Animal Cognition
https://doi.org/10.1007/s10071-019-01283-0

ORIGINAL PAPER

The use of a human's location and social cues by Asian elephants in an object-choice task

Oraya Ketchaisri[1] · Chomcheun Siripunkaw[1] · Joshua M. Plotnik[1,2]

Received: 13 December 2018 / Revised: 10 June 2019 / Accepted: 12 June 2019

Abstract

Asian elephants have previously demonstrated an ability to follow olfactory cues, but not human-provided social cues like pointing and gazing or orienting to find hidden food (Plotnik et al. in PLoS One 8:e61174, 2013; Anim Behav 88:91–98, 2014). In a study conducted with African elephants, however, elephants were able to follow a combination of these social cues to find food, even when the experimenter's position was counter to the location of the food. The authors of the latter study argued that the differences in the two species' performances might have been due to methodological differences in the study designs (Smet and Byrne in Curr Biol 23(20):2033–2037, 2013). To further investigate the reasons for these potential differences, we partially adapted Smet and Byrne (2013)'s design for a group of Asian elephants in Thailand. In a two-object-choice task in which only one of two buckets was baited with food, we found that, as a group, the elephants did not follow cues provided by an experimenter when she was positioned either equidistant between the buckets or closer to the incorrect bucket when providing the cues. The elephants did, however, follow cues when the experimenter was closer to the correct bucket. In addition, there was individual variability in the elephants' performance within and across experimental conditions. This indicates that in general, for Asian elephants, the pointing and/or gazing cues alone may not be salient enough; local enhancement in the form of the experimenter's position in relation to the food reward may represent a crucial, complementary cue. These results suggest that the variability within and between the species in their performance on these tasks could be due to a number of factors, including methodology, the elephants' experiences with their handlers, ecological differences in how Asian and African elephants use non-visual sensory information to find food in the wild, or some combination of the three.

Keywords Asian elephants · Cognition · Object-choice · Visual cues · Elephant behavior

Introduction

An active area of research aims to investigate whether or not non-human animals can follow visual cues to find out-of-sight food rewards (for a review, see Miklósi and Soproni 2006; Mulcahy and Hedge 2012). Many of these studies employ an object-choice task during which a human experimenter provides an animal with a cue about the location of food hidden in, under or behind one of the two buckets. These cues are usually visual (e.g., pointing, gazing/orienting or both—e.g., Itakura and Tanaka 1998; Hare and Tomasello 1999; Call et al. 2000; Krause et al. 2018), but sometimes acoustic (e.g., providing a cue about the food's location by shaking the buckets—Call 2004; Plotnik et al. 2014) or olfactory (by providing the animal with direct access to the smell of the buckets' contents—Plotnik et al. 2014). Results with a wide range of non-human primate species have been mixed on these tasks, with variability both within and between species most likely due to differences in methodology, experience with humans, and previous exposure to cues (e.g., chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*)—Itakura and Tanaka 1998, Call et al. 2000; capuchin monkeys (*Cebus apella*)—Itakura and Anderson 1996; Essler et al. 2017; and cotton-top tamarins (*Saguinus oedipus*)—Neiworth et al. 2002).

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10071-019-01283-0) contains supplementary material, which is available to authorized users.

✉ Joshua M. Plotnik
Joshua.Plotnik@gmail.com

1 Conservation Biology Program, Mahidol University, Kanchanaburi Campus, 199 Moo 9, Highway No. 323, Lum Sum, Sai Yok, Kanchanaburi 71150, Thailand

2 Department of Psychology, Hunter College, City University of New York, 695 Park Avenue, New York, NY 10065, USA

Published online: 19 June 2019

Interestingly, many domesticated animals have performed relatively well on similar object-choice tasks (e.g., dogs (*Canis familiaris*)—Hare et al. 2002, Virányi et al. 2008; goats (*Capra hircus*)—Kaminski et al. 2005; pigs (*Sus scrofa domestica*)—Nawroth et al. 2014; and horses (*Equus caballus*)—Maros et al. 2008, Proops et al. 2010). One explanation for the success of these latter species is the so-called domestication hypothesis (Hare et al. 2002), which argues that domesticated animals, through artificial selection for physical or behavioral traits preferred by humans, have gained (either directly or as an evolutionary byproduct) the social capacity for following human-provided cues (but see, for example, Hare et al. 2010; Udell et al. 2008; 2010 and Range and Virányi 2015, for discussions about this hypothesis).

