1 | Hand preference

The preferred hand for unimanual foraging was determined for each individual. If the HI score based on instances had the same sign as the HI score based on bouts, an individual was labeled as left or right-handed, or else they were labeled as ambiguous (Hopkins, 2013). Next, following the recommendations of Hopkins (2013), a possible correlation between the HI score based on instances and the HI score based on bouts was investigated by calculating Pearson's correlation coefficient. If a strong and positive correlation were found, all further analyses would be based on the HI calculated for instances rather than bouts (Hopkins, 2013; Meguerditchian et al., 2010). The possible effect of age and sex on HI was tested using a linear mixed effect model (LMM) with the *lmerTest* package of R (Kuznetsova et al., 2017). We added group as a random effect in the model. Finally, the possibility of a group-level hand preference was investigated using the Kolmogorov–Smirnov test, which reports whether the HI scores differ from a normal distribution (Schmitt et al., 2008).

We quantified the dominance rank relationships using a Bayesian Elo-rating framework with the R-package *EloSteepness* (Neumann & Fischer, 2023). The Bayesian approach is more robust and precise than the conventionally used David's scores-based steepness approach.

2.4.2 | Hand preference as a predictor of response to predators

We first compared the combined frequency of focus and tension behavior between the control, that is, the nonpredator novel object and test, that is, the two predator conditions. This step was essential to control for the potential effect of novelty which might be associated with the models presented. We conducted an LMM where tension and focus behavior (combined frequency/min) were included as the response variable, conditions (categorical: novel object/snake model/tiger model) as the fixed effect, and the group as a random effect. The null model included everything except for the fixed effect.

We used an LMM to investigate the relationship between hand preference and the behavioral response to predators. Only individuals observed for at least 5 min for a type of predator model were included. The frequency of tension and focus behavior was scaled by calculating z scores. We included this corrected combined frequency as the response variable, HI scores and predator types as fixed effects, sex, age, and dominance ranks as control variables, and individuals nested within groups as a random effect. We first checked the interaction effects between the independent variables, in case of no observed significance, the main effects were examined.

To examine the explanatory value of our model, we conducted null versus full model comparisons using likelihood ratio tests ("lrtest" function) from the R package *lmTest* (Zeileis & Hothorn, 2002). Additionally, model diagnostics (normality and dispersion) were checked using the *DHARMA* package of R (Hartig, 2022). The collinearity of the predictors was checked using the package *performance* (Lüdtke et al., 2020). Here, we only report models that differed significantly from the null model (comparisons and model diagnostics are presented in Supporting Information: Table S3 and S4). We performed all analyses in R (version 4.1.2; R Core Team, 2022) using the RStudio interface (version 2022.07.01, Build 554).

3 | RESULTS

3.1 | Hand preference

By comparing the HI scores based on bouts and instances of hand use, of the 22 individuals, 9 were labeled as left-handed, 11 as right-handed, and 2 were ambiguous for hand preference during unimanual foraging (Figure 2). The HI calculated based on bouts was strongly positively correlated with the HI based on instances (Pearson's product-moment correlation: $r = 0.91$, 95% confidence interval, CI [0.79, 0.99], $p < 0.001$). Therefore, in all further analyses, the HI based on instances rather than bouts were used (cf. Hopkins, 2013; Meguerditchian et al., 2010). All individuals were included in further analyses, including those labeled ambiguous based on their HI for foraging bouts. No group-level hand preference was found for the HI based on instances (Kolmogorov–Smirnov test: $D = 0.25$, $p = 0.11$). Using an LMM, the effect of age and sex on HI was tested while controlling for group identity. Age had no impact on the HI [LMM: $t(19) = 0.53$, $p = 0.60$], while for sex, a nonsignificant trend was found [LMM: $t(19) = 1.80$, $p = 0.09$] that showed that males might have a higher HI than females (effect = 0.38 ± 0.21 ; see Figure 2).

3.2 | Hand preference and the behavioral response to novel object and predators

We found that the individuals displayed a heightened frequency of tension and focus behavior during the predator exposure as compared to the nonpredator novel object condition (likelihood ratio test: $\chi^2 = 23.166$, $p < 0.0001$, Figure 3). The frequency of combined

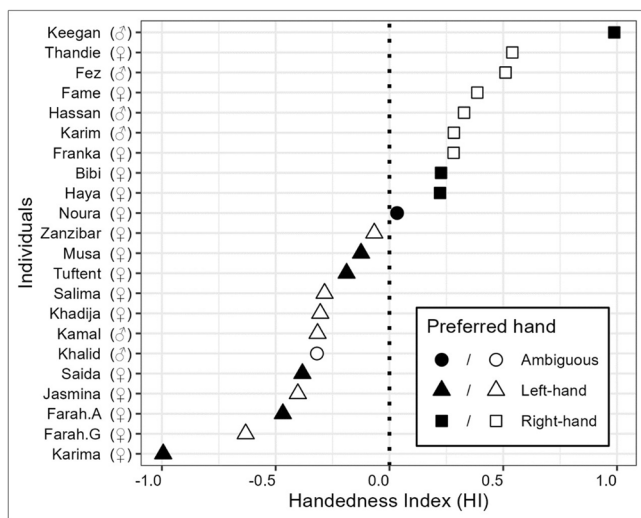


FIGURE 2 Scatterplot of the handedness index scores of each individual. The different shapes indicate the preferred hand of the individuals based on the labeling criteria. Filled shapes indicate individuals from Apenheul, and outlined shapes indicate individuals from Gaia Zoo. The dotted vertical line indicates HI = 0. To the left of this line, the HI indicates a left-hand bias and to the right, a right-hand bias. HI, handedness index.

