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Do African Savanna Elephants (*Loxodonta africana*) Show Interspecific Social Long-Term Memory for Their Zoo Keepers?

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ABSTRACT

"An elephant never forgets" is a popular phrase that refers not only to the elephant's extraordinary ability to remember migration routes but also to its pronounced social long-term memory (SLTM). Previous studies have shown intra- and inter-species SLTM performance, but the ability of elephants to have memories of individual humans has not yet been investigated. We tested this interspecific SLTM using auditory, olfactory, and visual stimuli, each from familiar and unfamiliar persons, in two African savanna elephant (*Loxodonta africana*) cows living in a zoo. The two-choice object tests revealed a higher interest in sensory stimuli from familiar keepers they had not seen for 13 years than in unfamiliar people. Statistically significant differences were found for olfactory stimuli. In addition, there was significantly more interest in visual stimuli from current keepers than in stimuli from unfamiliar people. Contrary to the results of a previous study with elephants, this was not observed for olfactory stimuli. Due to the small sample size and magnitude of the influencing factors, that is, outdoor experiment, only spatial separation of the animals, these results only represent indications of the possible interspecific SLTM. Nevertheless, we were able to provide the first empirical evidence that *L. africana* stores information about specific people over a long period of time. Further studies with larger sample sizes, cross-modal testing, and people disliked by the elephants could provide more insights.

1 | Introduction

For many wild animals, the ability to recognize potential threats in the form of another species (e.g., predators) has fitness consequences (reviewed by Lind and Cresswell 2005). For animals who live in social groups, it is additionally crucial to recognize conspecifics and to be able to discriminate among individuals (e.g., offspring, mates, rivals, etc.) (reviewed by Bee 2006). Gaining and storing information about conspecifics as part of the ability to recognize classes of individuals (i.e., familiar vs. unfamiliar) or specific individuals (i.e., individual recognition) is summarized as social knowledge (Menzel and Fischer 2011). In fission–fusion societies, group stability is low because individuals frequently separate (fission) only to regroup later (fusion). This makes it necessary to enable intra-species recognition over a long period of time (Archie, Moss, and Alberts 2006). Accessing social knowledge even after a long period of time—the social long-term memory (SLTM)—is important for various processes, such as dominance hierarchies (Höjesjö et al. 1998), reunification (Hörner et al. 2021; Moss, Croze, and Lee 2011), scent recognition (Hoerner et al. 2023), rearing (Berg et al. 2011) and territorial behavior

Summary

- In a two-choice object test using different sensory stimuli, both female African savanna elephants showed more interest for the olfactory stimulus from former keepers (no interaction for up to 13 years) than from unfamiliar persons.
- No difference in interest was found between unfamiliar persons and current keepers, except for visual stimuli.

(Frommolt, Goltsman, and Macdonald 2003). Elephants live in unusually fluid, fission-fusion societies and are known for their exceptional long-term memory (Archie, Moss, and Alberts 2006). In addition to recognizing conspecifics, these animals also have the ability of interspecific recognition. Observations of wild-living African savanna elephants (*Loxodonta africana* BLUMENBACH 1797) revealed that they can recognize features of human cohorts auditorily (McComb et al. 2014), olfactorily and visually (Bates et al. 2007) in assessing the level of threat. This raises the question if elephants are able to store information about specific humans in their SLTM and if so, which senses they use to recognize them after a long period of time.

All recognition as well as discrimination between familiar and unfamiliar stimuli involves the employment of one or more senses for communication (e.g., Cely and Tibbetts 2022). Due to the social structure of the fission-fusion herds, elephants often communicate over long distances, and so their communication senses have developed particularly well. Besides the trumpeting and antiphonal "rumble" that is audible to humans (Beeck et al. 2022; Soltis, Leong, and Savage 2005), they also use infrasonic sounds (< 20 Hz) for communication over long distances that for humans is not audible (Garstang 2004). In these low frequencies, the elephant is outstanding in hearing and localization compared to other animals. It can also perceive up to 10 kHz, but much more poorly (> 4 kHz) and not localized (Heffner and Heffner 1980). For comparison, humans can perceive not less than 20 Hz, but up to 20 kHz (Purves et al. 2001). The olfactory system of elephants is outstanding as well (Langbauer 2000). African savanna elephants (*L. africana*) have, with ~2000 functional olfactory receptor (OR) genes, an eminent position in the animal kingdom with regard to their sense of smell (Niimura, Matsui, and Touhara 2014). Plotnik et al. (2019) demonstrated the exceptional olfactory capacities of elephants when testing if the animals were able to detect differences in quantities of food using their olfactory sense alone. The results revealed that elephants chose the larger quantity of food by smelling for it (Plotnik et al. 2019). On the contrary, the visual sense does not seem to be as strongly developed. With 13.16–14.37 cycles per degree (cpd) (Pettigrew et al. 2010), *L. africana* have relatively poor vision among mammals (Caves, Brandley, and Johnsen 2018). A study that tested the ability of captive elephants to follow human-initiated visual cues, revealed that they are not able to follow pointing, body orientation or a combination of both as signals of location of hidden food (Plotnik et al. 2013, but see Smet and Byrne 2013). Although visual information is important for elephants when navigating their physical and social worlds, they rely more heavily on other senses, specifically audition and olfaction (reviewed by Ball et al. 2022).

Previous experiments investigated the extent to which elephants use their senses to recognize conspecifics and found that they react differently to cues from familiar conspecifics than from unfamiliar ones, not only visually but also olfactorily via cues such as urine (Bates et al. 2008) and feces (Hoerner et al. 2023), as well as auditorily (McComb et al. 2000; O'Connell-Rodwell et al. 2007).