There are in fact a number of other hypotheses that have also been proposed to account for species-level differences in performance on object-choice tasks in which non-human animals respond to a variety of cues about the location of rewards. Some of these hypotheses, as outlined by Mulcahy and Hedge (2012), focus on differences in social pressures within groups (cooperative vs. competitive relationships—Hare 2001; Hare and Tomasello 2004), or in the physical way in which the objects are presented in relation to the animal's perspective (Mulcahy and Call 2009), as well as the possibility that animals are simply distracted and thus affected by the presence of multiple containers during tasks (Mulcahy and Hedge 2012). Indeed, like the primates, it is likely that the variability both within and between species in responses to human-provided visual cues is due to a number of factors beyond domestication, including previous experience with human experimenters or handlers. This may partially explain why a number of non-domesticated, non-primate species have also successfully followed such cues (e.g., South African fur seals (*Arctocephalus pusillus*)—Scheumann and Call 2004; African gray parrots (*Psittacus erithacus*)—Giret et al. 2009; dolphins (*Tursiops truncatus*)—Herman et al. 1999; Tschudin et al. 2001; jackdaws (*Corvus monedula*)—von Bayern and Emery 2009; and Clark's nutcrackers (*Nucifraga columbiana*)—Tornick et al. 2011).

Captive Asian elephants (*Elephas maximus*) are unique test subjects for the domestication hypothesis in particular because, unlike other animals living with humans that have undergone artificial selection, they are often highly tame yet genetically indistinguishable from elephants in the wild (Lair 1997). In a previous experiment, a group of Asian elephants in Thailand did not follow human-provided visual social cues to find food (Plotnik et al. 2013). This was surprising given their close, often life-long relationships with their handlers ('mahouts'), but consistent with recent research suggesting that non-visual cues (specifically, olfactory cues) about the location of food may be more salient to elephants (Plotnik et al. 2014, 2019; von Dürckheim et al. 2018; Schmitt et al. 2018). Thus, it is possible that object-choice tasks in general require careful attention to species-relevant testing paradigms before direct comparisons can be made (Mulcahy and Hedge 2012).

Interestingly, Smet and Byrne (2013) conducted a similar visual cue study with captive African elephants and found that the elephants could follow different combinations of pointing and gazing cues directed toward a baited food bucket even when the experimenter was positioned near the incorrect, un-baited alternative. Both Plotnik et al. (2013) and Smet and Byrne (2013) used a simple object-choice task in which the experimenter stood between two buckets and provided a visual cue toward the hidden food's location. The elephant was then able to make a choice between the two buckets. The studies differed, however, in a number of ways. First, Plotnik et al. (2013)'s setup involved a sliding table stationed out of the elephant's reach on which the buckets were anchored to either end. The experimenter provided a cue to the elephant while always standing equidistant between the buckets, and removed the cue before pushing the table up to the elephant, so that he or she could make a choice. The experiment was conducted under an outdoor, shaded structure, and the elephants stood in a fixed location and thus had to wait for the table to be pushed toward them before they could interact with the buckets. The experimenter provided a pointing cue, an orient cue (i.e., a sustained gaze + body orientation toward the correct bucket), or a combination of the two for 5 s before pushing the table toward the elephants. Smet and Byrne (2013) conducted their experiment outside under normal daylight conditions, and allowed the elephants to approach the experimenter who stood, depending on the condition, either equidistant between the two buckets or closer to and behind either the baited or un-baited one. In addition, the experimenter provided the cue up until the time the elephant made a choice, so the elephant could see and potentially use the cue from both a distance and once they reached the buckets' location. Finally, the two experiments differed in how they presented the gazing/orient cue: Smet and Byrne (2013) provided an alternating cue by which the experimenter repeatedly shifted their gaze from the bucket to the elephant and back until the elephant had made a choice, while Plotnik et al. (2013) oriented the entire body, temporarily, approximately 45° toward the baited bucket.

Asian elephants live in relatively small, dynamic family groups, and often move within dense, low-visibility forests (de Silva and Wittemyer 2012; Sukumar 2003), where vision may not be as important as olfaction and audition. African savannah elephants (*Loxodonta africana*), on the other hand, often move across vast, open landscapes with varying-sized family groups (Moss et al. 2011), where visual cues from conspecifics may be substantially more relevant. Thus, it is possible that these ecological differences between Asian and African elephants could explain the differences in their performance on these experiments. We hypothesized, however, that it was more likely that the differences in the two species' performances on these tasks were due to methodology or prior experience rather than ecology or cognition.

Thus, we conducted a set of experiments to further investigate the performance differences of the Asian and African elephants on visual social-cuing tasks. Specifically, we were interested in providing a new group of Asian elephants—separate from those tested in (Plotnik et al. 2013, 2014, 2019) and at a different facility—with a setup that (a) allowed them to view the visual cue for a prolonged period from the time they were released toward the buckets until the time they made a choice, (b) included multiple experimenter positions as well as pointing, alternating gazing and both as conditions, and (c) tested the elephants without the confound of low light due to a shaded testing area. Although not exhaustive, these changes to the original procedure used with Asian elephants (Plotnik et al. 2013) were made to account for the most crucial methodological differences in Smet and Byrne (2013). Together, they provide an avenue for directly testing whether the differences in performance across the two elephant species on visual object-choice tasks are due to methodology. If they are not, and African elephants are actually better at following human-provided visual cues than Asian elephants, then future experiments should aim to investigate why.