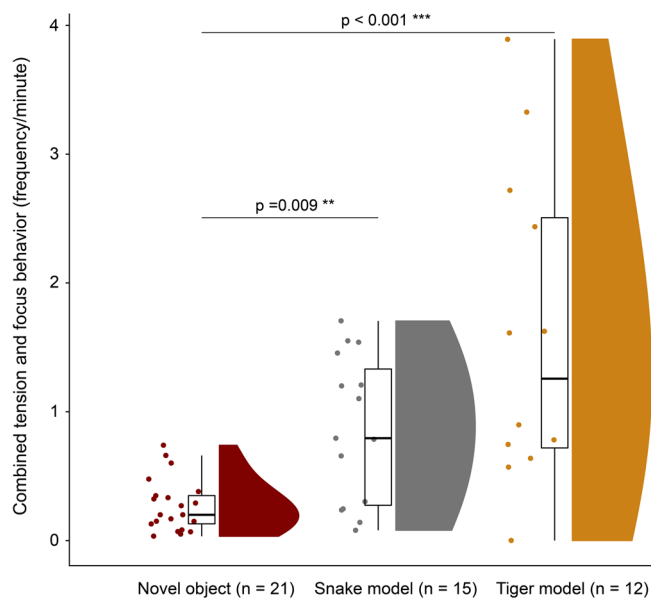


FIGURE 3 The combined frequency of tension and focus behavior displayed by the individuals in the nonpredator novel object, and the two predator conditions. Half-violin plots indicate the distribution of the data. Solid dots indicate the raw values of the data from the individuals, that is, each solid dot represents an individual (novel object, $n = 21$; snake model, $n = 15$; tiger model, $n = 12$). The different sample sizes indicate our strict consideration of individuals who were observed for at least 5 min in a particular condition. The boxes illustrate the interquartile range, horizontal bars inside the boxes indicate median values, and whiskers indicate the range of the data.

tension and focus was found to be higher when they were exposed to the snake (mean frequency \pm SD = 0.86 ± 0.57 ; LMM: $z = 2.595$, $p = 0.009$, Figure 3) and the tiger model (1.60 ± 1.23 ; LMM: $z = 5.432$, $p < 0.001$, Figure 3) than when exposed to the novel object (0.27 ± 0.20 , Figure 3). These results suggest that the two predator models indeed elicited an antipredator response, and the tension and focus behaviors displayed were not due to the (potential) novelty associated with the predator models.

In an initial model, we found no significant effect of the interaction between age and dominance rank; subsequently, the main effects were investigated. We dropped dominance rank as a control variable from the best-fitted model during selection based on the Akaike information criterion (AIC) values (Supporting Information: Table S2). We found a significant effect of HI on the behavioral responses to predator models (LMM: $t = -3.436$, $p = 0.002$; Supporting Information: Table S2). Individuals with a stronger left-hand preference elicited more frequent tension and focus behavior than right-handed individuals (Figure 4). Similar to HI, we also found an effect of the predator type ($t = -2.796$, $p = 0.01$; Supporting Information: Table S2). While the python model did affect individuals, the tiger model particularly had a stronger influence in eliciting

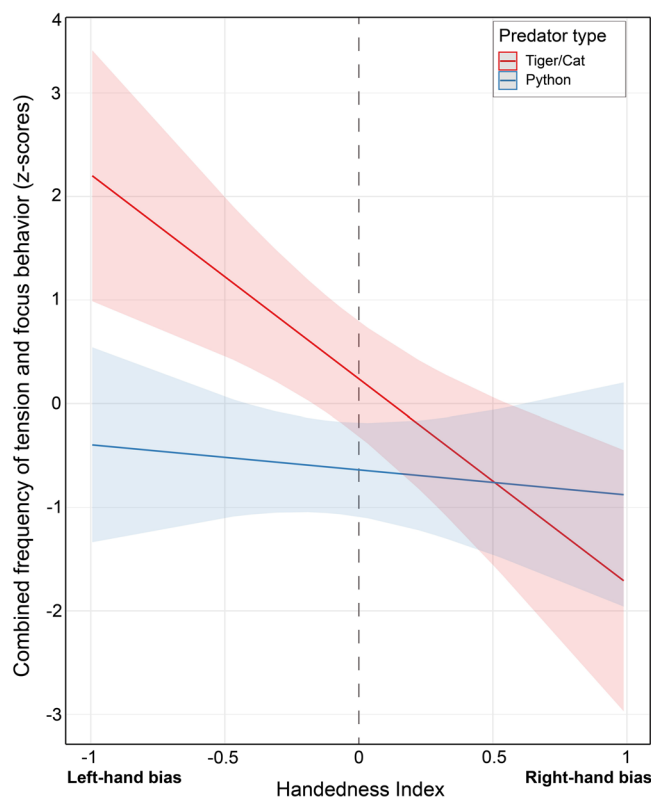


FIGURE 4 The combined frequency of tension and focus behavior (z scores) and its relation to an interaction between handedness index and predator type or context. The solid red and blue lines indicate the trend of the two different predator types (red = tiger, blue = python) surrounded by 95% confidence intervals. The left and right sides of the vertical dashed line denote left and right-hand preferences, respectively.

tension and focus behavior by the individuals (Figure 4). Furthermore, an interaction effect between HI and the type of predator model was observed (LMM: $t = 2.521$, $p = 0.019$; Supporting Information: Table S2). An in-depth analysis of the interaction effect revealed that the original main effect in which individuals with a stronger left-hand preference (i.e., $HI < 0$) elicited more frequent focus and tension behavior, was significantly stronger in response to the tiger than to the python model (t ratio = 2.631, $p = 0.02$; Figure 4, Supporting Information: Table S2). We did not find any effect of age ($t = 1.070$, $p = 0.29$, Supporting Information: Table S2). Finally, a nonsignificant trend was noticed for the effect of sex on the behavioral response to predators ($t = 1.918$, $p = 0.06$, Supporting Information: Table S2), with males exhibiting more frequent tension and focus behavior than females.

