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Thinking with their trunks: elephants use smell but not sound to locate food and exclude nonrewarding alternatives

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The two-way object choice paradigm has been used extensively in studies of animal cognition. The paradigm involves presenting two options, one rewarding and one nonrewarding, to a subject and allowing it to make a choice between the two, potentially by exploiting specific cues provided by the experimenter. Using the paradigm, we tested first whether Asian elephants, *Elephas maximus*, could use auditory and/or olfactory cues to find food. While elephants were unable to locate hidden food by following an auditory cue, they were capable of finding food when the cue was olfactory. The second part of the study involved providing the subjects with only olfactory information about one option before presenting them with a choice between two. In trials in which subjects were allowed to investigate only the nonrewarding option, they made choices by exclusion, either inferring the location of the rewarding option or simply avoiding the nonrewarding one. Elephants thus relied on olfaction to locate food and to exclude nonrewarding food locations, but failed to use auditory information (when it was the only cue presented) to do the same. This study represents important evidence of elephants using their sense of smell in a cognitive task.

The two-way object choice paradigm can be used to reveal which sensory modalities, and/or what social cues, animals rely on to locate hidden food. Subjects are presented with a choice between two containers, one baited with food, the other empty. They are guided towards the baited container by a cue provided within a single sensory domain (e.g. vision, audition, olfaction, etc.). The object choice paradigm has been used extensively, primarily in studies with primates, birds and dogs (for reviews see Hare & Tomasello 2005; Miklósi & Soproni, 2006) and, to a lesser extent, cetaceans and elephants (see Table 1 for examples across species).

If subjects can successfully locate hidden food by sight, sound or smell, these senses can then be exploited to test for cognitive abilities; for example, one can test the subject's ability to exclude one choice (the nonrewarding one) over another when presented with information solely from the former. These choices made by exclusion provide insight into how animals think about or process the sensory information they receive (see Call, 2004). In 'location tests', the subject receives information about both containers before making a choice. In 'exclusion tests', subjects are provided with information about only one of the two containers before they must make a choice. In the exclusion test's 'empty' trials, during which subjects only receive information about the empty container, the subjects must exclude this container in order to choose the baited one. Following the terminology outlined by Call (2004), a number of researchers who have used exclusion tests have adopted the terms 'inferential reasoning by exclusion' or simply 'inferential reasoning' (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Call, 2006; Erdőhegyi, Topál, Virányi, & Miklósi, 2007; Maille & Roeder, 2012; Petit, Call, & Thierry, 2005; Sabbatini & Visalberghi, 2008; Schloegl, Schmidt, Boeckle, Weiss, & Kotrschal, 2012). However, these choices by exclusion may operate either through a mechanism of avoidance, that is, through the learning of a simple rule to avoid the container that does not provide the reward, or through a mechanism of inference, that is, cognitively inferring the food's location, which is much more complex (Mikolasch, Kotrschal, & Schloegl, 2012; Paukner, Huntsberry, & Suomi, 2009; Penn & Povinelli, 2007; Schloegl, 2011; Schloegl et al., 2009; Schmitt & Fischer, 2009; Shaw, Plotnik, & Clayton, 2013).

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Table 1
Success and failure across species on two-way object choice tasks investigating abilities to 'locate' hidden food and to do so by 'exclusion' within the visual and auditory domains

Species	Visual cues				Auditory cues			
	Location		Exclusion		Location		Exclusion	
	Success	Failure	Success	Failure	Success	Failure	Success	Failure
Pan troglodytes	1	21	1, 10		1, 3		3, 10	
Pan paniscus	1		1		1, 3		1, 3	
Gorilla gorilla	1		1		1		1	
Pongo pygmaeus	1		10			1		
Symphalangus syndactylus	10		10					
Macaca tonkeana	2		2		2			2
Papio hamadryas anubis	9		9			9		
Cebus apella	6, 7, 13		6, 7, 13		6, 13		6	13
Ateles geoffroyi	10		10					
Eulemur macaco	14			14	14			14
Eulemur fulvus	14			14	14		14	
Psittacus erithacus	11		11		16		16	
Columba livia	5			5				
Corvus corax	8		8					
Nestor notabilis	8			8				
Corvus corone	15		15					
Corvus monedula	12			12				
Garrulus glandarius	18			18		18		
Canis familiaris	4, 5		4, 5		3			3
Elephas maximus		17						
Tursiops truncatus	19, 20							

This list provides examples, and is not an exhaustive review. (1) Call (2004); (2) Petit et al. (2005); (3) Bräuer et al. (2006); (4) Erdőhegyi et al. (2007); (5) Aust, Range, Steurer, and Huber (2008); (6) Sabbatini and Visalberghi (2008); (7) Paukner et al. (2009); (8) Schloegl et al. (2009); (9) Schmitt and Fischer (2009); (10) Hill et al. (2011); (11) Mikolasch, Kotrschal, and Schloegl (2011); (12) Schloegl (2011); (13) Heimbauer et al. (2012); (14) Maille and Roeder (2012); (15) Mikolasch et al. (2012); (16) Schloegl et al. (2012); (17) Plotnik et al. (2013); (18) Shaw et al. (2013); (19) Pack and Herman (2004); (20) Tschudin, Call, Dunbar, Harris, and van der Elst (2001); (21) Hare, Brown, Williamson and Tomasello (2002).