Materials and methods

Subjects

Our subjects were 7 captive, female Asian elephants aged between 22 and 66 years (Table 1). All of the elephants were housed at Elephants World, a facility for elephants in Kanchanaburi, Thailand, and tested between December, 2014 and May, 2015. Each elephant was handled and cared for by an individual mahout; he was responsible for the elephants' daily care and husbandry, as well as for handling them during all experimental sessions. Veterinary care was provided as needed for the elephants at the facility.

Design

Training stages

Training ensured the elephants recognized first that food could be found inside buckets, and second that when presented with a two-bucket choice, only one bucket would contain food. In single-bucket training, the experimenter (the first author—O.K.) stood behind a single, non-transparent bucket (40-cm tall, 30-L volume) and put a banana (food reward) into the bucket in full view of the elephant. The elephant and her mahout stood ~ 4–5 m beyond the bucket before the mahout was signaled to release the elephant toward it. Mahouts either stood at the starting point after

Table 1 Raw data for success across all elephants in the three experimental conditions

Subjects (age in years)	Body centered (experiment 1)				Asymmetric congruent (experiment 2)				Asymmetric incongruent (experiment 3)			
	T	G	T + G	C	T	G	T + G	C	T	G	T + G	C
Somboon (61)	17*	8	17*	11	22*	21*	21*	10	11	8	6**	12
Malee (46)	17*	18*	17*	12	12	18*	14	12	10	13	11	15
Nimochi (22)	12	12	9	6**	13	16	13	12	14	13	9	11
Kammoon (66)	17*	8	13	9	16	16	13	11	15	7**	10	11
Tangmo (55)	17*	12	20*	15	21*	19*	20*	13	9	13	15	12
To-Me (51)	15	10	15	12	18*	13	19*	10	20*	17*	17*	9
Gaina (55)	10	13	12	14	19*	13	19*	12	14	8	13	14
Median	17	12	15	12	18	16	19	12	14	13	11	12
IQR	5	5	5	5	8	6	7	2	5	5	6	3
W−	20	6	18.5	5.5	**21**	**28**	**28**	1.5	18.5	12.5	12	7.5
W+	1	9	2.5	9.5	**0**	**0**	**0**	8.5	9.5	15.5	16	7.5
P value	0.063	0.750	0.125	0.688	**0.031**	**0.016**	**0.016**	0.375	0.516	0.750	0.813	1.000

Total number of correct trials (out of 24 possible) per condition per elephant in each of the three experiments. *T* pointing only, *G* gazing only, *T* + *G* pointing-with-gazing, *C* control without any cues. *$P < 0.05$ in binomial tests in the expected direction (significantly better than chance), **$P < 0.05$ in the binomial tests in the other direction (significantly worse than chance). Wilcoxon signed-rank tests show the W− and W+ statistics (negative and positive ranks) and whether the elephants, as a group, scored significantly better than chance (12 out of 24 trials) in any given condition of each experiment (the exact, two-tailed *P* value is provided, and significant results are bolded). For the Wilcoxon test, tied ranks were averaged and scores tied with chance levels were dropped from the analyses the elephants' release, or walked behind the elephant. If necessary, in training only, mahouts could direct elephants toward the bucket containing the food. Elephants had 2 min to approach the bucket and retrieve the food before the elephant was returned to the starting point and the buckets were reset. Each elephant participated in 10 trials of one-bucket training, during which all of the elephants learned to approach and retrieve food from the bucket.

In two-bucket training, the experimenter stood equidistant between two buckets placed ~ 1.5 m apart and called the elephant's name three times before placing the banana in one of the two buckets in full view of the elephant. The experimenter then cued the mahout to release the elephant from the starting point, ~ 4–5 m beyond the buckets. While food was placed in only one of the buckets ('the correct one'), the elephant was allowed to search them both. After the elephant retrieved the food, the mahout called her back to the starting position. Elephants were given 12-trial sets and reached criterion when they successfully chose the correct bucket as their first choice in 10 out of 12 trials within a single set (> 80%). The seven elephants took between 1 and 8 sets to complete this stage (mean = 4.63).

Experiments

There were three main experiments based on the location of the experimenter in relation to bucket placement, and four conditions within each experiment. Each experiment consisted of four sets of 24 trials each, with each set consisting of 6 trials of each of the four conditions. Thus, each experiment consisted of a total of 96 trials, with 24 trials of each condition performed per experiment. Each set of 24 trials took approximately 30 min to perform per elephant, and only one set was conducted with each elephant on any given day. Elephants completed all sets within a given experiment before moving on to the next one.