4 | DISCUSSION

This study examined the relationship between hand preference and behavioral responses of Barbary macaques to potential predation threats. Individual hand preference for unimanual reaching was identified in 20 out of 22 individuals, with no observed group-level bias. Individuals clearly displayed antipredator behavior in response to the two predator models, supported by the very few occurrences of tension and focus behavior during the novel object condition. Individuals did differ, however, in their behavioral responses to potential predators, which were predicted by hand preference, predator type, and their interactions. In line with our hypothesis, the hand preference predicted the response to predators; individuals with a stronger left-hand than right-hand bias for unimanual foraging, in general, displayed more frequent tension and focus behavior. The tiger model particularly had a stronger effect on the individuals than the python. Furthermore, an interaction effect between hand preference and predator type implied that the tiger, compared to the python model, had a more substantial influence on individuals with a left-hand than a right-hand bias.

4.1 | Hand preference

Hand preference during unimanual reaching in Barbary macaques was hypothesized to be an estimator of hemispheric dominance. As such, hand preference for unimanual feeding was expected at an individual but not group level. In line with the predictions, no group-level hand preference was found in this study. Previous studies on Barbary macaque hand preference have also reported the absence of group-level lateralization for unimanual reaching (Baldachini et al., 2021). Here we found evidence of unambiguous hand preference for unimanual foraging in 20 of the 22 individuals tested. This translates to 91% of the sample, while earlier studies on Barbary macaques reported 35%, 47%, and 75% of individuals to be significantly lateralized (Baldachini et al., 2021; Regaiolli et al., 2018; Schmitt et al., 2008). The higher proportion of lateralized individuals

reported here compared to earlier research may be attributed to methodological differences rather than differences among the investigated populations. Overall, the presence of individual but not group-level lateralization for unimanual foraging that we observed aligned with the hypothesis that unimanual reaching is an estimator of hemispheric dominance in Barbary macaques.

4.2 | Predator type and hand preference as predictors of behavioral response

Both the predator models used in this study elicited antipredator behavior, substantiating their ecological relevance as threats. However, the intensity of effects on the individuals varied with the type of predator model; overall, the tiger model elicited a stronger response than the snake model. This observation was in line with previous studies that showed varying antipredator responses to different predators (LaBarge et al., 2021; Lemasson et al., 2009). Barbary macaques were found to display antipredator behavior even to play-backs of dog alarm calls, whereas snake alarm calls failed to elicit a response (Fischer & Hammerschmidt, 2001). Similarly, the tiger model may have posed a bigger immediate threat than the snake in the current study. Consequently, the tiger model caused a higher frequency of tension and focus behavior and, therefore, a stronger behavioral response by the individuals. These results highlight the importance of behavioral variation with regard to context-specificities, even with a single ecological event of predation.

In addition, independent of the type of predator model, individuals with a stronger left-hand preference displayed a higher frequency of tension and focus behavior than individuals with a stronger right-hand preference. This was in line with the expectation that left-handed individuals would be more reactive to (potential) predators than right-handed individuals, as the right hemisphere is specialized for predator detection and spontaneous behavioral responses (Rogers, 2002, 2010). Finally, a significant interaction effect between HI and predator type was observed, where individuals with a left-hand preference showed a more intense reaction to the tiger than to the snake model. The tiger model was indeed perceived as a greater threat than the snake and coupled with this, hand preference predicted the behavioral responses of Barbary macaques. This suggests an elevated level of reactivity in left-handed individuals while dealing with varying intensities of threat. Although these results indicate that the neural mechanisms may potentially differ when processing predation threats in left- and right-handed individuals, it is at the same time challenging to ascertain the specific underlying neural mechanisms noninvasively. Consistent with our findings, previous research on Geoffrey's marmosets found that left-handed individuals exhibit longer freezing behavior than right-handed individuals in response to hawk calls (Braccini & Caine, 2009). However, right-handed common marmosets are known to produce frequent mobbing calls and perform more head cocking and parallax movements than left-handed marmosets when confronted with a threat (Gordon & Rogers, 2010). This could contradict the pattern

found in Geoffrey marmosets, yet Gordon and Rogers (2010) argued that these right-handed individuals could be more proactive, as they were explorative toward threats instead of showing signs of withdrawal. Our parameters, that is, the focus and tension, can be seen as a measure of reactivity, withdrawal, or anxiety rather than a proactive investigative response. This is primarily due to the inclusion of behaviors—scratching and yawning, commonly grouped under self-directed behavior and used as indicators of anxiety or stress (Castles et al., 1999; Castles & Whiten, 2010; Maestriperi et al., 1992). As such, the relationship among HI, predator type, and behavioral response in Barbary macaques can be interpreted as left-handed individuals being more reactive than right-handed individuals, in line with the lateralized brain function and results of earlier studies.

