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Analogous laterality in trunk movements in captive African elephants: A pilot study

Maëlle Lefeuvre [a,b], Patrick Gouat[c], Baptiste Mulot[d], Raphaël Cornette[e] and Emmanuelle Pouydebat[a]

[a]UMR 7179 - MECADEV Adaptative Mechanisms and Evolution, CNRS/MNHN, Paris, France; [b]Institute of Environmental Sciences, Faculty of Biology, Jagiellonian University, Cracow, Poland; [c]Laboratoire d'Éthologie Expérimentale et Comparée E.A. 4443, Université Sorbonne Paris Nord, Villetaneuse, France; [d]Zooparc de Beauval & Beauval Nature, Saint-Aignan, France; [e]Institut de Systématique, Evolution, Biodiversité (ISYEB), UMR 7205, Muséum national d'Histoire naturelle, CNRS, SU, EPHE, UA, Paris, France

ABSTRACT

Lateralization of hand use in primates has been extensively studied in a variety of contexts, and starts to be investigated in other species and organs in order to understand the evolution of the laterality according to different tasks. In elephants, the orientation of the movements of the trunk has been observed mainly in feeding and social contexts, in free conditions. However, little is known about the influence of task complexity on trunk laterality. In this study, we compared the lateralization of the trunk in two conditions: standardized and free. We offered granules to six African elephants on each side of an opened trapdoor to create a constraining environment and reported the different behaviours employed and their orientation. In addition, we observed the same individuals in free conditions and noted the lateralization of the use of their trunk. We revealed a common right side preference in all our elephants, both in standardized and free conditions. This side bias was stronger in our constraining task, adding evidence for the task complexity theory. We finally described laterality in new behaviours in the literature on elephants, such as pinching, gathering or exploration with the trunk.

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KEYWORDS *Loxodonta africana*; lateralization; trunk; behaviour; constraining condition

Lateralization is a side preference repeatedly observed in the realization of a given behaviour by a given individual (Canning et al., 2011). It is caused by asymmetries in the brain areas related to the different tasks. Those asymmetries

CONTACT Maëlle Lefeuvre maelle.lefeuvre@doctoral.uj.edu.pl UMR 7179 - MECADEV Adaptative mechanisms and evolution, CNRS/MNHN, Paris, France; Institute of Environmental Sciences, Faculty of Biology, Jagiellonian University, Cracow 31-007, Poland

are triggered by the interaction of genetic, epigenetic and environmental factors (reviewed in Güntürkün, Ströckens, & Ocklenburg, 2020). For example, in birds, the visual asymmetry may be a consequence of the position of the embryo in the egg. One eye is oriented to the egg shell and receives more light stimulation (Rogers, Zucca, & Vallortigara, 2004). In zebrafish, several genes are implied in the development of lateralization while other genes induce the direction of the lateralization. Finally, sex hormones have been shown to influence the brain organization and could modify the strength of a side preference (reviewed in Güntürkün et al., 2020). As an indicator of brain asymmetries, the study of this behavioural feature is a derived, non-invasive way to understand the brain organization, functioning and evolution.

Many activities in several taxa imply lateralized movements, such as feeding, social interactions, predator surveillance or escaping. The movement is usually defined as left- or right-oriented and sometimes as clockwise or anticlockwise (Giljov, de Silva, & Karenina, 2017; Haakonsson & Semple, 2009; Keerthipriya, Tewari, & Vidya, 2015; Laska, 1998; Martin & Niemitz, 2003). Depending on the species and the activity, a side bias can be observed at an individual level or at a population or a species level when a large majority of the individuals displays a common side preference (e.g., right-handed writing in human, Annett, 1972).

Traditionally, lateralization has been investigated in humans' use of their hands (Annett, 1972, 1985; Forrester, Quaresmini, Leavens, Mareschal, & Thomas, 2013). The emergence of tool use in early *Homo* species is thought to have led to the development of a complex language, supported by the writing process and the major involvement of the right hand and the left brain hemisphere in communication (reviewed in Meguerditchian, Vauclair, & Hopkins, 2013). Consequently, apes and other primates have been studied with the objective of understanding the evolution of handedness. The extensive literature on this topic has covered monkeys (Laska, 1996; Pouydebat, Borel, Chotard, & Fragaszy, 2014; Schweitzer, Bec, & Blois-Heulin, 2007) and apes (Byrne & Byrne, 1991; Hopkins & de Waal, 1995; Hopkins et al., 2011; McGrew & Marchant, 1999; Pouydebat, Reghem, Gorce, & Bels, 2010; Prieur, Barbu, Blois-Heulin, & Pika, 2017; Rogers & Kaplan, 1996) in various contexts.

More task complexity has been shown in some cases to increase the side bias (Fagot & Vauclair, 1991; Giljov, Karenina, & Malashichev, 2013) and could help understanding the evolution of the brain and its asymmetries. In this perspective, different levels of task complexity and constraining situations have been offered to primates in order to evaluate the side preference consistency at the individual and population level, from the pinching of small items (Jones-Engel & Bard, 1996; Laska, 1996) to the retrieval of food rewards from a maze (Bardo, Pouydebat, & Meunier, 2015; Pouydebat et al., 2010). Among these tasks, the retrieval of food from a tube, implying both hands, is used as a standard and reliable test for hand preference and

differentiation in primates (Hopkins, 1995) and this task has been offered to a large number of species (Maille, Belbeoc'h, Rossard, Bec, & Blois-Heulin, 2013; McGrew & Marchant, 1997; Meguerditchian, Calcutt, Lonsdorf, Ross, & Hopkins, 2010; Meunier & Vauclair, 2007; Vauclair, Meguerditchian, & Hopkins, 2005). In comparison, studies on other mammals and taxa, other organs, and other postures and movements are rather limited (George, Lerch, Jozet-Alves, & Lumineau, 2021; Giljov, Karenina, & Malashichev, 2012, 2015; Rogers, Vallortigara, & Andrew, 2013; Ströckens, Güntürkün, & Ocklenburg, 2013).