Research by McComb et al. (2014) showed that during human–elephant interactions, *L. africana* can discriminate between threatening and non-threatening humans. The ability for interspecific recognition has also been observed in zoological facilities, where the animals are in close contact with their keepers. Over 90% of keepers form distinctive bonds with their animals, and this leads to more effective work with the respective animal and thus also to higher animal welfare and affectivity (Hosey and Melfi 2012). In elephants, such relationships have a positive effect on serum cortisol levels (Carlstead, Paris, and Brown 2019). However, there are also negative relationships between animals and keepers (Hosey and Melfi 2015). Therefore, it is not surprising that elephants interact differently with different people and even have certain "favorite attachment figures" (Rossman et al. 2017). In a playback two-choice object test, Asian elephants (*Elephas maximus*) showed that they can at least visually and olfactorily recognize their keepers (Polla, Grueter, and Smith 2018). In a matching-to-sample experiment using visual or olfactory cues from a familiar human or elephant, it is observed that *L. africana* can recognize conspecifics and familiar individual keepers (Perret 2017).

Although there are repeated reports in the media and books that elephants have recognized former keepers, mahouts or familiar people after a long time (Altevogt 1987; Chowdhury 2021; Report in New York Times 1935; Stickings 2019), there has not yet been any scientific confirmation that they can store memories of humans in their SLTM. Using a two-choice object test, the present study aims to provide evidence-based evaluations of interspecific long-term recognition in elephants to the stimuli of former keepers that they had not interacted with in over 13 years than to humans unfamiliar to them. Such information will provide us with further knowledge about the elephant-human relationship and the interspecific SLTM of elephants. This could lead to a change or adaptation of the management of the ex-situ husbandry of elephants and welfare benefits.

2 | Material and Methods

2.1 | Subjects and Housing

This study took place in the Serengeti-Park Hodenhagen, Germany, in 2022. Two *L. africana* cows (mother and daughter), Bibi (~36 years) and Panya (14.75 years), currently living in the safari-park/zoo participated in the present experiment. Three other females and two males were living together in their herd. The animals were kept in protected contact. Before their current location, Bibi and Panya, lived in Tierpark Berlin, Germany until November 2008, at which time they were transferred to

Zoo Halle, Germany. In November 2017, Bibi was relocated to the Serengeti-Park Hodenhagen. Panya (with her 1-year old male calf Ayo) was then reunited with Bibi in August 2020. The elephants were tested in an outside pre-enclosure individually, but could reach their trunks through the bars towards the experimental setup.

For this experiment, first an establishment phase was conducted for which three current keepers of the Serengeti-Park Hodenhagen were included. For the main experiment, three former keepers from the Tierpark Berlin (last interaction > 13 years), who had worked with the elephants until their move, were used as participants. They had accompanied the animals for 21, 10, and 8 years in the case of Bibi, and for 15 months in the case of Panya. For each keeper, an unfamiliar person was selected as a counterpart in the two-choice object test, this person had never been in one of the zoos where the elephants live/lived and has therefore never had any contact with the elephants. Familiar and unfamiliar people were matched according to approximate age and body stature. None of the persons were related to each other, and all were men.

2.2 | General Procedure and Experimental Set-Up

A set-up similar to that of a previous study was used and served as a basis (Polla, Grueter, and Smith 2018). In particular, Polla, Grueter, and Smith (2018) investigated whether two *E. maximus* cows at the Perth Zoo in Australia could distinguish between their current keepers and people unfamiliar with the elephants in a simultaneous two-choice object test. For this test, only single auditory, visual and olfactory stimuli were used. Here, we examined whether two *L. africana* cows could also make these differentiations, in addition to distinguishing between their former keepers and people unfamiliar to them.

The experiment took place in the pre-enclosure (186.7 m^2) next to the large shared main enclosure (~5500 m^2). The set-up itself consisted of two racks (150 cm high), each containing a sound box (Yamaha MS 202 II). Attached to each shelf was an aluminum pop-up poster frame in the front, which rose above the rack by another 80 cm. Also mounted inside the rack, were two hooks for the olfactory stimuli. Each of the two racks served as a holding device for a person's stimulus in the experiment (Figure 1). The set-up was positioned 280 cm apart from the fence, just near enough for Bibi, the larger of the two elephant cows, to reach the set-up with her trunk. Two cameras (GoPro HERO9 Black v01.72.00) were used to record the elephants' behaviors for later analysis. At a distance of approximately 5 m, one camera was located behind the set-up, and the other camera was located approximately 5 m beside the set-up to record all movements of the elephants (Figure 2). The point of view of the camera at the back also later determined the "left" and "right" positions of the experimental set-ups (see Figure 2B).

Each elephant was tested only once a day. The trial days within the individual test sections were randomized. No keepers were in direct visual contact with the elephant during the test. The area around the elephant enclosure was closed to visitors during the trials, to avoid any distraction.

2.2.1 | Stimuli

The experiment was conducted with three sensory stimuli: an auditory, an olfactory and a visual stimulus.