Predator attacks are highly stressful events (Cheney & Seyfarth, 2009), and the response to the presentation of a predator model can thus also be indicative of fear and anxiety (Barros et al., 2008; Carter et al., 2012). While the right hemisphere is dominant for predator detection and spontaneous behavioral responses, it is also involved in the expression of negative emotions such as fear and stress response (Ocklenburg et al., 2016; Rogers, 2002, 2010). Left-handed individuals, considered more reactive than right-handed individuals, could thus be expected to display both stronger behavioral and stress responses to such conditions. However, the relationship between behavioral syndromes, such as reactive and proactive coping styles, along with (neuroendocrine) stress reactivity, are hard to disentangle (Koolhaas et al., 2010; Rogers, 2018). Reactive individuals may show the highest hypothalamic–pituitary–adrenal (HPA) axis response, but this varies across species. For example, while there is a positive correlation between right frontal cortex activity and plasma cortisol levels in rhesus macaques (Kalin et al., 1998), a general trend of these levels being lowest in left-handed rhesus macaques is also evident (Westergaard et al., 2003, 2004). Furthermore, for some dimensions, stress reactivity is independent of whether an individual is considered to have a more reactive or proactive behavioral syndrome (Koolhaas et al., 2010).

Research into the potential link between hand preference and stress response has hitherto generated mixed results. In common marmosets, left-handed individuals have more prolonged elevated cortisol levels, possibly indicating that they are more reactive to stress than right-handed individuals (Rogers, 2009). However, a different study reported that the basal cortisol of left-handed common marmosets was lower than that of right-handed individuals and that there is no difference in reactivity between left- and right-handed individuals (Vaughan et al., 2019). In bonobos (*Pan paniscus*), no relationship between handedness and reactivity was found when investigating self-directed behavior and performance in cognitive tasks (Laméris et al., 2022). Regardless of whether the tension and focus behavior in response to predator models are solely indicative of the behavioral response or an affective one, our findings align with the lateralized brain function, that is, generated evidence of individuals with a left-hand preference being reactive. Nonetheless, to distinguish the behavioral syndrome of left- and right-handed

Barbary macaques from their stress reactivity, it would be valuable to conduct studies using both behavioral and physiological measures.

4.3 | Potential influence of sex on the behavioral response to predators

A nonsignificant trend was found, indicating that males may have a higher frequency of tension and focus behavior in response to the predators than females. Such response to predators is sex-specific in several primate species, such as Campbell's monkeys (Lemasson et al., 2009), white-fronted capuchins (*Cebus albifrons*), and tufted capuchins (*C. apella*) (Van Schaik & Van Noordwijk, 1989). In general, males show more vigilance and engage in riskier antipredator behavior than females, such as in multiple species of *Cercopithecus* monkeys (Gautier-Hion et al., 1983; Zuberbühler et al., 1997). Thus, the observed trend that suggests sex influenced the behavioral response to predators in Barbary macaques was in line with the general pattern of sexual differences in antipredator behavior in primates. Nevertheless, our study suffered from a low number of males, thus calling for caution during interpretation, and future studies with more males are needed.

4.4 | Potential shortcomings

Despite testing twice, only one round of predator exposure experiments at Gaia Zoo could be included. As a result of this and other limitations to the data, 27 observations of only 17 different individuals could be included in the final model that related handedness to the predator responses, while the full sample consisted of 22 individuals. It would thus be valuable to repeat this study in a larger sample of (Barbary) macaques. It could also be interesting to investigate the link between sex and response to predators in a larger sample of Barbary macaques since only five males were present in this study groups.

Only tension and focus behaviors were used to determine the response to predators, but different predators may elicit a range of antipredator behavior (Lemasson et al., 2009). Thus, in-depth information on antipredator behavior should be collected in future studies to determine the predictive ability of hand preference.

We conducted a group-level experiment; therefore, the individual responses might have been influenced by the presence and/or reaction of group members. Left-handed individuals are suggested to be less responsive to and of influence on their social group than right-handed individuals (Gordon & Rogers, 2010). Nonetheless, a group-level experiment best resembles how predators are detected and responded to under wild or semiwild circumstances, and as such, also mimics best the actual selection pressures during evolution. Therefore, this was an ecologically valid context to investigate the effect of lateralization of hand preference on individual differences in behavior. Finally, the two predator models used in the current study might not have represented the true predators of Barbary macaques.

However, the resemblance of these predator models to their true predators, and the addition of a nonpredator novel object condition assisted in drawing reliable inferences regarding the behavioral responses.

5 | CONCLUSIONS

Hand preference was a reliable predictor of the frequency of tension and focus behavior of Barbary macaques in the context of predation. The extent of left-hand preference was positively related to the frequency of focus and tension behaviors. The direction of this effect was in line with the right-hemispheric specialization for predator detection, spontaneous behavioral responses, and negative emotions. As such, our results were consistent with the lateralized brain function hypothesis and suggested that cerebral lateralization could be one of the neural mechanisms underlying individual differences in context-specific behaviors. Furthermore, an interaction between hand preference and the predator context translates to (i) a higher reactivity of left- than right-handed individuals and (ii) potentially different neural information processing mechanisms. As predator exposure is just one of many ecologically relevant contexts, lateralization may also result in interindividual variation in other context-specific behaviors, both in Barbary macaques and other nonhuman primates. Therefore, future research on other nonhuman primates and other ecologically relevant contexts building onto the current framework could reveal clues about the evolution of brain lateralization and potentially related behavioral predispositions.

AUTHOR CONTRIBUTIONS

Eva S. J. Dijk: Conceptualization (supporting); data curation (equal); formal analysis (supporting); investigation (equal); methodology (lead); writing—original draft (lead). **Debottam Bhattacharjee:** Conceptualization (equal); formal analysis (lead); funding acquisition (lead); methodology (equal); supervision (lead); validation (equal); writing—review and editing (equal). **Elena Belli:** Formal analysis (supporting); investigation (equal). **Jorg J. M. Massen:** Conceptualization (supporting); funding acquisition (supporting); methodology (equal); project administration (equal); resources (lead); supervision (supporting); validation (lead); writing—review and editing (equal).