Since the emergence of studies on birds in this field of research (Rogers et al., 2004), laterality has been investigated in an increasing number of species and situations, implying parts or the entire body (e.g., whales during hunting, Canning et al., 2011; turtles during escaping, Pellitteri-Rosa & Gazzola, 2018; ant larvae during righting, Miler, Kuszewska, & Woyciechowski, 2017; sheepdogs during herding, Siniscalchi, Bertino, d'Ingeo, & Quaranta, 2019). As for unpaired organs, they are usually centred on the body, and the lateralization of their movements is not an evident assumption at first. In those studies, the asymmetry of the movement and its dominant side are observed. As examples, one can mention the amplitude of the tail-wagging in dogs (Quaranta, Siniscalchi, & Vallortigara, 2007), the orientation of wrapping movement of monkeys' tail (Laska, 1998; Nelson & Kendall, 2018), the initiation of the sparring neck movement in giraffes (Granweiler, Thorley, & Rotics, 2021) or the use of the trunk by elephants (Giljov et al., 2017; Haakonsson & Semple, 2009; Martin & Niemitz, 2003).

The elephants' trunk is involved in various activities including feeding, social interactions, body care, sensory perception, vocalizing and tool use and manufacture (Fowler & Mikota, 2006; Haakonsson & Semple, 2009; Hart, Hart, McCoy, & Sarath, 2001; Plotnik, Lair, Suphachoksahakun, & de Waal, 2011; Rasmussen & Munger, 1996; Shoshani, 1998; Yang, Pitarch, Potratz, Beck, & Abdel-Malek, 2006). As for non-human primates, lateralization has been reported in feeding, social interactions, body care as well as in trunk resting postures (Giljov et al., 2017; Haakonsson & Semple, 2009; Keerthipriya et al., 2015; Martin & Niemitz, 2003). Feeding behaviours are mainly characterized through the wrapping movement around a vertical food item, usually grass. In this case, lateralization corresponds to either clockwise or anticlockwise movement and is consistent within individuals for feeding activity (Giljov et al., 2017; Haakonsson & Semple, 2009). However, a decomposition of the feeding sequence into movements (touching and pulling off the plant – bringing it to the mouth – leaving the mouth to reach another plant) showed a variable strength of the side bias between each step of the sequence, food acquisition being the most lateralized step (Martin & Niemitz, 2003).

Elephants are social animals living in family groups, in which tactile and olfactory communication is substantial (Buss, 1961). Touching of conspecifics has been associated with many purposes such as reassurance, learning, playing, health or hormonal state checking (Yasui & Idani, 2017). In their study, Giljov et al. (2017) revealed a side preference inconsistency in the most common social contact (trunk-to-mouth) and the absence of population-level lateralization, contrary to what could have been expected, with the exception of the trunk-to-genitalia behaviour from males to females. This side bias might be explained by olfactory or cerebral asymmetries, the second one being influenced by sexual hormones (Güntürkün et al., 2020; Karenina, Giljov, de Silva, & Malashichev, 2018). Finally, lateralization has been observed in body care and resting positions in elephants, but to a lesser extent and with a weaker side preference than for feeding behaviours (Haakonsson & Semple, 2009).

In mammals, the pyramidal tract controls the muscles of the limbs with a higher sensitivity than the other motor control systems. As the tip of the elephants' trunk is capable of skilful precise movements comparable to primates' abilities (Haakonsson & Semple, 2009; Lefeuvre, Gouat, Mulot, Cornette, & Pouydebat, 2020; Martin & Niemitz, 2003), their pyramidal tract is thought to be connected with the facial motoneurons. In addition, projections and the highly developed nucleus in elephants' mesodiencephalo-olivo-cerebellar circuitry remind one of the red nucleus in human's brain, known to be involved in limb movements and more particularly in hands use (reviewed in Onodera & Hicks, 1999). This analogy is reinforced by the similarities between primates' hand and elephants' trunk. First of all, one has to notice the skilful manipulation (Chevalier-Skolnikoff & Liska, 1992; Christel, Kitzel, & Niemitz, 1998; Pouydebat et al., 2010, 2011; Pouydebat & Bardo, 2019; Racine, 1980) and the various behaviours performed by those organs (Adams & Berg, 1980; Lefeuvre et al., 2020; Nekaris, 2005; Pouydebat, Reghem, Borel, & Gorce, 2011). One can also mention their developed sense of touch, related to the amount of sensitive corpuscles in their skin (Hoffmann, Montag, & Dominy, 2004; Rasmussen & Munger, 1996). The main difference of trunk compared to hands is the absence of bones, increasing the flexibility of this organ. It makes the proboscis a good model for laterality studies, as the muscles organization enables oriented movements (Kier & Smith, 1985).

Despite a parallel between primates' hand and elephants' trunk, drawn in the literature at the morphological, sensory and neural levels, we are only starting to shed the light on the lateralization of the movements of the trunk. To our knowledge, very little is known about the impact of the task complexity on the side preference in the trunk's usages and the implied neural mechanisms. The orientation of the trunk has always been observed in free conditions, with no repeatable and quantifiable constraints (Giljov

et al., 2017; Haakonsson & Semple, 2009; Keerthipriya et al., 2015; Martin & Niemitz, 2003). The influence of standardized conditions on side preference is sorely lacking in the elephant's literature, although the position of the manipulated item has a direct effect on lateralization (Chapelain et al., 2012; Regaiolli, Spiezio, & Vallortigara, 2016).

Our study is a first step in the quantification of lateralization of trunk movements in captive African elephants of savannah (*Loxodonta africana*), underrepresented in the literature (Bielert, Costo, & Gallup, 2018; Musser, 2017). Our aim was to describe this phenomenon during feeding activity in a controlled environment. Taking advantage of the infrastructures available in captivity and the routine training of the elephants, we designed a new test in order to assess the side preference during feeding under standardized conditions. In addition, elephants were observed during their daily activity in order to study the orientation of spontaneous lateralized behaviours under less constrained conditions in comparison to our experiment. According to the "Task complexity theory" (Fagot & Vauclair, 1991), we expect a more consistent side preference in food manipulation under constrained condition due to the complexity of the task and the standardized position of the food target.

Methods

Animal subjects and housing

Our study has been conducted at the ZooParc of Beauval from the 1st of February to the 31st of May 2019, and involved six African elephant females used in a previous study (Lefeuvre et al., 2020). M'Kali, N'Dala and Marjorie lived at the zoo since 2003 while Juba, Ashanti and Tana arrived in 2017 and all the individuals were familiar with training and the infrastructures at Beauval. The three new elephants (Juba (A1), Ashanti (A2) and Tana (A3)) and M'Kali (A4) constituted one group and Marjorie (B1) and N'Dala (B2) a second one. The two groups were kept in different parts of the building, separated into boxes to facilitate cleaning and manipulation of the elephants. Marjorie and N'Dalawere housed in 4 boxes (58.5 m^2 each) and the four other elephants had access to 5 boxes (four boxes of 58.5 m^2 and one box of 307 m^2). One box of each group had been designed for medical training, surrounded by narrow oblique bars with trapdoors for the interventions on different parts of the elephants' body.