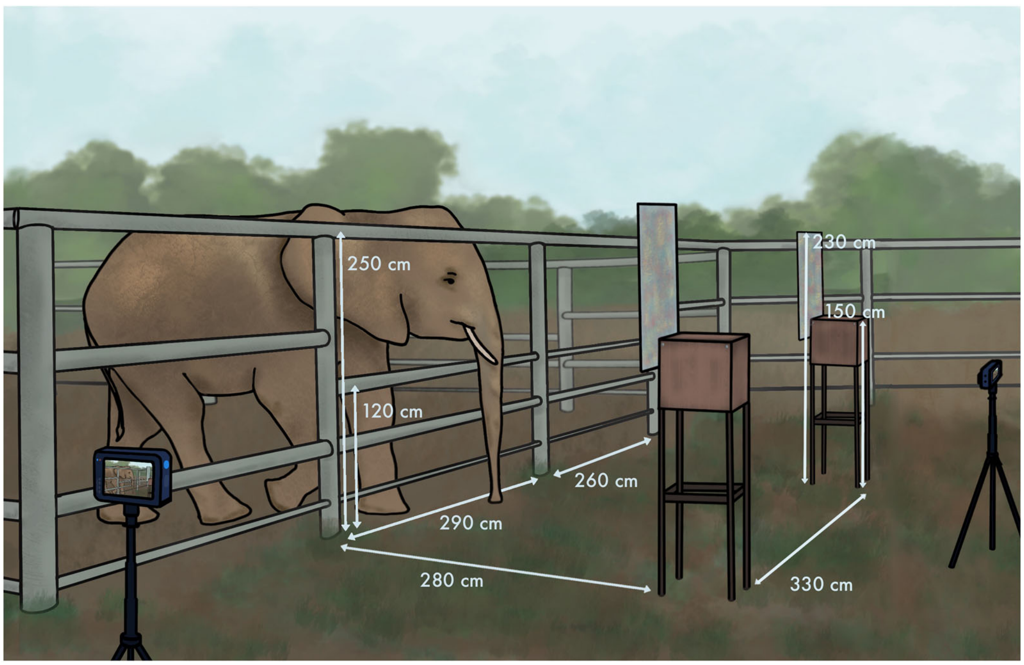

FIGURE 1 | Schematic representation of the experimental set-up. The elephant was standing in the pre-enclosure with two openings in the fence that allowed it to reach the experimental set-ups (two racks in a distance of 330 cm to each other). The behavior was recorded using one camera in front of the animal (in the center behind the two racks) and one camera lateral to the animal (perpendicular to the other camera). Designed by Luise Kränzlin. [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 2 | (A, B) Images excerpts from an establishment trial of Panya. One frame from the side camera (A) and one frame from the back camera (B) at the same second. Panya was seen reacting excitedly to the auditory stimulus when exposed to it for the first time. In the main enclosure next to it are the bull and Bibi. The time code of these frames is shown in the bottom right-hand corner. [Color figure can be viewed at wileyonlinelibrary.com]

To provide the animal with a high variability of voice tone in the auditory trials, a whole sentence in German was recorded as a stimulus: “Hallo, guten Morgen, wie geht es dir?” (English = “Hello, good morning, how are you?”). All recordings were done with the internal microphone of a Sony α 77. The test persons spoke the sentence several times so that a new recording could be played each time during the experiment to avoid the effect of recognizing characteristic background noises. For each day of the experiment, the test persons played four repetitions each. For each repetition, the sentence was repeated six times, the volume of both speakers has been equalized. The sound files were cut with the audio software “REAPER” v6.56 (REAPER 6.56, 2022).

For the olfactory test, the test persons were asked to wear a prepared white T-shirt (100% cotton) for 8 h during the night in their private surrounding, not in a zoo or in contact with other animals. Before wearing the T-shirt, the test person should take a shower and was asked not to use deodorant and perfume. We are aware that the elephants would perhaps be familiar with the holistic odor of the keeper. However, it is very likely that the composition of the care products themselves as well as the routine of the test person may have changed over the last 13 years. In addition, all three keepers were now working with other animals. Thus, we opted for the essential odor to avoid that changes of care products influenced our study. Each time after wearing the T-shirt, they had to place them (four in total) in individual plastic zip bags. These bags were stored before the test for an average of 4 weeks.

For the visual trials, photos were taken with a Sony α 77 standing on a tripod about 100 cm from the person being photographed. The persons stood in front of a white wall and looked directly into the camera. The abdomen and head were photographed (see as an example Figure S1). Each person wore either dark or brown clothing, and any imprints, such as zoo logos, were subsequently removed with the image editing software Luminar Neo v1.0.5.9506 (Luminar Neo 1.0.5.9506 2022). The individual images were printed in color and DIN A1 format (594 × 841 mm) and could later be attached to the frame on the experimental set-up.

2.3 | Trial Sections

The trial series started in May 2022 and ended in June 2022. A total of 35 trial days were conducted consecutively (Table 1). The start time of the trials was between 9:00 and 10:30 a.m. and was adjusted according to the keepers' work schedule. In the experiment, each animal was alone in the pre-enclosure for 4 min and was free to decide whether it interacted with the experimental set-up or not.

To familiarize the animals with the experimental set-up and routine, an acclimatization period was carried out before the actual experiment. For this purpose, the planned routine without stimuli was conducted on 8 days.

For the establishment, three current keepers and three random people (unfamiliar), were asked to provide each of the three different stimuli. The stimuli were randomized as well as the arrangement of the test persons on the test set-ups (right and left).

Right after the establishment, the trial days of the experiment started, in which stimuli from the former keepers and new unfamiliar people were used. The trial days and the arrangement of the test persons were also randomized. The experiment was then repeated with the same elephants again to obtain a higher number of trails. The order of the trial days and the arrangement of the test persons were again randomized.