ACKNOWLEDGMENTS

We thank Lisette van den Berg for welcoming us to the Apenheul primate park. We are thankful to Emile F. Prins and Thomas Remmits for allowing and supporting the studies at Gaia Zoo. We sincerely thank all the caretakers and zookeepers from the Apenheul and Gaia Zoo for their help during the study. This research was funded by European Union's Horizon 2020 research and innovation program, Marie Skłodowska-Curie Actions, grant number H2020-MSCA-IF-2019-893016, awarded to D. B.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.



DATA AVAILABILITY STATEMENT

The data presented in the study are available in the supplementary files. Supplementary File [S1](#): Datasets. Supplementary File [S2](#): R-scripts.

ETHICS STATEMENT

This study was noninvasive, requiring no ethical approval according to the European Directive 2010/63. Permission to conduct research was obtained from the Apenheul Primate Park and Gaia Zoo, and approval letters have been provided. Internal staff members from the approval committee closely monitored the experiments with predator models. The experimenters followed all internal protocols and guidelines of the zoos while working with the nonhuman primates. The research was consistent with the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

ORCID

Debottam Bhattacharjee  <https://orcid.org/0000-0002-4555-7983>
Elena Belli  <http://orcid.org/0000-0001-5945-6529>

REFERENCES

- Anderson, C. M. (1986). Predation and primate evolution. *Primates*, 27(1), 15–39. <https://doi.org/10.1007/BF02382520>
- Baldachini, M., Regaiolli, B., Llorente, M., Riba, D., & Spiezio, C. (2021). The influence of target animacy and social rank on hand preference in Barbary macaques (*Macaca sylvanus*). *International Journal of Primatology*, 42(2), 155–170. <https://doi.org/10.1007/s10764-020-00193-0>
- Barros, M., Maior, R. S., Huston, J. P., & Tomaz, C. (2008). Predatory stress as an experimental strategy to measure fear and anxiety-related behaviors in non-human primates. *Reviews in the Neurosciences*, 19(2–3), 157–169. <https://doi.org/10.1515/REVNEURO.2008.19.2-3.157>
- Bautista, J. (2019). Golden eagles (*Aquila chrysaetos*) as potential predators of barbary macaques (*Macaca sylvanus*) in northern Morocco: Evidences of predation. *Go-South Bulletin*, 15, 181–188.
- Bisazza, A., Rogers, L. J., & Vallortigara, G. (1998). The origins of cerebral asymmetry: A review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neuroscience and Biobehavioral Reviews*, 22(3), 411–426. [https://doi.org/10.1016/S0149-7634\(97\)00050-X](https://doi.org/10.1016/S0149-7634(97)00050-X)
- Braccini, S. N., & Caine, N. G. (2009). Hand preference predicts reactions to novel foods and predators in marmosets (*Callithrix geoffroyi*). *Journal of Comparative Psychology*, 123(1), 18–25.
- Cameron, R., & Rogers, L. J. (1999). Hand preference of the common marmoset (*Callithrix jacchus*): Problem solving and responses in a novel setting. *Journal of Comparative Psychology*, 113(2), 149–157. <https://doi.org/10.1037/0735-7036.113.2.149>
- Canteloup, C., Vauclair, J., & Meunier, H. (2013). Hand preferences on unimanual and bimanual tasks in Tonkean macaques (*Macaca tonkeana*): Handedness in Tonkean macaques. *American Journal of Physical Anthropology*, 152(3), 315–321. <https://doi.org/10.1002/ajpa.22342>
- Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlshaw, G. (2012). How not to measure boldness: Novel object and antipredator responses are not the same in wild baboons. *Animal Behaviour*, 84(3), 603–609. <https://doi.org/10.1016/j.anbehav.2012.06.015>
- Caspar, K. R., Pallsadies, F., Mader, L., Sartorelli, H., & Begall, S. (2022). The evolution and biological correlates of hand preferences in anthropoid primates. *ELife*, 11. CLOCKSS. <https://doi.org/10.7554/elife.77875>