Medical training consists of learning and repeating movements and postures in order to facilitate the veterinary interventions. Elephants learnt, for instance, to pass their ear through the dedicated vertical trapdoor to allow blood sampling on its back side, to stay still upon contact with a needle, to lay a foot on the sill of a larger trapdoor for feet care, to raise their trunk for tusks and teeth inspection or to follow the steps of insemination

procedure. Frequently repeating these orders reduces the stress during veterinary interventions and makes it more comfortable for the vets and the animals.

Elephants were exclusively trained in the box available for their group. Only N'Dala was occasionally trained for insemination in the other box. This box was the only one equipped with a trapdoor designed to have access to the back and genitalia of the females. Nevertheless, the other trapdoors were similar, and we were able to apply our protocol in both boxes identically. N'Dala lost her eyesight one year before our study because of retinal detachment on one eye and cataract on the other. However, she was able to participate in training sessions in the same conditions as the others, thanks to her knowledge of her environment and keepers' vocal cues. One should also mention the asymmetry of the distal part of her trunk due to an old injury (Figure 1). Laterality inconsistencies have been observed in elephants with injured trunks (Racine, 1980), thus we will take this feature into account in our discussion.

Training occurred every morning at around 9am. Each elephant was trained once or occasionally twice per week. The running order changed almost every week, depending on the veterinary routine interventions and other manipulations. Training was conducted individually to avoid

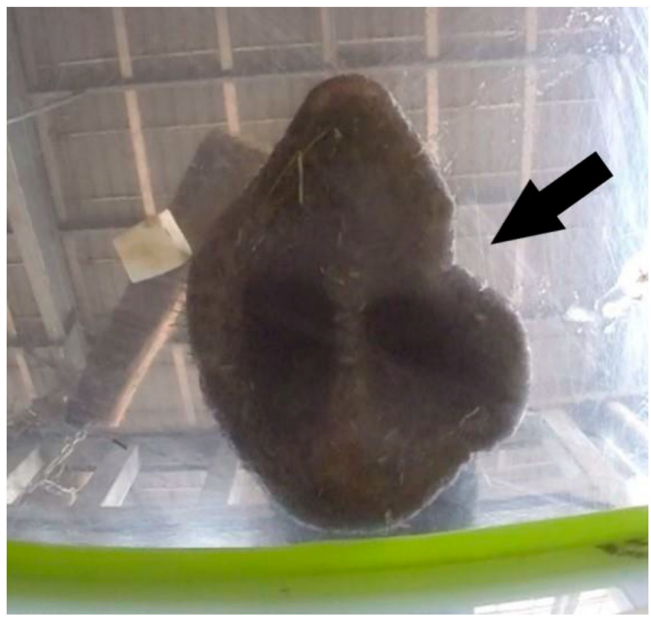

Figure 1. Picture of the distal part of N'Dala's trunk, with a little-cube item (2 × 2 cm), used in another experiment. The black arrow points at a deformation resulting from an old injury. [To view this figure in color, please see the online version of this journal.]

disturbance. During the session, holding the position was rewarded by apple slices regularly distributed, unpleasant exercises were rewarded by vegetables highly appreciated by the elephants, such as celery stick, and at the end of the session, the individual was given her daily granules ration. Meanwhile, the other elephants received their ration in a bucket held by keepers to avoid competition. This is the moment we chose to perform the experiment detailed below.

Additionally, different food items constituted the daily ration of the elephants. They had access to hay ad libitum, provided in nets in height. Branches of European trees species and bamboo were distributed twice per day, and seasonal vegetables cube pieces were scattered in their enclosure three times per day. Finally, apple slices were distributed during the transfer of elephants between boxes, to keep their attention away from the opening and closing of the doors. More details of food item properties have been stated in a previous article (Lefeuvre et al., 2020).

Experiment

We used granules (Royal Horse, S-200 Sport & Loisir) as a food item to investigate the side preference in manipulation. We chose a trapdoor with less free space under it in order to constrain the movement and to favour a grasping behaviour. After the last reward distribution, the elephant was placed perpendicularly to the wall and centred in front of the opened door. One keeper was asking for a trunk-up position and rewarded this action with apple slices. At the same time, another keeper was separating the granules ration into two equal piles, one pile on each side of the door (Figure 2).

Figure 2. Establishment of the experiment. One keeper asks for the trunk-up position and gives apple slices, while another keeper installs the two piles on each side of the opened trapdoor. [To view this figure in color, please see the online version of this journal.]

Then the elephant was allowed to eat the piles of granules. We recorded the manipulation and consumption of the granules with a camera Sony FDR-AX 53 on a tripod until the elephant finished the granules, then lost interest in the door and left the position. We performed this experimentation10 times for each individual, once at the end of 10 of their training sessions.

Based on the videos, we reported the type and orientation of each manipulation of granules, differentiating grasping movements and vacuums (oriented or not). We described grasping as enrolling the trunk around the target (i.e., granules). We considered a right-side preference if the trunk was laid on its left side and wrapped with a clockwise movement, from the left to the right (Figure 3). We assumed that grasping movements were always oriented whereas vacuum movements were considered as oriented only when the distal part of the trunk was laid on one side and the movement was unidirectional. Vacuums referred to a suction of granules with the trunk. We considered a right-oriented vacuum when the tip of the trunk was laid on the left side and conversely. The trunk was either static or performing a sweeping movement from the left to the right (Figure 4).

In our setup, contrary to unconstrained situations, the elephants cannot place themselves in front of the food they want to catch. Thus, the position of the granules may force elephants to adapt their strategy and could introduce a bias in the direction or strength of the side preference. Then we also reported the position of the manipulated pile of granules (on the left or on the right of the elephant) for each movement.

Observations

In addition to our experiment, we observed the uses of the trunk by the elephants during their daily activity in their building and in the parklands, from

Figure 3. Right-oriented grasping movement around the left pile of granules. The trunk is wrapping clockwise. [To view this figure in color, please see the online version of this journal.]