2.4 | Data Analysis

The recordings of the trial days were randomized and analyzed blindly via the software "BORIS" (Behavioral Observation Research Interactive Software) v7.13.6 (Friard and Gamba 2016). Three parameters were determined for the quantitative statistical analysis. The most important parameter is the "trunk reach duration" (TRD), which describes the time the elephant directs the tip of its trunk towards the stimulus. Linked to this is the "trunk reach frequency" (TRF), that is, how often the elephant points the tip of its trunk at the stimulus. The TRD and TRF were measured whenever the tip of the trunk was 90 cm from the base of the trunk, 70 cm above the ground and pointed directly at the stimulus. The third parameter is the "time of interest" (TOI), that is, the time the elephant is facing a stimulus. The TOI was measured from the time the elephant crossed the bars of the fence until the time its head was behind the bars again. In addition, the initial interest in responses to stimuli by the elephants was recorded, that is, the first TRD/TRF. Due to the temporally different appearance of the auditory

TABLE 1 | Randomized stimuli schedule.

		Acclimatization								Establishment								
Day		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Bibi	Left									1O	2A		3V			3O	2O	
	Right											2V		3A	1A			1V
Panya	Left									1O	3A			2O			1V	
	Right											1A	3V		2V	3O		2A

		Experiment trial 1									Experiment trial 2								
Day		18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Bibi	Left		5O		5A	4V				6O	4A				6V		6A	5O	
	Right	6V		4A			4O	6A	5V			6O	5V	4O		4V			5A
Panya	Left	4A	6O				5V	4O		6V		6O	6A				6V		5A
	Right			5O	4V	6A			5A		4V			5V	5O	4A		4O	

Note: For the four experimental sections: Acclimatization, Establishment, Experiment trial 1 and Experiment trial 2. Divided is whether the familiar person's stimulus was on the left or right experimental setup. Also indicated is the experimental group (Current keepers 1–3, Old keepers 4–6). In addition, the stimuli carried out on the respective day: auditory (A/light gray), olfactory (O/dark gray) or visual (V/white).

stimulus, the initial interest could not be evaluated for these stimuli.

2.5 | Statistical Analysis

The statistical analysis and graphs were done with R v4.3.1 (R Core Team 2023). All statistical tests were preceded by a check for normal distribution using the Shapiro-Wilk test. None of the data were normally distributed, so non-parametric tests were used. For the entire study, permutation tests using a for-loop were applied. For each sensory stimulus (auditory, olfactory, and visual) and parameter (TOI, TRD, and TRF), the distribution of the mean differences between the groups (familiar and unfamiliar) was determined. The values within each group were permuted and the significance level was then determined from the observed and expected differences (an example r code can be found in File S4). For each test, 10,000 permutations were performed. The significance level was set at $\alpha = 0.05$.

During acclimatization, it was determined whether the animals showed a side preference to the experimental set-ups. For this purpose, TRD, TRF and TOI for right and left were tested for statistical significance. If the null hypothesis—no preference for one side—was not rejected for both animals, it could be assumed for further experiments that both animals had no preference and their data from the following phases could be pooled as one data set. For the establishment phase, it was tested if there was a difference in behavior towards familiar (current keepers) and unfamiliar individuals. Since the three parameters were constant for all stimuli and, assuming that the elephants could in principal identify familiar people through all three senses, the data from the three different stimuli were analyzed together. For the main experiment, it was tested for a difference between behavior towards familiar (former keepers) and unfamiliar people, as in the establishment. The two data sets from Experiment 1 and Experiment 2 were combined resulting in $n = 12$ trials. Again, both the individual stimuli alone and all three stimuli together were analyzed.

3 | Results

The "trunk reach duration" (TRD), "trunk reach frequency" (TRF) and "time of interest" (TOI) were recorded at any time by the cameras and were subsequently evaluated. Both elephants walked into the enclosure freely on all days of the trials.

3.1 | Acclimatization

Both elephant cows were given 8 days of acclimatization with 4 min each day to get used to the experimental set-ups and the slightly different morning routine. Neither of the two elephants showed a statistically significant preference for one side for any of the three parameters (permutation test, $n = 8$. TRD: $p_{Bibi} = 0.204$, $p_{Panya} = 1$; TRF: $p_{Bibi} = 0.559$, $p_{Panya} = 1$; TOI: $p_{Bibi} = 0.994$, $p_{Panya} = 1$).

3.2 | Establishment

The establishment phase was first carried out with samples from the three current keepers and three people unfamiliar to the animals. Since neither of the two elephants showed a side preference for an experimental setup, the results from the establishment of both elephants were combined. For both the individual stimuli and all stimuli combined, no statistically significant difference in behavior was found for any parameter for the different groups of people, except for the visual stimuli where the animals showed significantly more TRD and TRF for the familiar stimuli (Table 3). The average TRD for the visual familiar stimuli was 21.9 times as long ($\varnothing_{Familiar} = 1.22 \pm 1.30$ s, $\varnothing_{Unfamiliar} = 0.06 \pm 0.14$ s) and the average TRF was 7.9 times as often ($\varnothing_{Familiar} = 1.33 \pm 0.82$, $\varnothing_{Unfamiliar} = 0.17 \pm 0.41$) as for the unfamiliar stimuli, however, with large standard deviations.

In addition, the animals showed during the trials with visual stimuli interest first in the familiar stimuli four times each, once in the unfamiliar stimuli first, and once Panya showed no TRD/TRF at all. In the case of auditory stimuli, there was a direct inverse correlation of the first interest, four times first for unfamiliar, once for familiar.