Each of the three experiments differed as to the location of the experimenter in relation to the buckets. In 'experiment 1', the experimenter provided one of the three cues toward the correct, baited bucket while standing equidistant between and slightly behind the two buckets, placed ~ 1.5 m apart (Supplementary Movie 1). In 'experiment 2', the experimenter stood behind the bucket containing food while providing the cue toward it (also known as the asymmetrical congruent condition). In 'experiment 3', the experimenter stood directly behind the incorrect, unbaited bucket while providing the cue toward the correct, baited one (also known as the asymmetrical incongruent condition). The experimenter presented either one of three cues or a control (the four conditions), with each one presented pseudo-randomly six times per set but never more than twice in a row. The three cues were: pointing (the experimenter used her whole arm to indicate the correct bucket with a sustained, ipsilateral point by extending her arm outward from the same side of her body—Fig. 1), gazing (the experimenter alternated looking down and toward the correct bucket and back toward the elephant), and pointing-with-gazing (the experimenter performed both cues simultaneously—Supplementary Movie 1). The experimenter provided no cue as to the correct location of the food and stood equidistant between the two buckets in each control condition of the three experiments. This condition controlled for the potential use of

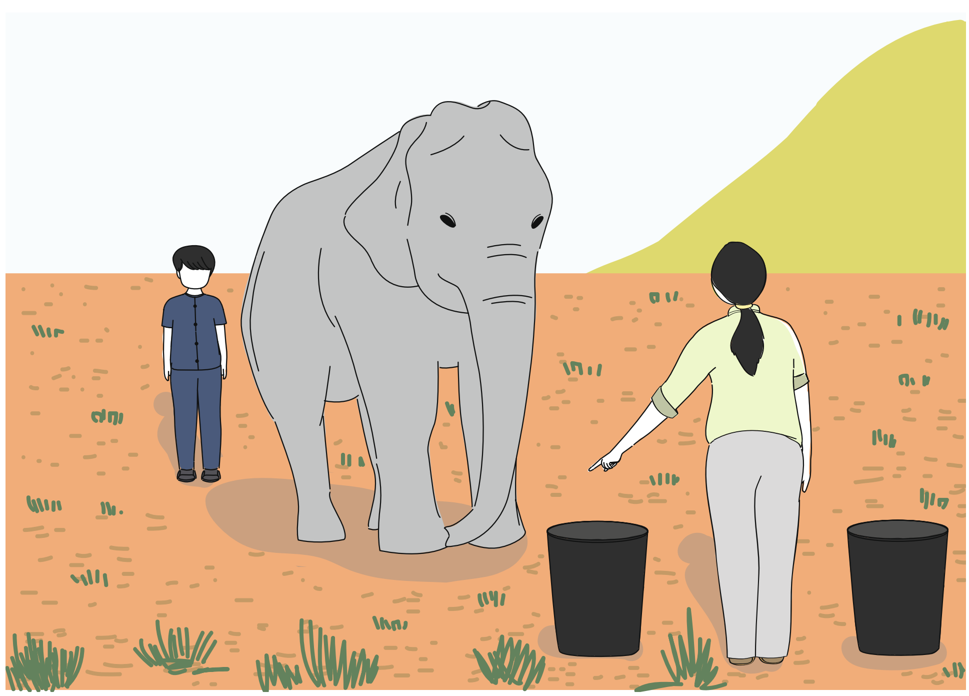

Fig. 1 An 'experiment 1' trial in which the experimenter provides a pointing cue. Illustration by N. Doungcharoen

olfactory or other, unintentional cues (such as the mahout's involvement) about the food's correct location.

In all of the experiments, the experimenter first walked in front of the two buckets and placed a 70 × 150 cm black cardboard barrier with a bamboo base in front of the two buckets to ensure the elephants could not see them being baited. The experimenter then removed the barrier by walking it to the side and away from the buckets, and took her position between or behind the buckets (depending on the condition and experiment) and indicated to the mahout that the elephant could be released. As soon as the elephant began her approach, the experimenter gave a sustained cue up until when the elephant arrived at the buckets and made a choice. If the elephant chose correctly, they were able to voluntarily retrieve the banana from the bucket. If they chose incorrectly, the correct bucket was removed before the elephant could search it. In either case, the elephant was then recalled to the starting point after her first choice to begin the next trial.

For testing, we placed the elephants into three groups to control for potential order effects in the presentation of the three experiments: (a) 1, 2, 3 (three elephants), (b) 1, 3, 2 (two elephants), and (c) 3, 1, 2 (two elephants). We were unable to do a quantitative analysis of these results due to the small overall sample size.

Analysis

We used the one-sample Wilcoxon signed-rank test to assess the elephants' performance compared to chance on each condition within each of the three experiments. Binomial tests were used to investigate individual elephant performance at the level of each condition, and Friedman tests were used to assess group-level performance between conditions within experiments. The Mann–Whitney *U* test was used to investigate whether or not the elephants' performance on experiment 1 conditions in the current study differed significantly from that of a different sample of elephants in comparable conditions in Plotnik et al. (2013). All tests were performed using SPSS version 24 (IBM, 2017), and reported *P* values are exact. Finally, the heterogeneity *G* test, which takes both success and the directionality of the results (heterogeneity) into account (Sokal and Rohlf 1995), was used to test whether the elephants' performance suggested side biases.