Figure 4. Right-oriented vacuum movement on the left pile of granules. The tip of the trunk is laid on its left side and the sweeping movement goes to the right. [To view this figure in color, please see the online version of this journal.]

the 1st of February to the 4th of May 2019. The method of observation and the complete behavioural repertoire are reported in detail in Lefeuvre et al. (2020). We noted the direction of the movements in seven potentially oriented behaviours: four manipulative behaviors and three explorative behaviours (see Figure 5). Resting postures and social interactions were too rare to be included in this study.

Manipulative behaviours included Side pinch (catching little items between the fingers of the trunk, the tip laying down on one side), Grasp (same as grasping in the experiment), Sweep (sweep movement with the side of the trunk to gather items before catching them) and Gather (same as Sweep but with the tip of the trunk only).

Exploration of the ground (aim for finding food, end of the trunk probing the ground until contact with an item or abandonment) was displayed by all the elephants. In addition, two Guide behaviours were performed only by N'Dala, the blind elephant, when walking: Guide (similar to Exploration of the ground but aimed for avoiding obstacles) and Back guide (similar to Guide but holding the trunk in the other side, the dorsal part in the front and the tip rolled against the ventral part of the trunk).

The manipulative behaviours were considered as right-oriented when the trunk was laid on its left side, and the movement was performed clockwise, except for Side pinch which was a more static behaviour. Explorative behaviors were oriented when the elephants were drawing circles with their trunk. Thus, the side bias was characterized by the direction of the movement, clockwise being considered as a right orientation of the movement. When Guide behaviours were static or recalled a white cane, going from a side to the other with a balancing movement, we considered them as non-

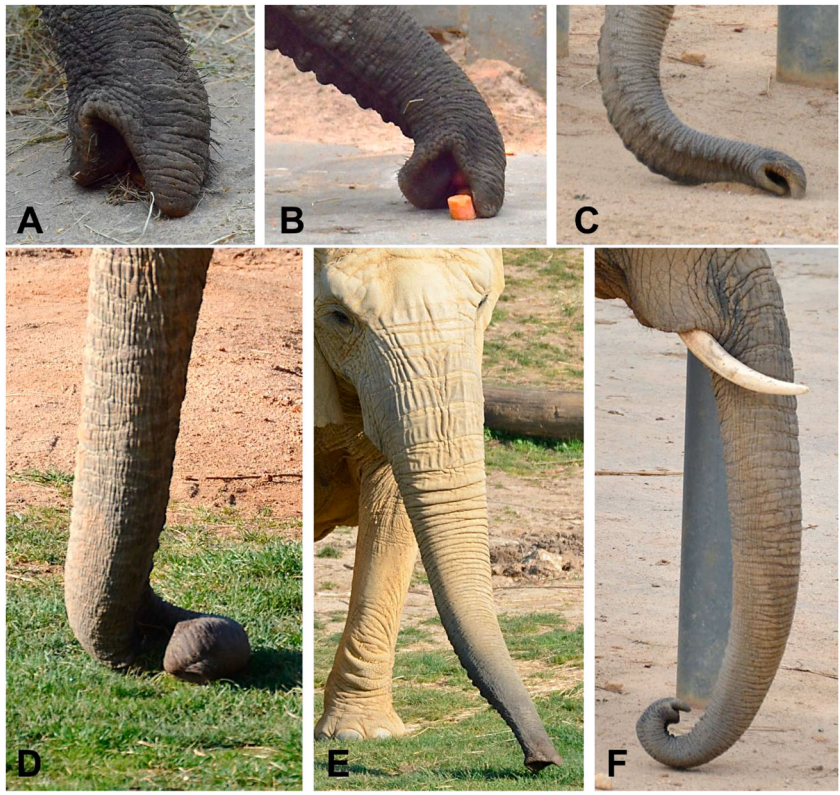

Figure 5. Example pictures of the observed behaviours. (a) represents a Side Pinch behaviour, with one side of the trunk tip laid on the floor while catching an item between the fingers. Here the Side pinch movement is right-oriented. (b) Represents a Gather behaviour, the tip of the trunk is used to push and gather items before gripping them. Here the Gather movement is right-oriented. (c) Represents a Sweep behaviour, with a longer part of the trunk sweeping the floor to gather items, here sand. Here the Sweep movement is right-oriented. (d) Represents a Grasp behaviour, for which the trunk is wrapped around the item, here grass. Here the Grasp movement is right-oriented. (e) Represents both Exploration of the ground and Guide behaviours, as they were performed in a similar way, with the trunk tip oriented to the floor. (f) Represents a Back guide behaviour, used to detect obstacles but with the dorsal side of the trunk and the end of the trunk curled. [To view this figure in color, please see the online version of this journal.]

oriented, because we were not able to assess a potential difference in the amplitude of the movement on the left or the right.

Statistical analysis

During the experiment, the number of occurrences of vacuum and grasping behaviours was quantified according to their orientation (left or right) or not

(unoriented). Because the number of occurrences of a given behaviour varied greatly from one session to the other, we used the total number of occurrences in the analysis.

In order to detect a side preference at the individual level, we compared the occurrences of right and left oriented behaviors using a binomial test.

We also compared the effect of the position of the piles (right or left) on the use of the behaviours. When only right-oriented behaviour was observed (i.e., grasping behaviour), the number of behaviours was compared between the two piles using a Fisher-Pitman permutation test for paired samples (i.e., each animal being an independent sample, $N = 6$). When possible (i.e., when suitable data were available), we made the analysis for each individual independently, using the same statistical procedure whereas each sample was a session ($N = 10$). In both case the statistic of the test and the exact probability were given. When several types of behaviour (i.e., unoriented and oriented left or right) were involved, we used a Chi^2 test with exact procedure.

During observations, we reported the side preference in the occurrences of behaviours. In a first step, the proportion of oriented occurrences of each behaviour was calculated for each individual. In a second step, the side preference in the population of oriented behaviours was assessed by a binomial test (with a binomial probability under Ho of .5) for each behaviour and each individual.

All the statistical tests were performed with StatXact 8 (Cytel Studio).

Ethical note

Observations were made from the safety zone with no contact or interaction with the elephants. The manipulation of the animals was performed only by the keepers. No deprivation of granules or other punishment occurred in case of refusal to attempt or the use of an alternative strategy during our experiment.

Results

Experiment

We observed a total of 240 graspings (121 for the left pile and 119 for the right pile). For each of the elephants, grasping was always oriented to the right. For a given individual, the number of grasping differed between the left and the right piles (Figure 6) but no statistically significant difference was found neither at the group level ($N = 6$; stat = .1525; $p = .93$) nor at the individual level for N'Dala (B2) who displayed the most important difference between the two piles ($N = 10$; stat = .1287; $p = .27$).