The majority of primate studies using object choice tests have focused on perception of cues within the visual and auditory domains while studies in nonprimates have largely focused on the visual domain only (but see Bräuer et al., 2006; Schloegl et al., 2012; Shaw et al., 2013 for exceptions). While the Old World and New World primate species have excelled in both location and exclusion tests within the visual domain, results within the auditory domain are mixed (Table 1). The lemur species tested, for example, excelled in the auditory domain while struggling to follow visual cues, a result that highlights the ecological differences between prosimians and their monkey and ape relatives (Maille & Roeder, 2012). This may indicate that attention to behavioural ecology is important in the design of any cognitive experiment that uses similar paradigms across species. In the object choice tasks specifically, what senses do these animals use in the wild to navigate or locate food, and can these senses be exploited in the laboratory? Elephants, for instance, present an interesting challenge in such experiments, as they are highly inquisitive animals that may rely on primarily nonvisual information in their physical and social decision-making processes (Plotnik et al., 2013).

Thus, the results of any two-way object choice tasks presented to elephants would be likely to reflect the different ecological pressures faced by these animals compared with those faced by primates and birds. To our knowledge, olfactory abilities have yet to be tested following the two-way object choice paradigm in any species, but elephants stand as a prime candidate for testing within this domain.

Elephants are highly social animals that rely heavily on their communicative abilities to maintain their social structure. While interactions between elephants are mediated by scent, sound, sight and touch, both olfactory and acoustic communication seem to be more critical than visual communication (e.g. Plotnik et al., 2013; Vidya & Sukumar, 2005). It is important for elephants to recognize individuals and keep track of the locations of family members in order to maintain social cohesion (Bates et al., 2008; Buss, Rasmussen, & Smuts, 1976). An array of behavioural evidence suggests that elephants (*Loxodonta* genus, *Elephas maximus*) rely strongly on their sense of smell for social discrimination (e.g. Arvidsson, Amundin, & Laska, 2012; Bates et al., 2007). For example, olfactory cues from urine allow elephants to identify the location of up to 30 individual elephants (Bates et al., 2007).

Olfaction also plays an important role in reproduction; elephants can detect various pheromones, enabling them to judge the different reproductive states of males and females (Bagley, Goodwin, Rasmussen, & Schulte, 2006; Poole, Kasman, Ramsay, & Laslay, 1984; Rasmussen & Schulte, 1998). Elephants are also able to discriminate between different odours and can use olfactory cues to distinguish between different human ethnic groups in Kenya (Bates et al., 2007). They show olfactory learning capabilities and long-term olfactory memory (Arvidsson et al., 2012), and probably use olfaction when identifying food and water sources from great distances (e.g. Gaalema, Perdue, & Kelling, 2011; Poole, 1996; Sukumar, 2003).

Elephants also possess extremely effective acoustic abilities, important both for short- and long-distance communication (Poole, Payne, Langbauer, & Moss, 1988). They can produce sounds that range in frequency from 14 to 9000 Hz, can attain an intensity of 103 dB (Payne, Langbauer, & Thomas, 1986; Poole et al., 1988) and can travel distances (Langbauer, Payne, Charif, Rapaport, & Osborn, 1991) of up to 10 km without significant attenuation (Garstang, Larom, Raspet, & Lindeque, 1995; Larom, Garstang, Payne, Raspet, & Lindeque, 1997). Both Asian (Payne et al., 1986) and African elephants (Poole et al., 1988) can produce low-frequency vocalizations below the range of human hearing, some of which can be transmitted seismically through the ground (O'Connell-Rodwell, 2007). Elephants can distinguish between the calls of up to 100 adult females from different family or bond groups (McComb, Moss, Sayialel, & Baker, 2000). Owing to these factors, elephants serve as a particularly interesting test species for the investigation of olfactory and auditory perception in an object choice task. However, although there is substantial evidence of elephants using vocalizations in the gathering of social knowledge, there is little or no evidence that they use acoustic information for any nonsocial or primarily physical purposes, such as finding food. Although we might not expect that elephants would use sound to locate food in their natural environment, their exceptional acoustic sense and general behavioural flexibility, specifically in social contexts, may enable them to generalize their use of acoustic cues to nonsocial contexts.