Ethical statement

This research formed the basis of the first author's Master's thesis, and the study was approved by the conservation biology program at Mahidol University. At the time this study was conducted in Thailand and to the best of our knowledge, there was no established animal ethics review process available for such projects, but we made sure that the study design and the elephants' participation were in-line with previously reviewed and approved elephant cognition research conducted at other institutions by the last author (e.g., Plotnik et al. 2011, 2013, 2014). Participation by elephants in the experiments was completely voluntary; although it never happened, if elephants had failed to approach the buckets or otherwise did not participate in the experiments, they would not have been made to do so.

Results

Individually, some of the elephants scored significantly better than chance (binomial test, $P < 0.05$) on cues provided during experiments 1, 2 and 3, but as a group, the elephants only did so on the three social cue conditions—pointing (T), gazing (G) and pointing-with-gazing (T + G)—in experiment 2 (when the experimenter stood behind the bucket with the food; see Table 1). As a group, the elephants did not score significantly better than chance in any control condition (Table 1). The elephants also did not perform better on any given condition (excluding controls from the analysis) within any of the three experiments (Friedman test: Experiment 1 (T, G, T + G): $X^2 = 0.58$, $df = 2$, $P = 0.819$; Experiment 2 (T, G, T + G): $X^2 = 0.58$, $df = 2$, $P = 0.809$; Experiment 3 (T, G, T + G): $X^2 = 2.00$, $df = 2$, $P = 0.393$).

We also looked at whether or not the elephants had a particular side bias toward one or the other bucket based on the side on which it was presented. By pooling all data across all elephants in the three experiments, we found elephants had a significant side bias to one side (Heterogeneity *G* test Gh = 126.53, $df = 6$, $P < 0.001$, Gt = 274.06, $df = 7$, $P < 0.001$), with six out of seven elephants showing a significant side bias, and five of them choosing the right bucket (i.e., the bucket to the experimenter's right) significantly more often than the left one (binomial test for right-bucket choices across 288 total trials: $P < 0.05$ for five of seven elephants—Somboon, Nimochi, Tangmo, To-Me, Gaina; binomial test for left-side choices across 288 total trials: $P < 0.05$ for one of seven elephants—Malee; non-significant binomial test for side bias across 288 total trials for one of seven elephants—Kammoon).

Finally, to investigate differences between the performance of the elephants in Plotnik et al. (2013) and the current study, we compared the performance of the elephants on the three conditions in the only experiment in which there was relative consistency across the two studies: pointing, gazing/orienting and both when the experimenter was equidistant between the buckets (experiment 1 in the current study). There was no significant difference between the performances of the two groups of elephants in any condition (median from current study (Mc), median from Plotnik et al. 2013 (Mo), and IQR (interquartile range); Mann–Whitney

U statistic): pointing: Mc = 17, IQR = 5; Mo = 14, IQR = 3; $U = 17.5$, $n = 7$, $P = 0.394$; gazing/orienting: Mc = 12, IQR = 5; Mo = 12, IQR = 2; $U = 20.0$, $n = 7$, $P = 0.590$; both: Mc = 15.0, IQR = 5, Mo = 12, IQR = 5; $U = 11.5$, $n = 7$, $P = 0.107$). It is important to note that these two studies differed in study location, setup, experimenter, type of gazing/orienting and the length of pointing time before the elephant could make a choice in each trial; so, this statistical comparison across studies should be considered carefully.

Discussion

Here, in a replication of Plotnik et al. (2013) with significant changes to the experimental methodology to account for concerns raised by Smet and Byrne (2013), we found that Asian elephants seem limited in their capacity to follow human-provided social cues such as pointing, gazing and a combination of the two to find food in a two-bucket object-choice task. In the current study, with a group of elephants in Thailand that, to our knowledge, had never participated in cognition studies before, we positioned the buckets outside in an open-air environment and provided a sustained visual cue from the time when the elephants approached the buckets through when they made a choice. Although some individual elephants performed significantly better than chance in some of the conditions, the elephants as a group only chose the correctly baited buckets significantly more often than chance in the asymmetric congruent experiment. As a group, they did not choose the correctly baited bucket significantly more often than chance in any condition of experiment 1 or 3. They also did not perform better on any given condition within each of the three experiments.

First, we recognize that the non-significant group-level statistics should be interpreted cautiously due to the lack of power of the non-parametric analyses at a low sample size ($N \leq 7$, due to scores tied with chance being removed). The fact that several elephants individually performed above chance in the body centered and asymmetric congruent conditions (and one, To-Me, did well in the asymmetric incongruent condition) suggests that some of the elephants may have been able to follow pointing, or pointing and gazing cues. Because of the individual variability in performance, a considerably larger sample size is needed to investigate more definitively how well elephants follow human-provided social cues.