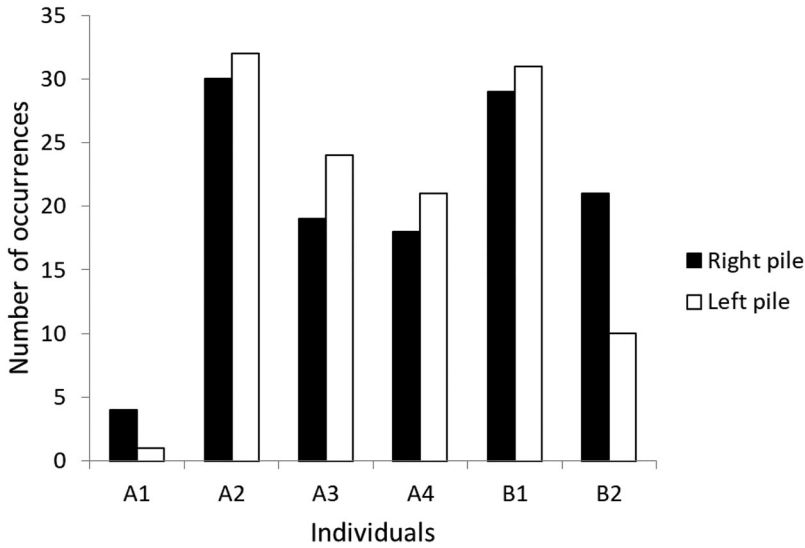

Figure 6. Number of occurrences of grasping behaviour for each individual and for each of the two piles of granules (right or left).

Contrary to grasping behaviour, vacuums were not always oriented and the proportion of oriented vacuum varied greatly between the elephants (Figure 7).

All the elephants had a preferred orientation of the vacuum behaviour (Figure 8). For all of them with the exception of N'Dala (B2), the right oriented vacuum behaviour was the most common. This preference was highly significant for each individual ($p < .001$) with the exception of M'Kali (A4) for whom the number of oriented vacuums was too low ($N = 4$).

The proportions of each type of vacuum behaviour (i.e., left or right oriented, and unoriented) differed significantly between the left and the right piles in three individuals (Figure 9). They displayed more right oriented vacuums and less unoriented vacuums when eating the right pile (A1: $Chi^2 = 9.7$, df = 2, $p = .004$; A2: $Chi^2 = 9.8$, $df = 2$, $p = .004$; A3: $Chi^2 = 4.9$, $df = 1$, $p = .035$). A similar tendency was observed in Marjorie (B1) but the number of vacuum behaviours was too small to bring a significant difference between the two piles.

Observations

Among the four behaviours displayed by all the individuals (Figure 10), only Side pinch was always oriented. In the three other behaviours, the proportion of unoriented behaviour varied from 0% to 99.4% and was the highest for Exploration of the ground.

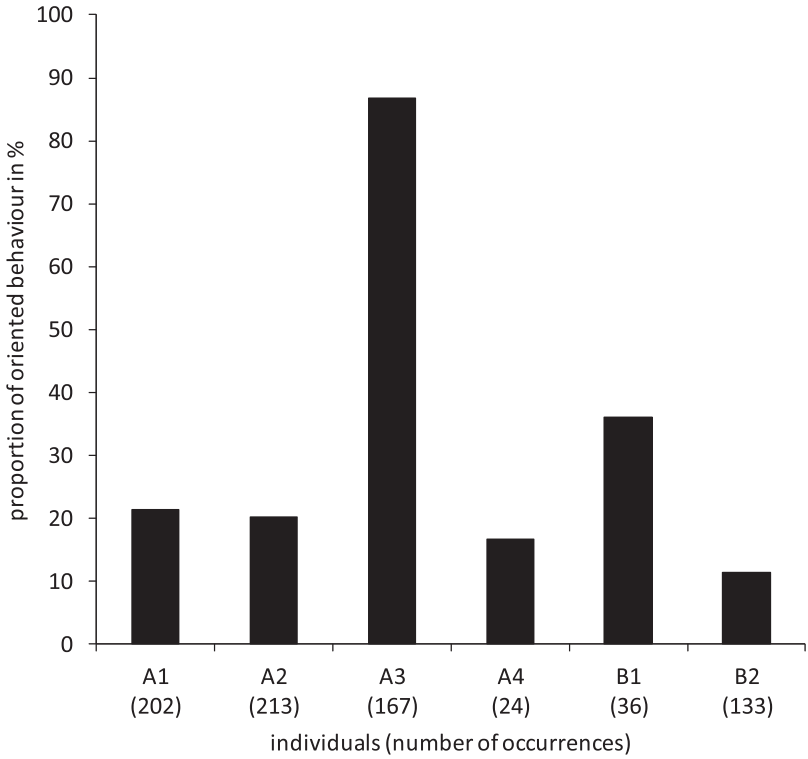

Figure 7. Proportions of oriented vacuums for each individual. The total number of vacuum behaviours is given between brackets under the individual code.

When the number of occurrences exceeded 30, a right-side preference was the rule and always exceeded 75% of the oriented occurrences. A right-side preference was also observed in less displayed behaviours, but the number of occurrences was too small to allow any conclusion.

Gather was only performed by Ashanti, however, the 6 oriented occurrences out of 72 observations were too scarce to conclude on her side preference, even if she oriented this movement only to the right ($p = .031$).

The two Guide behaviours were performed only by N'Dala (B2), the blind elephant. From the 168 occurrences of the Guide behaviour observed, 108 were unoriented and 52 were right oriented ($p < .001$). The proportion of oriented Back Guide behaviour was of 24% (179 unoriented vs. 58 oriented) but no side preference was detected (left: 24; right: 34; $p = .24$).