Generally regarded as one of the most cognitively complex animals, elephants show problem solving and reasoning skills (e.g. Byrne, Bates, & Moss, 2009; Plotnik, Lair, Suphachoksahakun, & de Waal, 2011), but little is known about how their acoustic or olfactory abilities may mediate or underlie their physical or social cognition. In the present study, we aimed to better our understanding of how elephants use their sensory abilities in a food-finding task. First, we sought to determine whether elephants are able to locate food in a two-way object choice task by either audition or olfaction. If significant results were obtained in either domain, the second aim of our study was to investigate whether elephants can use these senses to make choices by exclusion.

METHODS

Experiment 1: Acoustic Cuing

Subjects

Between February and March 2012, we tested seven elephants (six females, one male), ranging in age from 6 to 25 years old, at the Think Elephants International research facility, based at the Golden Triangle Asian Elephant Foundation (GTAEF) in Chiang Saen, Thailand. The facility is home to 26 elephants, some of which are rented as part of the elephant camp programmes at the Anantara Golden Triangle Elephant Camp and Resort and the Four Seasons Golden Triangle Tented Camp, and most of which were rescued from a life of street begging in Bangkok. The elephants are provided with a combination of artificial shelter and access to natural habitat environment on a daily basis. They are fed four to seven times a day (natural grasses and fruits), and bathed two or three times a day. The elephant's mahout (the daily caretaker who is also usually the elephant's owner), two full-time staff veterinarians and senior management provide daily care and ensure proper elephant welfare practice is in place. This study was approved by the National Research Council of Thailand, and by the University of Cambridge Zoology Animal Users Committee (Z003/2011).

Apparatus and materials

A sliding table was used to extend and retract baited buckets towards and away from the subject (Fig. 1). The table, measuring 2.97 × 0.90 m, was fitted with wheels that rolled within grooves on a support frame. The square frame measured 3 m along each side and stood 0.54 m off of the ground. With the table resting on top of the frame, the entire structure reached a height of 0.67 m. Attached to the rear of the table were two cylindrical arms (2.02 m) that served as push/pull handles. Two metal baskets (21.5 cm in diameter) were bolted to the top of the table, one at either end (2.46 m apart). A pair of opaque buckets (tapered from a lip diameter of 26 cm to a base diameter of 19 cm) served as food containers that could be inserted interchangeably into the metal baskets on the table. A curtain (length 4.66 m, height 2.77 m) was rigged up on a pulley system, a distance of 1.24 m to the front of the table frame (positioned between the subject and the table).

General procedure

The subjects were previously trained in an earlier experiment to remove the lids from the opaque buckets when the lids were placed upside-down on top of them and the sliding table was extended (Plotnik et al., 2013). In the current experiment, one of the buckets was baited with sunflower seeds in the middle of and directly behind the table and then both were closed with the upside-down lids. The two buckets were then placed into the two baskets at either end of the table, and the curtain was opened to give the subject visual access to the apparatus. One after the other, each bucket was lifted out of its basket, shaken five times with an up-and-down motion, and then returned (Fig. 1a). The table was extended, allowing the elephant to remove the lid from one bucket to retrieve any reward inside. The table was retracted before the subject could remove the lid from the second bucket.

The procedure for control trials was identical to that of test trials, except that no cues were provided; the buckets remained in their baskets for the trial duration and the experimenter remained still behind the table, facing the subject. These trials allowed us to disqualify the possibility that the elephants were able to locate the baited bucket because of confounding olfactory and/or visual cues or any auditory cues provided inadvertently when the buckets were baited.

Each subject completed four sets, with each set comprising 12 test trials and three control trials. In test trials, the location of the baited bucket and the sequence in which the buckets were shaken was pseudorandomized (six trials of each location and shake sequence per set, and no more than three consecutive occurrences of the same location and/or shake sequence). The control trials were pseudorandomly interspersed between the last eight of the 12 test trials, with no two control trials ever occurring consecutively. Note that the visual component of the buckets being shaken was still available to the elephants as a synchronous cue to the sound of the seeds rattling.