3.3 | Experiment Trials 1 and 2

The trial phases were carried out with samples from the three former keepers and three new unfamiliar persons. By testing the differences between Trial 1 and Trial 2, no significant difference could be found (Table 2), therefore the data was merged. With the merged data, a significance can only be found for TRD for the olfactory stimuli (Table 3 and Figure 3). The average TRD for the familiar stimuli was 5.9 times as long as for the unfamiliar stimuli ($\varnothing_{Familiar} = 1.39 \pm 1.52$ s, $\varnothing_{Unfamiliar} = 0.24 \pm 0.41$ s), however, with large standard deviations.

When all stimuli were examined together, a statistically significant difference could be seen for both TRD and TRF to the familiar versus unfamiliar stimuli (Table 3 and Figure 4). In total, the average TRD for the familiar stimuli was 3.2 times as long ($\varnothing_{Familiar} = 1.17 \pm 1.37$ s, $\varnothing_{Unfamiliar} = 0.36 \pm 1.02$ s) and the average for TRF was 2.4 times as often ($\varnothing_{Familiar} = 0.94 \pm 1.26$, $\varnothing_{Unfamiliar} = 0.39 \pm 0.69$) as for the unfamiliar stimuli, however, with large standard deviations.

TABLE 2 | *p* values of the permutation tests between the samples of the Experimental trial 1 and the Experimental trial 2.

	Auditory			Olfactory			Visual		
	TOI	TRD	TRF	TOI	TRD	TRF	TOI	TRD	TRF
Familiar	0. 982	0.350	0. 275	0.466	0.678	0.709	0.781	0.371	0.455
Unfamiliar	0.955	1.000	1.000	0.180	0.733	1.000	0.607	0.878	1.000

TABLE 3 | *p* values of the permutation tests in the establishment and experiment (Trials 1 and 2) for individual (auditory, olfactory, and visual) and combined (all) stimuli.

		Auditory	Olfactory	Visual	All
Establishment	TOI	0.762	0.804	0.672	0.887
	TRD	0.071	0.454	0.027*	0.438
	TRF	0.257	0.730	0.042*	0.482
Experiment	TOI	0.176	0.464	0.674	0.602
	TRD	0.120	0.021*	0.321	0.006**
	TRF	0.259	0.281	0.212	0.028*

*$p < 0.05$; **$p < 0.01$.

During the trials with olfactory and visual stimuli, the animals showed initial interest in the familiar stimuli six times and twice in the unfamiliar stimuli; four times they showed no interest in any stimuli.

The average results of the test series as well as the results as raw data can be found in the supplementary materials (see Tables S2 and S3).

4 | Discussion

The current study indicates that *L. africana* in zoos may recognize and distinguish between familiar and unfamiliar humans even after at least 13 years. When all three stimuli were analyzed in their entirety, there was a significantly longer duration and frequency that the two animals moved their trunks to the potentially familiar stimuli, demonstrating primarily a higher interest in familiar than in unfamiliar people, a possible indication of long-term memory abilities.

Although the animals showed significantly longer TRD for the olfactory stimuli of former keepers compared to unfamiliar people, we could not detect this behavior for the visual and auditory stimuli. Elephants are reported to show incredible olfactory discrimination in other experimental tests (Arvidsson, Amundin, and Laska 2012; Rizvanovic, Amundin, and Laska 2013), human scent matching to sample (von Dürckheim et al. 2018), olfactory recognition of people (Perret 2017; Polla, Grueter, and Smith 2018) and also in olfactory SLTM capabilities in mother-daughter relationships (Hoerner et al. 2023). Our results on olfactory sense agree with the findings from these studies. It should be noted that on the last experimental day with the visual stimulus, Bibi managed to push herself particularly far between the poles and knocked over the experimental set-up of the unfamiliar person. For this, she used comparatively more time ($t_{27} = 5.789$ s). If this trial is considered an outlier and thus excluded, there is a significant difference between familiar and unfamiliar persons for TRD ($p = 0.010$; $n = 11$) for the visual stimuli. The difference for TOI ($p = 0.720$; $n = 11$) and TRF ($p = 0.107$; $n = 11$) remained nonsignificant. The finding that the difference in TRD is significant would also be consistent with the fact that the initial interest in olfactory and visual stimuli was equally high. The fact that the animals were three times as often (12:4) interested in the familiar stimulus first not only shows the high level of interest in the former keepers but also that they must have already analyzed the stimulus before TRD/TRF.

In the establishment phase of the study, only the visual stimuli showed a higher initial interest and a significant positive difference for TRD and TRF for the familiar stimuli. Why there were lower initial interest in familiar stimuli and no significant difference in parameter for the olfactory stimuli, like in the main experiment, or even a difference for the auditory stimuli is unclear. One possible explanation could be that there is also interest in strangers, because visitors at the zoo interact with the elephants, through protected contact, and have permission to feed them with specific food purchased at a nearby kiosk. In addition, scents of former keepers (experimental phase) may be easier to distinguish from those of unfamiliar persons, than the scents of the current keepers (establishment phase) to unfamiliar persons. This may be due to long-term memory processes, and because the elephants were tested in the same environment as the current keepers and also have daily interaction with visitors. So in the establishment phase, they may have relied more on subtle visual cues than on olfactory cues. This remains to be further tested. Another possibility is with differences in the method of the experimental set-up. A study by Plotnik et al. (2014) observed that *E. maximus* were unable to locate food via acoustic signals derived directly from the food, suggesting that elephants failed to use auditory information when it was the only cue presented to them. However, in a previous object choice task, they were able to locate food with vocal cues, after they received prior training with the cues (Plotnik et al. 2013). Thus, future studies may pair multi-modal cues or include prior training to improve reaction to stimuli from familiar humans, as experiences are not based on only one sensory system. In a similar experiment, Polla, Grueter, and Smith (2018) showed that *E. maximus* was able to distinguish current keepers from unfamiliar people, relying on olfactory and visual stimuli. Our findings are comparable with the results from Polla, Grueter, and Smith (2018) in their nature as two-choice object tests, despite slight differences in the methodology, such as variation in type of stimuli and evaluation of a different elephant species. For example, the T-shirts used in our study for the olfactory cues were stored in plastic zip bags for an average of 4 weeks before use, whereas in the study by Polla, Grueter, and Smith (2018), cutouts from the armpit area of the T-shirts were used on the same day they were worn. Furthermore, the current study used a whole sentence in German for auditory cues, whereas Polla, Grueter, and Smith (2018) used one word: "Hello." Although the behavior in tests of the two elephant species is comparable in some experiments (see Snyder et al. 2021), discrepancies in the results of comparable experiments with both species have been shown in the past.