Discussion

Our study revealed a strong right side preference in all our elephants to grasp food in standardized situation. In our experiment, although changing the

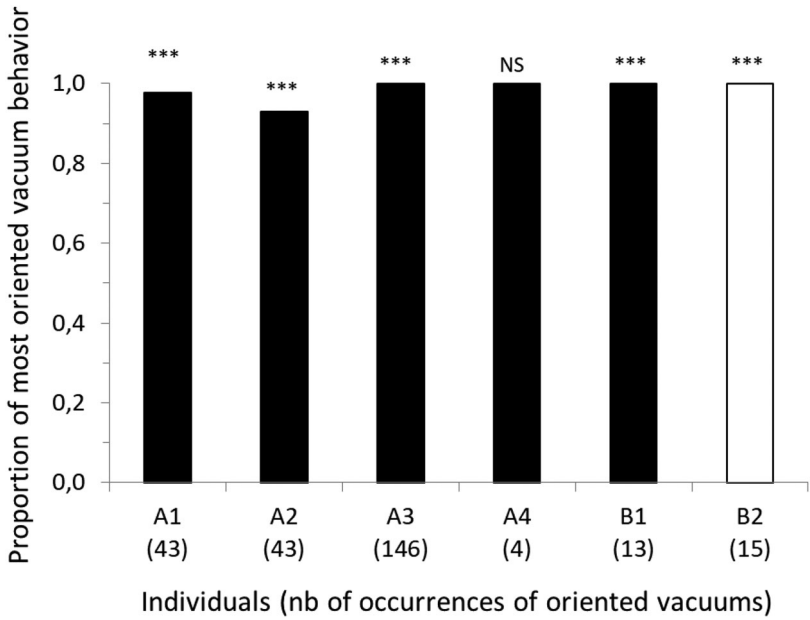

Figure 8. Proportion of the most common oriented vacuum behaviours for each individual. The right oriented vacuum (black bars) was the most common for all individuals except for N'Dala (B2) (dominant left oriented vacuum, white bar). The total number of oriented vacuums is given between brackets under the individual code. ***$p < .001$; NS: $p = .125$.

grasping direction according to the position of the pile seemed to be the most efficient way to collect granules, right orientation was always the rule on the two piles and no attempt to grasp granules with a left oriented movement was observed in any of our individuals. The absence of pile's position effect on the number of grasping shows the strength of this side preference implied in food retrieval regardless of the position of the target.

Our results add evidence for the "Task Complexity Theory" (Fagot & Vauclair, 1991) in the feeding context in African elephants. This theory predicates a stronger lateralization of complex movements. For large animals such as Proboscideans, the manipulation of small items can be considered as a complex task due to the required skilful control of the trunk. Indeed, the strength of the side preference has been shown to be higher during feeding and manipulation of sand than in other tasks in free situation (Giljov et al., 2017; Haakonsson & Semple, 2009). The granules we used in our experiment were not as tiny as sand, but they were still small items and their manipulation required fine coordination and imposed a relative constraint to the elephants, in addition to the wall and the position of the trapdoor.

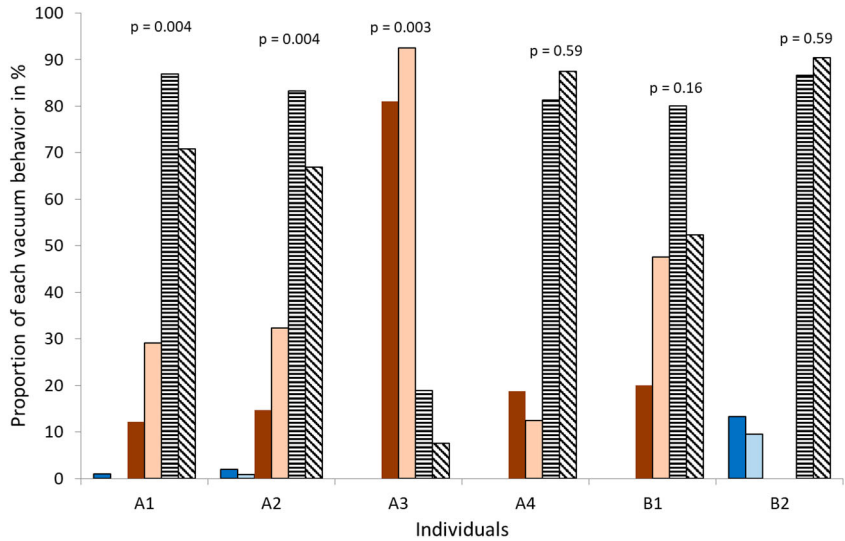

Figure 9. Distribution of the different types of vacuum behaviours used by each elephant according to the position of the piles of granules. Striped horizontal/oblique: unoriented behaviour on the left pile/right pile; dark blue/pale blue: left-oriented behaviour on the left pile/right pile; dark red/pale red: right-oriented behaviour on the left pile/right pile. The *p*-value of the Chi^2 is given above the columns for each individual. [To view this figure in color, please see the online version of this journal.]

In primates, gripping small items between the fingers has also been investigated to assess laterality and a side bias was not very often observed (Jones-Engel & Bard, 1996; Laska, 1996; Pouydebat et al., 2010). However, in more complex tasks such as catching moving items (Pouydebat et al., 2014) or using tools (Bardo et al., 2015; Pouydebat et al., 2010), primates showed a consistent side preference. Our study combined the complexity of the manipulation of small items using the trunk and the postural constraint of a wall with a low hatch. In this way, our experimental design is in accordance with other laterality studies carried out in the large field of primates.

Contrary to the grasping movement, the vacuums were not necessarily oriented, even rarely for some individuals. To our knowledge, this result is new and can hardly be compared to other results in the field of laterality research. Indeed, the vacuum movement is similar in some extent to gripping with a hand, but in studies of paired organs, the hand used but not its orientation is reported to assess the side preference. When unpaired organs are studied, either a wrapping movement is observed (monkeys' tail: Laska, 1998; elephants' trunk: Giljov et al., 2017; Haakonsson & Semple, 2009; Keerthipriya et al., 2015; Martin & Niemitz, 2003), or the organ is not endowed with manipulative abilities (giraffes' neck during sparring: Granweiler et al., 2021; dogs' tail wagging: Quaranta et al., 2007). As shown in this