In addition, it is important to highlight the significant results regarding the elephants' side biases toward one bucket. As we discussed in Plotnik et al. (2013), when elephants perform well on one experiment or condition but not others (as they did in the current study), as well as demonstrate an ability to follow the placement of food in pre-testing trials, it is unlikely that the elephants have an inherent, natural side bias toward one side. We would expect such a bias to be consistent across all conditions and result in chance performance, thus ultimately obscuring our ability to interpret whether the elephants could follow visual cues in an object-choice task at all. Our results instead suggest that the elephants chose one side significantly more often than the other when they were unable to interpret or did not follow the provided cues (Tebbich et al. 2007). The fact that six of seven elephants showed a significant side bias across all 288 trials (when there were an equal number of left and right correct choices) suggests that they did not consistently understand or follow the provided social cues.

There are two possible explanations for the elephants' success as a group on the asymmetric congruent experiment. First, the elephants may have prioritized paying attention to the experimenter's proximity to a particular bucket and associated this with the food's location (local enhancement). If this were the case, we would expect a result significantly better than chance in the asymmetric congruent experiment, and a result significantly worse than chance in the asymmetric incongruent condition. In other words, if the elephants were simply making choices based on the experimenter's position alone, we would expect the elephants in the latter experiment to prefer the incorrect bucket since the experimenter was consistently standing next to it. However, the fact that the elephants as a group did not score significantly worse than chance (i.e., they did not choose the incorrect bucket significantly more than chance) in the asymmetric incongruent experiment suggests that it may be the combination of the experimenter's position and the pointing and/or gazing cue that creates a sufficiently salient cue for the elephants in the asymmetric congruent condition. Interestingly, two elephants did perform significantly worse than chance in the asymmetric incongruent experiment but in only one, different condition each. This suggests that their performance was probably not related exclusively to the experimenter's position, which remained consistent across test conditions in this experiment. We did not perform an additional control condition in which the experimenter did not provide a pointing and/or gazing cue but stood next to the correct or incorrect bucket because we were concerned that the elephants might learn to use local enhancement even when it led to an incorrect choice. This would make it difficult to interpret their use of human-provided social cues (the main focus of this study). Nonetheless, the elephants' inconsistent performance across experimental conditions suggests that they were not using local enhancement alone to guide their choices. Overall, these results are different from those found with the African elephants, whereby the elephants seemed capable of using both the experimenter's location and the social cue (when it included a point) to find the food, but were able, when given conflicting information, to prioritize the latter (Smet and Byrne 2013).

Second, although the elephants' inability to find the food in the control condition suggests that they were not using the olfactory cues from the food alone to find it, they may have used aspects of the food's smell and the spatial, olfactory information from the experimenter to guide them toward the correct bucket in the asymmetric congruent condition. Recent research suggests that olfactory cues, especially in object-choice or match-to-sample tasks, may play an important role in elephant cognition (e.g., Plotnik et al. 2014, 2019; von Dürckheim et al. 2018).

Originally, we had hypothesized that methodological differences between the previous studies could have accounted for the differences in results. Although we did not include all of the numerous conditions in which the African elephants in Smet and Byrne (2013) were tested, we chose what we believed to be the most important methodological changes (i.e., those related to environment, presentation and cue) that could account for the species-level differences in performance. Given the mixed results across the two Asian elephant studies, experimental design may help explain some of the species-level differences in performance. The fact that several individual elephants performed well on certain conditions in the current study suggests that some of the changes to the methodology may have had an impact on these elephants' performances (Table 1); however, methodology is unlikely to be the sole explanation for the species-level differences.

Nonetheless, it is difficult to identify the specific reasons for why the African and Asian elephants showed differences in their performance on these tasks. There are very likely several factors that contribute to whether and how animals respond to human social cues. For instance, there may be significant ecological or husbandry differences that impact how animals use visual information in their physical and social decision-making processes. Given the differences in the elephants' natural environments, there is likely significant variability in the two species' foraging behaviors. Savannah elephants (*Loxodonta africana*) in relatively large social groups often seek out food within open savannah environments (Moss et al. 2011), where visual information about resource location may be relevant. Asian elephants (*Elephas maximus*), on the other hand, usually live in dense forest or jungle environments where visibility is limited (Sukumar 2003), and thus vision may not be as relevant as olfaction for locating food. Thus, there may be ecological differences between the two species that could account for the differences seen in Smet and Byrne (2013), Plotnik et al. (2013), and the current study. Interestingly, one similarity in performance across the three studies involved the conditions in which only a gaze cue was provided; in these conditions, the elephants appeared unable to use gaze cues alone to find food, suggesting this human-provided social cue is insufficiently salient for either species.