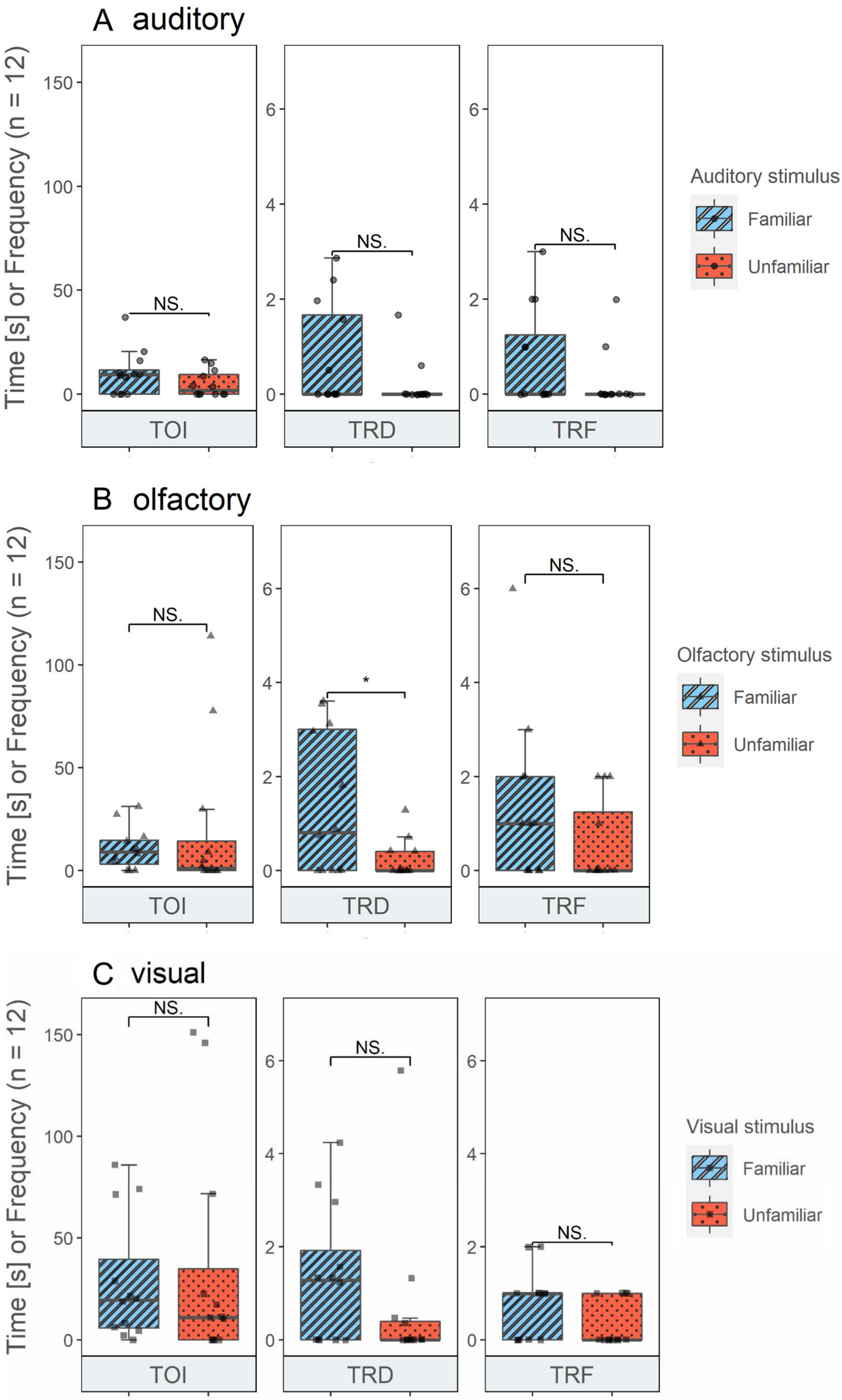

FIGURE 3 | (A–C) Boxplot of TOI, TRD and TRF parameters for (A) auditory, (B) olfactory, and (C) visual stimuli in the experimental phase. Blue-striped bars represent the familiar people (former keepers). Red-dotted bars represent the unfamiliar people. TOI is the time of interest, TRD is the trunk reach duration, and TRF is the trunk reach frequency ($n = 12$). NS. = $p > 0.05$, *$p < 0.05$. Error bars = SD. In black are the data points. [Color figure can be viewed at wileyonlinelibrary.com]