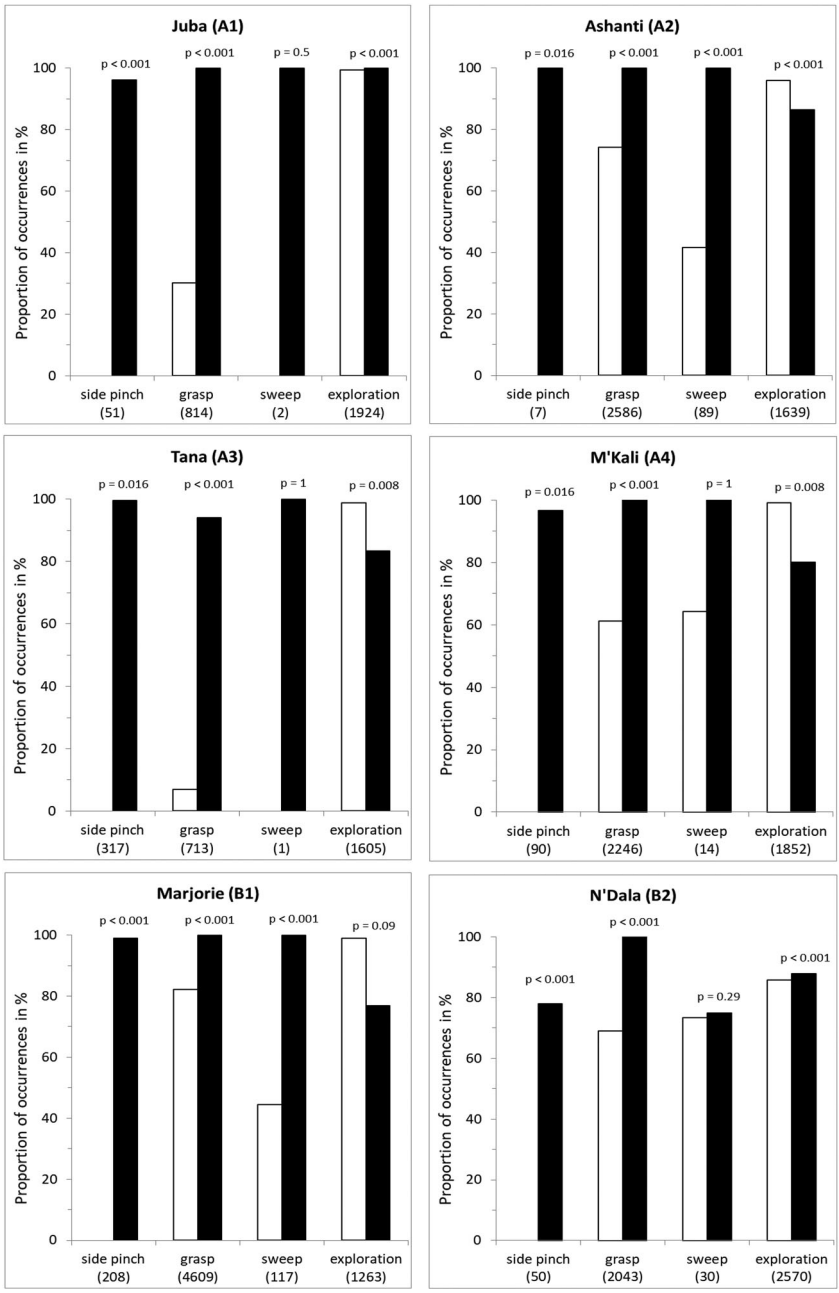

Figure 10. Proportions of unoriented behaviours (white bars) and right preference for oriented behaviours (black bars) during observations. Each graph corresponds to a different individual (name and code are given at the top of the graph). The name of the behaviour is given under each pair of bars with the total number of occurrences between brackets. The result of a binomial test (exact probability) is given above each black bar.

study, grasping and vacuuming differed in the proportion of oriented occurrences, the strength of the lateralization and the influence of the target's position, but this would need further investigation with larger sample sizes.

The low proportion of oriented vacuums in some individuals could be explained by the lower constraint level of our setup on vacuums than grasping. Elephants are able to extend their trunk to reach items in front of them without positioning issues (Kier & Smith, 1985). Compared to vacuums, grasping requires a longer part of the trunk laying on the floor and an adaptation of the posture, and the wall might be more constraining for this behaviour.

As for grasping movement, oriented vacuums were right biased for all our individuals except N'Dala, who displayed a left side preference when vacuuming the granules in our experiment. Previous studies have shown that lateralization of the movements of the trunk is generally consistent within activities for a given individual (e.g., feeding, social interactions, Haakonsson & Semple, 2009; Keerthipriya et al., 2015), yet N'Dala made an exception for this particular feeding behaviour. In fact, the distal part of her trunk was split on the left side due to an old injury (shown in Figure 1). We assume that this morphological feature may only complicate the prehension of items as tiny as granules, as we observed a right-side preference in the Side pinch behaviour with bigger food. Hence, N'Dala adapted her movement to her injury only in the case of this injury being disrupting for her feeding activity.

Our results showed that the position of the piles influenced the amount of oriented vacuums, which were observed less often on the left pile. A right-oriented vacuum is less constraining if the goal of the movement is on the right of the elephant, because the trunk does not need to bypass the pile. Oriented vacuums to consume the left pile may be less rewarding and require more efforts than non-oriented vacuums and thus be less frequently performed. Macaques have been observed inverting the hand they used to catch food according to its position, opting for the hand closer to the item at first (Chapelain et al., 2012; Fagot & Vauclair, 1991). Our elephants remained consistent in their side preference but the position of the food appears to influence the use of oriented or non-oriented movement.

In our experiment, we limited the freedom of movement of our elephants in order to encourage grasping behaviours, leading to alternative strategies. Elephants tried to align themselves with one pile, moved aside in front of their goal, and passed the trunk between the bars of the wall (Figure 11). They all abandoned those alternative strategies, leading to the conclusion that they were probably less efficient and more constraining. As do elephants, primates use postures that will facilitate their movements and the retrieval of food. They adopt balanced positions in trees (Pouydebat et al., 2014; Rogers & Kaplan, 1996) or more comfortable or adapted postures during tests (Bardo et al., 2015; Laska, 1996).

Figure 11. Alternative strategy to reach the granules. The elephant moves on the side to be in front of the pile and tries to pass the trunk between the bars. [To view this figure in color, please see the online version of this journal.]

In free observations, a global tendency for a right-side preference appeared in all our individuals, however, we reported less oriented occurrences than expected. As discussed before, the constraints of the environment and the individuals' posture may decrease the utility of lateralized movements in some situations.

Side pinch and Grasp behaviours were the most frequent movements, as they are crucial feeding behaviours and the cornerstone of item manipulation. For large mammals such as Proboscideans, a higher nutrient intake represents a considerable benefit for fitness, and lateralization is an effective strategy to increase this benefit. Our findings are in accordance with previous studies, showing strong side preference with rare inconsistencies in the main feeding behaviours. Only one exception can be noticed in the use of Side pinch by N'Dala, but as illustrated before, her old injury can force her sometimes to change her side preference to manipulate tiny items.