The differences in the African and Asian elephants' responses to pointing cues in these studies, as well as the individual variability within them, could also be due to differences in training. Captive elephants undergo different training regiments over the course of their lifetimes, and the African elephants tested may have had more opportunity to learn the specific function of the pointing cues. Although Smet and Byrne (2013) suggest that the elephants in Africa were not trained with a pointing cue prior to their study and that the elephants' training primarily involved the use of vocal commands, our own experience working with elephants and their mahouts suggests that it can be difficult to verify past experience. Although the elephants may not have been trained on pointing explicitly, it is possible that pointing or other visual cues served as unintentional, secondary reinforcers in the elephants' previous training processes. In addition, although Asian elephants in captivity have worked closely with humans for thousands of years (Lair 1997), it is quite possible that this relationship is predominantly guided by tactile, olfactory and acoustic communication rather than visual cues like pointing and gazing. This would make sense in light of recent research across elephant species that suggests that olfaction and audition are important sensory modalities for elephants (e.g., Bates et al. 2007, 2008; O'Connell-Rodwell 2007; Plotnik et al. 2014, 2019). It is clear that further research on elephants' use of visual information in both physical and social cognition tasks is needed to determine how relevant such information is to them.

Although both popular and scientific literature often assume that all three living elephant species are similar, recent experimental and ethological research across the two elephant genera suggest that there may be significant species-level differences in Asian and African elephant behavior and ecology (e.g., de Silva and Wittemyer 2012; Pardo et al. 2019). Thus, future studies that attempt to draw comparisons about the cognitive abilities of animals, and elephants in particular, as well as the human–animal bond should be careful to take the individual species' ecology, behavior and experiences into account. Specifically, ecologically relevant paradigms should be used appropriately, even if all of the species involved have similar eyes, ears and trunks.

Acknowledgements We thank the mahouts, staff and volunteers at Elephants World in Kanchanaburi, Thailand for their assistance with this study. We also thank the faculty and students of the Conservation Biology Program at Mahidol University's Kanchanaburi Campus for their support. Finally, we appreciate the comments of anonymous reviewers that helped improve an earlier version of this manuscript.

Compliance with ethical standards

Conflict of interest JP is the founder of Think Elephants International, a US public charity that focuses on elephant conservation. CS is co-founder of the Banana Orchard Project in Kanchanaburi, an ecotourism venture for captive elephants in Thailand. CS's involvement in the latter project did not begin until after the current study was completed.

Ethical statement All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

References

Bates LA, Sayialel KN, Njiraini NW, Moss CJ, Poole JH, Byrne RW (2007) Elephants classify human ethnic groups by odor and garment color. Curr Biol 17:1938–1942

Bates LA, Sayialel KN, Njiraini NW, Poole JH, Moss CJ, Byrne RW (2008) African elephants have expectations about the locations of out-of-sight family members. Biol Let 4:34–36

Call J (2004) Inferences about the location of food in the great apes (Pan paniscus, Pan troglodytes, Gorilla gorilla, and Pongo pygmaeus). J Comp Psychol 118(2):232–241

Call J, Agnetta B, Tomasello M (2000) Cues that chimpanzees do and do not use to find hidden objects. Anim Cogn 3:23–34

de Silva S, Wittemyer G (2012) A comparison of social organization in Asian elephants and African savannah elephants. Int J Primatol 33(5):1125–1141

Essler JL, Schwartz LP, Rossettie MS, Judge PG (2017) Capuchin monkeys' use of human and conspecific cues to solve a hidden object choice task. Anim Cogn 20(5):985–998. https://doi.org/10.1007/s10071-017-1118-2

Giret N, Miklósi A, Kreutzer M, Bovet D (2009) Use of experimenter-given cues by African gray parrots (*Psittacus erithacus*). Anim Cogn 12:1–10

Hare B (2001) Can competitive paradigms increase the validity of social cognitive experiments on primates? Anim Cogn 4:269–280

Hare B, Tomasello M (1999) Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. J Compar Psychol 113(2):173–177

Hare B, Tomasello M (2004) Chimpanzees are more skillful in competitive than in cooperative cognitive tasks. Anim Behav 68:571–581

Hare B, Brown M, Williamson C, Tomasello M (2002) The domestication of social cognition in dogs. Science 298(5598):1634–1636

Hare B, Rosati A, Kaminski J, Bräuer J, Call J, Tomasello M (2010) The domestication hypothesis for dogs' skills with human communication: a response to Udell et al. (2008) and Wynne et al. (2008). Anim Behav 79(2):e1–e6

Herman LM, Abichandani SL, Elhajj AN, Herman EYK, Sanchez JL et al (1999) Dolphins (*Tursiops truncatus*) comprehend the referential character of the human pointing gesture. J Comp Psychol 113:347–364

Itakura S, Anderson JR (1996) Learning to use experimenter-given cues during an object-choice task by a capuchin monkey. Curr Psychol Cogn 15:103–112

Itakura S, Tanaka M (1998) Use of experimenter-given cues during object choice tasks by chimpanzees (*Pan troglodytes*), an orangutan (*Pongo pygmaeus*), and human infants (*Homo sapiens*). J Comp Psychol 112:119–126

Kaminski J, Riedel J, Call J, Tomasello M (2005) Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. Anim Behav 69(1):11–18

Krause MA, Udell MA, Leavens DA, Skopos L (2018) Animal pointing: changing trends and findings from 30 years of research. J Compar Psychol 132:326–345