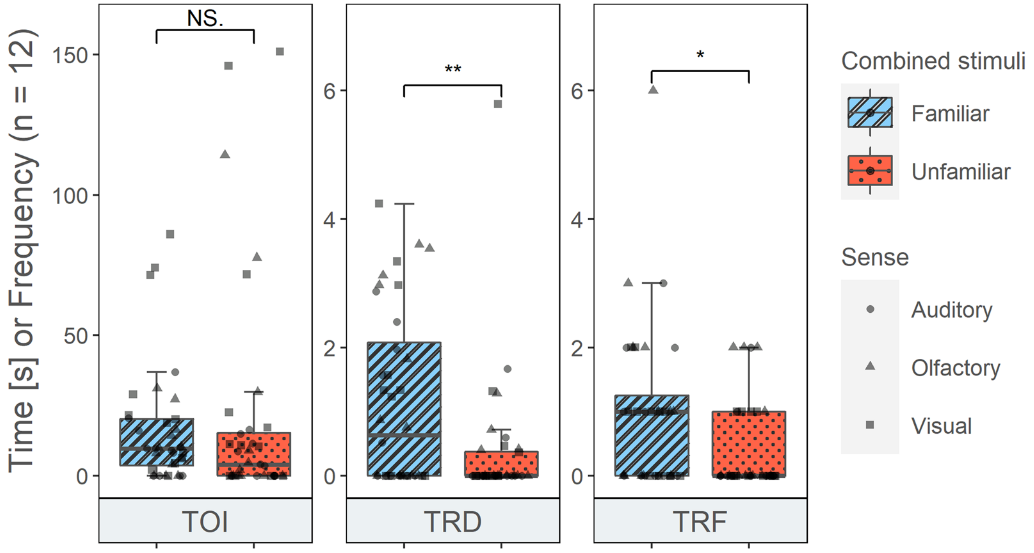

FIGURE 4 | Boxplot of TOI, TRD, and TRF parameters for all three stimuli combined in the experimental phase. Blue-striped bars represent the familiar people (former keepers). Red-dotted bars represent the unfamiliar people. TOI is the time of interest, TRD is the Trunk reach duration, and TRF is the trunk reach frequency ($n = 36$). NS. = $p > 0.05$, *$p < 0.05$, **$p < 0.01$. Error bars = SD. In black are the data points. [Color figure can be viewed at wileyonlinelibrary.com]

Plotnik et al. (2013) showed that *E. maximus* cannot use visual cues from humans to find food, but in the same year Smet and Byrne (2013) showed that *L. africana* is able to do so. However, in adapted replicate experiments with *E. maximus*, no ability to use the visual cues was again shown for this species by another study (Ketchaisri, Siripunkaw, and Plotnik 2019). The authors argued that this could be due to the different species but could also have something to do with the methodology and the environment of the animals. This also applies to the present experiments. *E. maximus* in the experiment from Polla, Grueter, and Smith (2018) spent more time interacting with the stimuli ($\mathrm{TOI}_{\varnothing} = 169.751$, $s = 77.582$, $n = 9$) than *L. africana* in the present experiment ($\mathrm{TOI}_{\varnothing} = 62.310$, $s = 56.778$, $n = 9$). Thus, in addition to the differences in the experimental procedure, differences in the behavior of two species may also have led to the different results between the experiments. Both species exploit similar niches and are highly social animals, but the structure of the societies they live in is different (de Silva and Wittemyer 2012). In contrast to *L. africana*, *E. maximus* live in smaller, more fluid groups (de Silva and Wittemyer 2012). It is not clear, but maybe the stronger fission-fusion dynamics in *E. maximus* allows for increased associations in small groups (Nandini, Keerthipriya, and Vidya 2017) and more time spent in recognizing other individuals, which could extend to social bonds across species, that is, human relationships (Stoeger et al. 2012). Another aspect is the difference in personality and in coping with anthropogenic challenges. A review of published findings on *L. africana* and *E. maximus* from 1980 to 2023 revealed that stress responses vary within and across individuals exposed to similar stimuli, and not always in a predictable fashion (Pokharel and Brown 2023). Thus, individual behavioral characteristics may explain the differences observed in time interacting with the stimuli.

Due to the often-small sample sizes, statistical challenges are quite common in zoo science, but should be avoided where feasible (Kuhar 2006). In the present experiment, the animals were given the opportunity to react to the same stimulus on different days. This repetition of the main experiment (i.e., increased number of trials) aimed at increasing the robustness of the results. However, it should be kept in mind that a higher number of trials does not equal a greater sample size. And also the likely different effect sizes between the stimuli should be considered. Analyzing the three together is therefore statistically questionable.

4.1 | General Observations and Differences in the Elephants

Since Panya was with her 5-year-old son during the day and night, she showed clear discomfort at the beginning of the acclimatization phase when she was spatially separated from him. She displayed this discomfort on the first days by vocalizing loudly, flaring her ears, and prancing around wildly. As the days went by, this behavior subsided, and Panya visibly became more relaxed with the situation. On the first day of testing with the auditory stimulus, Panya and Bibi showed imposing behavior, this involved erect ears and short mock attacks to the set-ups, however, also here a habituation set in quickly. This habituation can also be observed in other experiments with elephants and audio speakers (Goodyear and Schulte 2015).