- Castles, D. L., Whiten, A., & Aureli, F. (1999). Social anxiety, relationships and self-directed behaviour among wild female olive baboons. *Animal Behaviour*, 58(6), 1207–1215. <https://doi.org/10.1006/anbe.1999.1250>
- Castles, D. L., & Whiten, A. (2010). Post-conflict Behaviour of Wild Olive Baboons. II. Stress and Self-directed Behaviour. *Ethology*, 104(2), 148–160. <https://doi.org/10.1111/j.1439-0310.1998.tb00058.x>
- Cheney, D. L., & Seyfarth, R. M. (2009). Chapter 1: Stress and coping mechanisms in female primates. In H. J. Brockmann, T. J. Roper, M. Naguib, K. E. Wynne-Edwards, J. C. Mitani, & Leigh W. Simmons (Eds.), *Advances in the study of behavior* (Vol. 39, pp. 1–44). Academic Press. [https://doi.org/10.1016/S0065-3454\(09\)39001-4](https://doi.org/10.1016/S0065-3454(09)39001-4)
- Désiré, L., Boissy, A., & Veissier, I. (2002). Emotions in farm animals: A new approach to animal welfare in applied ethology. *Behavioural Processes*, 60(2), 165–180. [https://doi.org/10.1016/S0376-6357\(02\)00081-5](https://doi.org/10.1016/S0376-6357(02)00081-5)
- Fernández-Lázaro, G., Latorre, R., Alonso-García, E., & Barja Núñez, I. (2019). Nonhuman primate welfare: Can there be a relationship between personality, lateralization and physiological indicators. *Behavioural Processes*, 166, 103897. <https://doi.org/10.1016/j.beproc.2019.103897>
- Fischer, J., & Hammerschmidt, K. (2001). Functional referents and acoustic similarity revisited: The case of Barbary macaque alarm calls. *Animal Cognition*, 4(1), 29–35. <https://doi.org/10.1007/s100710100093>
- Fischer, J., & Hammerschmidt, K. (2002). An overview of the Barbary macaque, *Macaca sylvanus*, vocal repertoire. *Folia Primatologica*, 73(1), 32–45. <https://doi.org/10.1159/000060417>
- Fooden, J. (2007). Systematic review of the Barbary macaque, *Macaca sylvanus* (Linnaeus, 1758). *Fieldiana Zoology*, 113(113), 1–60. [https://doi.org/10.3158/0015-0754\(2007\)113\[1:SROTBM\]2.0.CO;2](https://doi.org/10.3158/0015-0754(2007)113[1:SROTBM]2.0.CO;2)
- Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7(11), 1325–1330. <https://doi.org/10.1111/2041-210X.12584>
- Fu, W., Xu, J., Wang, X., Li, Y., He, S., Wang, C., Ren, Y., Yang, B., Wu, T., Wang, Y., & Li, B. (2022). Consistency of limb preference across unimanual feeding, bipedal locomotion, and social grooming in golden snub-nosed monkeys (*Rhinopithecus roxellana*). *Laterality*, 28(1), 32–47. <https://doi.org/10.1080/1357650X.2022.2141251>
- Gautier-Hion, A., Quris, R., & Gautier, J.-P. (1983). Monospecific vs polyspecific life: A comparative study of foraging and antipredatory tactics in a community of *Cercopithecus* monkeys. *Behavioral Ecology and Sociobiology*, 12(4), 325–335. <https://doi.org/10.1007/BF00302901>
- Gordon, D. J., & Rogers, L. J. (2010). Differences in social and vocal behavior between left- and right-handed common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology*, 124(4), 402–411. <https://doi.org/10.1037/a0019736>
- Gordon, D. J., & Rogers, L. J. (2015). Cognitive bias, hand preference and welfare of common marmosets. *Behavioural Brain Research*, 287, 100–108. <https://doi.org/10.1016/j.bbr.2015.03.037>
- Hartig, F. (2022). DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. <https://CRAN.R-project.org/package=DHARMA>
- Hook, M. A., & Rogers, L. J. (2000). Development of hand preferences in marmosets (*Callithrix jacchus*) and effects of aging. *Journal of Comparative Psychology*, 114(3), 263–271.
- Hopkins, W. D. (2013). Independence of data points in the measurement of hand preferences in primates: Statistical problem or urban myth? *American Journal of Physical Anthropology*, 151(1), 151–157. <https://doi.org/10.1002/ajpa.22248>
- Hopkins, W. D., & Bennett, A. J. (1994). Handedness and approach-avoidance behavior in chimpanzees (*Pan*). *Journal of Experimental Psychology: Animal Behavior Processes*, 20(4), 413–418. <https://doi.org/10.1037/0097-7403.20.4.413>
- Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, 51(1), 1–35. <https://doi.org/10.1016/j.jhevol.2005.12.012>
- Kalin, N. H., Larson, C., Shelton, S. E., & Davidson, R. J. (1998). Asymmetric frontal brain activity, cortisol, and behavior associated with fearful temperament in rhesus monkeys. *Behavioral Neuroscience*, 112(2), 286–292. <https://doi.org/10.1037/0735-7044.112.2.286>
- Kappeler, P. M., & van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology*, 23(4), 707–740. <https://doi.org/10.1023/A:1015520830318>
- Kluiver, C. E., de Jong, J. A., Massen, J. J. M., & Bhattacharjee, D. (2022). Personality as a predictor of time-activity budget in lion-tailed macaques (*Macaca silenus*). *Animals*, 12(12), 1495. <https://doi.org/10.3390/ani12121495>
- Koolhaas, J. M., de Boer, S. F., Coppens, C. M., & Buwalda, B. (2010). Neuroendocrinology of coping styles: Towards understanding the biology of individual variation. *Frontiers in Neuroendocrinology*, 31(3), 307–321. <https://doi.org/10.1016/j.yfrne.2010.04.001>
- Kuběňová, B., Lhota, S., Tomanová, V., Blažek, V., & Konečná, M. (2022). Lion-tailed macaques show a stable direction and reinforcement of hand preference in simple reaching tasks over several years. *Journal of Vertebrate Biology*, 71(21076). <https://doi.org/10.25225/jvb.21076>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82(13), 1–26. <https://doi.org/10.18637/jss.v082.i13>
- LaBarge, L. R., Allan, A. T. L., Berman, C. M., Hill, R. A., & Margulis, S. W. (2021). Extent of threat detection depends on predator type and behavioral context in wild samango monkey groups. *Behavioral Ecology and Sociobiology*, 75, 13.
- Laméris, D. W., Verspeek, J., Salas, M., Staes, N., Torfs, J., Eens, M., & Stevens, J. (2022). Evaluating self-directed behaviours and their association with emotional arousal across two cognitive tasks in bonobos (*Pan paniscus*). *Animals*, 12, 21. <https://doi.org/10.3390/ani121213002>
- Larivière, S., & Calzada, J. (2001). *Genetta genetta*. *Mammalian Species*, 680(680), 1–6. [https://doi.org/10.1644/1545-1410\(2001\)680%3C0001:GG%3E2.0.CO;2](https://doi.org/10.1644/1545-1410(2001)680%3C0001:GG%3E2.0.CO;2)
- Leliveld, L. M. C., Langbein, J., & Puppe, B. (2013). The emergence of emotional lateralization: Evidence in non-human vertebrates and implications for farm animals. *Applied Animal Behaviour Science*, 145(1), 1–14. <https://doi.org/10.1016/j.applanim.2013.02.002>
- Lemasson, A., Ouattara, K., & Zuberbühler, K. (2009). Anti-predator strategies of free-ranging Campbell's monkeys. *Behaviour*, 146(12), 1687–1708. <https://doi.org/10.1163/000579509X12469533725585>
- Lüdecke, D., Makowski, D., Waggoner, P., & Patil, I. (2020). Performance: Assessment of regression models performance. R Package Version 0.4, 5.
- Maestriperì, D., Schino, G., Aureli, F., & Troisi, A. (1992). A modest proposal: Displacement activities as an indicator of emotions in primates. *Animal Behaviour*, 44(5), 967–979. [https://doi.org/10.1016/S0003-3472\(05\)80592-5](https://doi.org/10.1016/S0003-3472(05)80592-5)
- Majolo, B., McFarland, R., Young, C., & Qarro, M. (2013). The effect of climatic factors on the activity budgets of Barbary macaques (*Macaca sylvanus*). *International Journal of Primatology*, 34(3), 500–514. <https://doi.org/10.1007/s10764-013-9678-8>
- Masilkova, M., Šlipogor, V., Lima Marques Silva, G. H., Hadová, M., Lhota, S., Bugnyar, T., & Konečná, M. (2022). Age, but not hand preference, is related to personality traits in common marmosets (*Callithrix jacchus*). *Royal Society Open Science*, 9(10), 220797. <https://doi.org/10.1098/rsos.220797>
- McManus, I. C. (2009). The history and geography of human handedness. In E. C. Sommer, & R. Kahn (Eds.), *Language lateralisation and psychosis* (pp. 37–57). Cambridge University Press.