Previous studies have defined the grasping movement as a reliable indicator of feeding lateralization (Giljov et al., 2017; Haakonsson & Semple, 2009; Keerthipriya et al., 2015; Martin & Niemitz, 2003). Indeed, in Asian elephants, this is the main strategy to retrieve food. However, African elephants, in contrast with Asian elephants, are equipped with two fingers and show finer manipulative skills (Fowler & Mikota, 2006; Racine, 1980), and it is

unsurprising to observe oriented pinch behaviour in a species using this strategy substantially.

Sweep and Gather behaviours were less often observed and the low number of occurrences for some individuals unable us to conclude on their side preference. Nevertheless, elephants who displayed more often these behaviours showed a strong right-side preference, consistent with the lateralization of the other feeding behaviours. Gathering food may be a time-consuming task in a feeding sequence, and reducing its duration with lateralized movements might lead to a globally more efficient food retrieval. To our knowledge, the only other observation of similar lateralized gathering behaviours was reported in free-ranging Asian elephants (Keerthipriya et al., 2015). In this study, grasping and gathering were combined in a unique wrapping movement which was strongly lateralized, regardless of the aim of the movement.

The Exploration of the ground was rarely oriented, and the strength of the side preference was lower than for feeding behaviours, with more inconsistencies in the orientation of the movement. Lateralization in social mammals is thought to represent an advantage either in the speed and efficiency of a movement (foraging faster and better, thus foraging more, Martin & Niemitz, 2003) or in the synchronization of an activity (more efficient communication, Ghirlanda & Vallortigara, 2004; Karenina et al., 2018; Prieur, Pika, Barbu, & Blois-Heulin, 2016). Nevertheless, exploratory behaviours might not need to be fast or synchronized, but to be accurate. With their massive olfactory bulb (Shoshani, Kupsky, & Marchant, 2006), elephants have undoubtedly an accurate sense of smell, but this does not seem to be strongly lateralized in the case of exploration of their environment.

Brain asymmetries related to the sensory input processing are widespread in the animal kingdom, among vertebrate and non-vertebrate taxa (reviewed in Güntürkün et al., 2020). As a result, a lateralized olfactory information gathering has been observed in different species. For instance, dogs have been shown to use a specific nostril according to the situation and the type of odour (Siniscalchi, D'Ingeo, & Quaranta, 2017). In addition, the investigation of new olfactory stimuli is associated with the right nostril in dogs and horses (Siniscalchi, 2017). In elephants, the investigation of females' hormonal state by males was always oriented to the right, which favours the use of the right nostril (Giljov et al., 2017).

We observed similar results in the Guide behaviour as in the Exploration of the ground. One reason can be the similarity between these two movements, which might then be performed identically, with the same direction and strength of the orientation. The other reason could be a combination of those behaviours, detecting obstacles and food at the same time, leading to an overlapping of the Exploration of the ground and the Guide behaviours.

Moreover, the Back guide movement was not lateralized. We assume that this posture, with the end of the trunk curled and an exploration of the ground with the dorsal part, protects the tip of the trunk from objects and injuries, but only tactile exploration might be involved in this situation. Lateralization of haptic sense has been observed in capuchin monkeys and humans (reviewed in Güntürkün et al., 2020), and elephants are equipped for fine tactile discrimination (Rasmussen & Munger, 1996). Nevertheless, the corpuscles dedicated to haptic sensation are numerous in the tip of the trunk, and this part is not involved in the Back guide behaviour. We can hypothesize that the orientation of explorative behaviours is strongly related to sensory asymmetries, but further research is needed on this topic.

Surprisingly, all our elephants showed a general tendency for a right lateralization of most of the behaviours we have reported. According to previous studies, elephants can manifest different side preferences depending on the activity (Haakonsson & Semple, 2009; Martin & Niemitz, 2003). Moreover, no population-level laterality has been found in Asian elephants (Giljov et al., 2017; Haakonsson & Semple, 2009; Racine, 1980), except in some social contexts such as females' genitalia inspection by males (Giljov et al., 2017) or the positioning of calves on one side of their mother while walking (Karenina et al., 2018). The analogous lateralization highlighted in our study might be a bias of our small sample size. To our knowledge, the only other study reporting a common side preference in the use of the trunk compared four Asian elephants and two African elephants in captivity (Racine, 1980), but this study was supplemented with a survey implying 72 captive elephants from 7 zoos and circuses and no population-level laterality appeared. In the study of Racine (1980), behavioural transmission has been observed between the two species housed together, however, laterality mimicry is unlikely to occur. Laterality in free-ranging (Giljov et al., 2017) or captive elephants (Haakonsson & Semple, 2009) has not been observed to be harmonized within groups. One also has to mention that our individuals originated from different places and countries, did not have blood tie, and arrived at the zoo at different periods, thus imitation is definitely unexpected. Furthermore, side preference has been shown to establish during the first two months of life (Keerthipriya et al., 2015) and has not been observed varying along the life of elephants.

Conclusion

Elephants have been shown to have lateralized movements of their trunk during feeding (Keerthipriya et al., 2015; Martin & Niemitz, 2003; Musser, 2017; Racine, 1980), social interactions (Giljov et al., 2017), body care and natural relaxed movement during walking (Haakonsson & Semple, 2009). We added explorative behaviours to the list, as well as constraining

conditions during food retrieval. Previous studies found individual, context dependent side preferences, with elephants being robust in their laterality for a given task such as feeding or body care, but potentially changing their side preference for different tasks (Haakonsson & Semple, 2009). No population-level side bias was observed in either captive or free-ranging elephants (Bielert et al., 2018; Haakonsson & Semple, 2009; Keerthipriya et al., 2015; Martin & Niemitz, 2003), except in some social contexts with a strong influence of the sex of the individuals (Giljov et al., 2017; Karenina et al., 2018). Contrary to those studies, we found a consistent side preference within and between individuals, but larger sample sizes are needed to generalize our results. This pilot study shows the relevance of describing lateralization of elephants under standardized constraining conditions as it has been done on primates, and open the way for further studies on Proboscideans.

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Data availability statement

The data that support the findings of this study are available from the corresponding author, M. L., upon reasonable request.

ORCID

Maëlle Lefeuvre http://orcid.org/0000-0003-4291-134X

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