Bibi was sometimes quite fearless to the set-ups, whereas Panya was much more cautious. The keepers described Bibi as an elephant that may be dominant in her interactions. As a mother of five children, she is a very experienced elephant cow, unlike Panya who is only half her age and is probably not yet able to assess such situations as well as her mother. This may lead to Panya spending more time on the set-ups than Bibi and thus having a significantly higher TOI during all phases than her mother ($t\varnothing_{\mathrm{Bibi}} = 33.496\,\mathrm{s}$, $t\varnothing_{\mathrm{Panya}} = 73.397\,\mathrm{s}$, permutation test: $p = 0.008$, $n = 35$). Another explanation could be that since

Bibi displays stereotypical behavior (head weaving), she may not have enough time to spend on the set-ups. We could not observe a relationship between the stereotypical behavior and a familiar, or unfamiliar person. With the exception of the overturning of the experimental set-up, no other changes in behavior could be observed that were possibly related to a positive or negative attitude of the elephant towards the test persons, such as temporal gland secretions, or signs of a greeting ceremony.

Conducting experiments outdoors is usually not free from environmental influences. This was the case in this experiment due to the structural circumstances in the zoo. The influence of short-term separation on the elephant cows from other herd members cannot be fully evaluated. The bull, for example, distracted the two elephant cows a few times during their trials, but no change in behavior could be observed after the contact and the lost time in the trial had to be accepted. Elephants engaged in other behaviors such as leaning against a grid in the pre-enclosure and eating grass. This happened on the opposite side of the experimental set-up, but also near the set-up itself dedicated directly to the experimental set-up were impacted. However, such behaviors were accepted within the set 4 min time limit. Furthermore, when the elephants ate grass at the experimental set-up, the time was always included in the TOI. It was repeatedly observed that after eating and during the time it took to pull their heads back through the bars, the animals quickly checked the set-up again with their trunk (TRD). We therefore assume that eating grass at the set-up was partly due to the presence of the set-up. Yet, we cannot fully determine whether this had an influence on the decision of the animals about their position to the experimental set-up.

4.2 | Perspectives

Elephants have sex-specific lifestyles, with females living in family fission-fusion herds under an older matriarch and males separating from the group at adolescence and living in bachelor groups, often under older bulls, or sometimes as solitary individuals (Evans and Harris 2008; Murphy, Mumby, and Henley 2019). So far, no sex-specific differences have been studied in recognition studies. However, and because of the different lifestyles, bulls should be included in a further study to investigate whether there are sex-specific differences. In addition, the results should be confirmed in a study with a larger sample size in elephants and former keepers. Besides, an adaptation of the experiment with e.g. cross-modal sensory stimuli or the possibility to have the keepers present would be conceivable. When elephants in zoos undergo reunification after years of separation, they exhibited signs of the greeting ceremony that is common in the wild (Hörner et al. 2021). If signs of the greeting ceremony could also be evaluated in the meeting with the former keepers, it would provide further scientific evidence for the special bond between keeper and elephant. In contrast to this positive relationship, a comparison could be made with individuals negatively linked to the animals, such as disliked keepers or veterinarians. For wild *L. africana*, such emotion-cognition linked recognitions are made between harmless (Kamba, Kenya) and dangerous people (Maasai, Kenya), and this is observed auditorily (McComb et al. 2014), olfactorily and visually (Bates et al. 2007). This distinction is essential for survival, as there could be significant differences between people with different levels of preference and relationships for the elephants in the zoo.

5 | Conclusion

Previously, strong performance in SLTM has been observed in several species of birds and mammals in the wild and in captivity. Common ravens (*Corvus corax*) can discriminate between familiar and unfamiliar calls after a period of time of at least 3 years (Boeckle and Bugnyar 2012). Northern sea bears (*Callorhinus ursinus*) and cotton-top tamarins (*Saguinus oedipus*) can recognize calls from their conspecifics after a period of time of at least 4 years (*C. ursinus*: Insley 2000; *S. oedipus*: Matthews and Snowdon 2011). Bottlenose dolphins (*Tursiops truncates*) show a different response to calls from familiar individuals than from unfamiliar ones, even after more than 20 years (Bruck 2013). Chimpanzees (*Pan troglodytes)* and bonobos (*Pan paniscus*) show a significantly higher interest in pictures of conspecifics that they know but have not seen for partly over 25 years than in individuals that are unfamiliar to them (Lewis et al. 2023). The so-called greeting ceremony was observed during the reunion of *L. africana* in European zoos after a separation of 2 and 12 years (Hörner et al. 2021), which has also been observed in the wild when they reunite (Moss, Croze, and Lee 2011). In *L. africana*, in particular, social knowledge and the SLTM may play a crucial role because memory duration can affect reproductive success, thus affecting fitness (e.g., McComb et al. 2001). The results of the present study hint at interspecific SLTM for their zoo keepers. In the establishment phase during trials with the visual stimuli, the two elephant cows exhibited higher initial interest and significantly greater TRD and TRF in stimuli from their current keepers than in stimuli from persons unfamiliar to them. During the experimental phase, they showed significantly greater TRD on olfactory stimuli from former keepers than from unfamiliar persons. If the 1 day of trials when Bibi overturned the experimental set-up with the unfamiliar stimuli was excluded, then significantly greater TRD was also shown during trials with visual stimuli. Initial interest for the olfactory and visual stimuli, was three times more often for the familiar compared to the unfamiliar stimuli. These findings suggest that female *L. africana* in zoos can store memory of humans in their SLTM. This is especially surprising since Panya was only 1 year old when she left Tierpark Berlin and her former keepers. However, there were many influencing factors that could have affected the animals' behavior, so the findings of this experiment are to be interpreted with caution.

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Ethics Statement

This study was discussed with the responsible ministry ("Niedersächsische Landesamt für Verbraucherschutz und Lebensmittelsicherheit") in Lower Saxony, Germany, and it was determined that no further approval was needed for its implementation.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in the Supporting Information of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.