- Meguerditchian, A., Calcutt, S. E., Lonsdorf, E. V., Ross, S. R., & Hopkins, W. D. (2010). Brief communication: Captive gorillas are right-handed for bimanual feeding. *American Journal of Physical Anthropology*, 141(4), 638–645. <https://doi.org/10.1002/ajpa.21244>
- Meguerditchian, A., Vauclair, J., & Hopkins, W. D. (2013). On the origins of human handedness and language: A comparative review of hand preferences for bimanual coordinated actions and gestural communication in nonhuman primates. *Developmental Psychobiology*, 55(6), 637–650. <https://doi.org/10.1002/dev.21150>
- Nelson, E. L. (2022). Insights into human and nonhuman primate handedness from measuring both hands. *Current Directions in Psychological Science*, 31(2), 154–161. <https://doi.org/10.1177/09637214211062876>
- Neumann, C., & Fischer, J. (2023). Extending Bayesian Elo-rating to quantify the steepness of dominance hierarchies. *Methods in Ecology and Evolution*, 14(2), 669–682. <https://doi.org/10.1111/2041-210X.14021>
- Ocklenburg, S., Korte, S. M., Peterburs, J., Wolf, O. T., & Güntürkün, O. (2016). Stress and laterality—The comparative perspective. *Physiology & Behavior*, 164, 321–329. Scopus. <https://doi.org/10.1016/j.physbeh.2016.06.020>
- Öhman, A., & Mineka, S. (2003). The malicious serpent: Snakes as a prototypical stimulus for an evolved module of fear. *Current Directions in Psychological Science*, 12(1), 5–9. <https://doi.org/10.1111/1467-8721.01211>
- R Core Team. (2022). A language and environment for statistical computing. <http://www.R-project>
- Raymond, M., & Pontier, D. (2004). Is there geographical variation in human handedness? *Laterality: Asymmetries of Body, Brain and Cognition*, 9(1), 35–51. <https://doi.org/10.1080/13576500244000274>
- Regaiolli, B., Spiezio, C., & Hopkins, W. D. (2018). Hand preference on unimanual and bimanual tasks in Barbary macaques (*Macaca sylvanus*). *American Journal of Primatology*, 80(3), e22745. <https://doi.org/10.1002/ajp.22745>
- Roberts, S., McComb, K., & Ruffman, T. (2008). An experimental investigation of referential looking in free-ranging Barbary macaques (*Macaca sylvanus*). *Journal of Comparative Psychology (Washington, D.C.: 1983)*, 122, 94–99. <https://doi.org/10.1037/0735-7036.122.1.94>
- Rogers, L. J. (2002). Lateralization in vertebrates: Its early evolution, general pattern, and development. *Advances in the study of behavior* (Vol. 31, pp. 107–161). Elsevier. [https://doi.org/10.1016/S0065-3454\(02\)80007-9](https://doi.org/10.1016/S0065-3454(02)80007-9)
- Rogers, L. J. (2009). Hand and paw preferences in relation to the lateralized brain. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 364(1519), 943–954. <https://doi.org/10.1098/rstb.2008.0225>
- Rogers, L. J. (2010). Relevance of brain and behavioural lateralization to animal welfare. *Applied Animal Behaviour Science*, 127(1), 1–11. <https://doi.org/10.1016/j.applanim.2010.06.008>
- Rogers, L. J. (2011). Does brain lateralization have practical implications for improving animal welfare? *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources*, 6(036), 1–10. <https://doi.org/10.1079/PAVSNNR20116036>
- Rogers, L. J., & Andrew, R. (2002). *Comparative vertebrate lateralization*. Cambridge University Press. <http://ebookcentral.proquest.com/lib/uunl/detail.action?docID=217820>
- Rogers, L. J. (2018). Chapter 4—Manual bias, behavior, and cognition in common marmosets and other primates. In G. S. Forrester, W. D. Hopkins, K. Hudry, & A. Lindell (Eds.), *Progress in brain research* (238, pp. 91–113). Elsevier. <https://doi.org/10.1016/bs.pbr.2018.06.004>
- Van Schaik, C. P., & Van Noordwijk, M. A. (1989). The special role of male Cebus monkeys in predation avoidance and its effect on group composition. *Behavioral Ecology and Sociobiology*, 24(5), 265–276. <https://doi.org/10.1007/BF00290902>
- Schmitt, V., Melchisedech, S., Hammerschmidt, K., & Fischer, J. (2008). Hand preferences in Barbary macaques (*Macaca sylvanus*). *Laterality: Asymmetries of Body, Brain and Cognition*, 13(2), 143–157. <https://doi.org/10.1080/13576500701757532>