Lair RC (1997) Gone astray: the care and management of the Asian elephant in domesticity. Food and Agriculture Organization of the United Nations, Rome

Maros K, Gácsi M, Miklósi Á (2008) Comprehension of human pointing gestures in horses (*Equus caballus*). Anim Cogn 11(3):457–466

Miklósi Á, Soproni K (2006) A comparative analysis of animals' understanding of the human pointing gesture. Anim Cogn 9:81–93

Moss CJ, Croze H, Lee PC (eds) (2011) The amboseli elephants: a long-term perspective on a long-lived mammal. University of Chicago Press, Chicago

Mulcahy NJ, Call J (2009) The performance of bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*) in two versions of an object choice task. J Compar Psychol 123:304–309

Mulcahy NJ, Hedge V (2012) Are great apes tested with an abject object-choice task? Anim Behav 83:313–321

Nawroth C, Ebersbach M, von Borell E (2014) Juvenile domestic pigs (*Sus scrofa domestica*) use human-given cues in an object choice task. Anim Cogn 17:701–713

Neiworth JJ, Burman MA, Basile BM, Lickteig MT (2002) Use of experimenter given cues in visual co-orienting and in an object-choice task by a new world monkey species, cotton top tamarins (*Saguinus oedipus*). J Comp Psychol 116:3–11

O'Connell-Rodwell CE (2007) Keeping an "ear" to the ground: seismic communication in elephants. Physiology 22:287–294

Pardo MA, Poole JH, Stoeger AS, Wrege PH, O'Connell-Rodwell CE, Padmalal UK, de Silva S (2019) Differences in combinatorial calls among the 3 elephant species cannot be explained by phylogeny. Behav Ecol. https://doi.org/10.1093/beheco/arz018

Plotnik JM, Lair R, Suphachoksahakun W, de Waal FBM (2011) Elephants know when they need a helping trunk in a cooperative task. Proc Natl Acad Sci 108(12):5116–5121

Plotnik JM, Pokorny JJ, Keratimanochaya T, Webb C et al (2013) Visual cues given by humans are not sufficient for Asian elephants (*Elephas maximus*) to find hidden food. PLoS One 8:e61174

Plotnik JM, Shaw RC, Brubaker DL, Tiller LN, Clayton NS (2014) Thinking with their trunks: elephants use smell but not sound to locate food and exclude nonrewarding alternatives. Anim Behav 88:91–98

Plotnik JM, Brubaker DL, Dale R, Tiller LN, Mumby HS, Clayton NS (2019) Elephants have a nose for quantity. Proc Natl Acad Sci 10:10. https://doi.org/10.1073/pnas.1818284116

Proops L, Walton M, McComb K (2010) The use of human-given cues by domestic horses, *Equus caballus*, during an object choice task. Anim Behav 79(6):1205–1209

Range F, Virányi Z (2015) Tracking the evolutionary origins of dog-human cooperation: the "Canine-Cooperation" Hypothesis". Front Psychol 5:e1582

Scheumann M, Call J (2004) The use of experimenter-given cues by South African fur seals (*Arctocephalus pusillus*). Anim Cogn 7:224–230

Schmitt MH, Shuttleworth A, Ward D, Shrader AM (2018) African elephants use plant odours to make foraging decisions across multiple spatial scales. Anim Behav 141:17–27

Smet AF, Byrne RW (2013) African elephants can use human pointing cues to find hidden food. Curr Biol 23(20):2033–2037

Sokal RR, Rohlf FJ (1995) Biometry: the principles of statistics in biological research. WH Freeman and Co, New York

Sukumar R (2003) The living elephants: evolutionary ecology, behaviour, and conservation. Oxford University Press, Oxford

Tebbich S, Seed AM, Emery NJ, Clayton NS (2007) Non-tool-using rooks, *Corvus frugilegus*, solve the trap-tube problem. Anim Cogn 10(2):225–231

Tornick JK, Gibson BM, Kispert D, Wilkinson M (2011) Clark's nutcrackers (*Nucifraga columbiana*) use gestures to identify the location of hidden food. Anim Cogn 14:117–125

Tschudin A, Call J, Dunbar RIM, Harris G, van der Elst C (2001) Comprehension of signs by dolphins (*Tursiops truncatus*). J Comp Psychol 115:100–105

Udell MAR, Dorey NR, Wynne CDL (2008) Wolves outperform dogs in following human social cues. Anim Behav 76:1767–1773

Virányi Z, Gácsi M, Kubinyi E, Topál J, Belényi B, Ujfalussy D, Miklósi Á (2008) Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). Anim Cogn 11(3):373

von Bayern AMP, Emery NJ (2009) Jackdaws respond to human attentional states and communicative cues in different contexts. Curr Biol 19:602–606

Von Dürckheim KEM, Hoffman LC, Leslie A, Hensman MC, Hensman S, Schultz K, Lee S (2018) African elephants (*Loxodonta africana*) display remarkable olfactory acuity in human scent matching to sample performance. App Anim Behav Sci 200:123–129