- Šlipogor, V., Gunhold-de Oliveira, T., Tadić, Z., Massen, J. J. M., & Bugnyar, T. (2016). Consistent inter-individual differences in common marmosets (*Callithrix jacchus*) in Boldness-shyness, stress-activity, and exploration-avoidance. *American Journal of Primatology*, 78(9), 961–973. <https://doi.org/10.1002/ajp.22566>
- Soto, C., Gázquez, J., & Llorente, M. (2022). Hand preferences in coordinated bimanual tasks in non-human primates: A systematic review and meta-analysis. *Neuroscience and Biobehavioral Reviews*, 141, 104822. <https://doi.org/10.1016/j.neubiorev.2022.104822>
- Stanford, C. B. (2002). Avoiding predators: Expectations and evidence in primate antipredator behavior. *International Journal of Primatology*, 23(4), 741–757. <https://doi.org/10.1023/A:1015572814388>
- Stein, A. B., & Hayssen, V. (2013). *Panthera pardus* (Carnivora: Felidae). *Mammalian Species*, 900(900), 30–48. <https://doi.org/10.1644/900.1>
- Thierry, B., Iwaniuk, A. N., & Pellis, S. M. (2000). The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology*, 106(8), 713–728. <https://doi.org/10.1046/j.1439-0310.2000.00583.x>
- Tomaz, C., Verburg, M. S., Boere, V., Pianta, T. F., & Belo, M. (2003). Evidence of hemispheric specialization in marmosets (*Callithrix penicillata*) using tympanic membrane thermometry. *Brazilian Journal of Medical and Biological Research*, 36, 913–918. <https://doi.org/10.1590/S0100-879X2003000700012>
- Vaughan, E., Le, A., Casey, M., Workman, K. P., & Lacreuse, A. (2019). Baseline cortisol levels and social behavior differ as a function of handedness in marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 81(9), e23057. <https://doi.org/10.1002/ajp.23057>
- Wang, L., Luo, Y., Lin, H., Xu, N., Gu, Y., Bu, H., Bai, Y., & Li, Z. (2023). Performance on inhibitory tasks does not relate to handedness in several small groups of Callitrichids. *Animal Cognition*, 26, 415–423. <https://doi.org/10.1007/s10071-022-01682-w>
- Waterman, J. O., Campbell, L. aD., Maréchal, L., Pilot, M., & Majolo, B. (2020). Effect of human activity on habitat selection in the endangered Barbary macaque. *Animal Conservation*, 23(4), 373–385. <https://doi.org/10.1111/acv.12543>
- Westergaard, G. C., Chavanne, T. J., Houser, L., Cleveland, A., Snoy, P. J., Suomi, S. J., & Higley, J. D. (2004). Biobehavioural correlates of hand preference in free-ranging female primates. *Laterality: Asymmetries of Body, Brain and Cognition*, 9(3), 267–285. <https://doi.org/10.1080/13576500342000086a>
- Westergaard, G. C., Chavanne, T. J., Lussier, I. D., Houser, L., Cleveland, A., Suomi, S. J., & Higley, J. D. (2003). Left-handedness is correlated with CSF monoamine metabolite and plasma cortisol concentrations, and with impaired sociality, in free-ranging adult male rhesus macaques (*Macaca mulatta*). *Laterality: Asymmetries of Body, Brain and Cognition*, 8(2), 169–187. <https://doi.org/10.1080/713754484>
- Wright, L., Watt, S., & Hardie, S. M. (2013). Influences of lateral preference and personality on behaviour towards a manual sorting task. *Personality and Individual Differences*, 54(8), 903–907. <https://doi.org/10.1016/j.paid.2013.01.005>
- Zeileis, A., & Hothorn, T. (2002). Diagnostic checking in regression relationships. *2(3)*, 7–10.
- Zonato, A., Gagliardo, A., Bandoli, F., & Palagi, E. (2022). Reaching versus catching: flexible hand preference in ring-tailed lemurs. *Ethology Ecology & Evolution*, 1–22. <https://doi.org/10.1080/03949370.2022.2098382>

Zuberbühler, K., Noë, R., & Seyfarth, R. M. (1997). Diana monkey long-distance calls: Messages for conspecifics and predators. *Animal Behaviour*, 53(3), 589–604. <https://doi.org/10.1006/anbe.1996.0334>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: van Dijk, E. S. J., Bhattacharjee, D., Belli, E., & Massen, J. J. M. (2023). Hand preference predicts behavioral responses to threats in Barbary macaques. *American Journal of Primatology*, e23499. <https://doi.org/10.1002/ajp.23499>