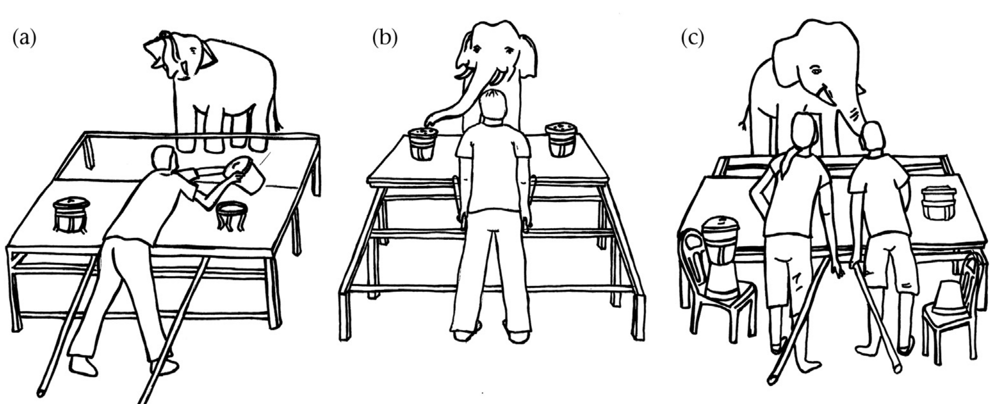

Figure 1. Diagrams of experimental set-up in each of the three test conditions. (a) Acoustic cuing with one experimenter (experiment 1). (b) Olfactory cuing with one experimenter (experiment 2). (c) Exclusion with two experimenters (experiment 3). Drawing by A. Hennessy, edited by E. Gilchrist.

Experiment 2: Olfactory Cuing

Subjects

Two additional elephants were tested along with the seven elephants from the acoustic experiment (seven females, two males) between February and March 2012. The nine elephants for this experiment ranged in age from 6 to 42 years old.

Apparatus and materials

A translucent bucket was placed into each of the metal baskets and bolted, along with the basket, to the sliding table. Two concentric rings of pencil-size holes were burned into both bucket lids. Ten holes made up the inner ring (8 cm diameter) and 16 holes made up the outer ring (13 cm diameter). Slightly smaller opaque, orange buckets were inserted into the translucent buckets to control for residual olfactory cuing; one of the orange buckets always held the bait ('baited bucket') while the other remained empty ('empty bucket'). Neither of the outer, translucent buckets came into contact with food at any point. See Fig. A1 in the Appendix for diagrams of the bucket set-up.

General procedure

For the Test Condition, the experimenter baited the 'baited bucket' (behind and directly central to the table) with the food reward (pineapple and sunflower seeds, $N = 7$; only sunflower seeds, $N = 2$) and inserted it into one of the outer buckets. The 'empty bucket' was inserted into the opposite outer bucket. The lid of each outer bucket was secured into place with two cable ties, the curtain was opened, and the table was pushed towards the subject. In each trial, the subject was given 15 s to investigate the two buckets (the 'investigation phase'; Fig. 1b), starting from the full extension of the table. The table was then pulled back, the cable ties were cut and the bucket lids were overturned. The table was again extended, allowing the subject to remove the lid from one bucket to retrieve any reward inside (the 'choice phase'). If the subject failed to touch at least one bucket during the 'investigation phase' then the trial was restarted. Subjects were run on four sets of 10 trials.

For the Control Condition, two small (11.7 cm diameter), translucent containers with screw-top lids were introduced into the procedure as a means of blocking the olfactory cue. As with the orange buckets, one of these smaller containers served as the 'baited container' and the other the 'empty container' in each trial. The 'baited container' was secured with its lid and placed into the orange 'baited bucket'. Together, the unit was then inserted into either of the two outer buckets on the table. Solid lids were used to cover the outer buckets in place of the perforated lids. After the 'investigation phase' the screw-top lids were removed (without lifting the translucent containers out of the orange buckets). The procedure was otherwise identical to that of the Test Condition. Subjects were run on a single set of 10 trials.

For both the Test Condition and the Control Condition, both the location of the baited bucket and the sequence in which the bucket lids were overturned were pseudorandomized (five trials of each location and lid removal sequence per set, and no more than three consecutive occurrences of the same location and/or lid removal sequence).

Experiment 3: Olfactory Exclusion

Subjects

Between March and May 2012, subjects that were successful in experiment 2 ($N = 7$; five females, two males, 11–42 years old) were tested further (one subject, NamFon, was not available to participate in experiment 3).

Apparatus and materials

Two experimenters operated the sliding table with one stationed behind each bucket. Off of the table, two stands were positioned, one directly behind each of the two buckets. During the 'choice phase', the outer perforated lids were not simply overturned, but replaced with solid lids. The smaller containers used in the Control Condition of experiment 2 were used in every experiment 3 condition. These containers were not covered with their screw-top lids in any test trials, but the lids were on during the 'investigation phase' of control trials to ensure that in these trials, the elephants were unable to receive olfactory information. During the 'choice phase' of control trials, the screw-top lids were removed entirely. See Fig. A2 in the Appendix for diagrams of the bucket set-up.

General procedure

The procedure for the Baseline Condition was identical to that of the Test Condition in experiment 2 except for the presence of an additional experimenter and aforementioned materials. The Baseline Condition allowed for direct comparison with the Test Condition by instituting these experimenter and material changes, modifications that remained consistent within the Test Condition procedure. Subjects were given up to four sets (10 trials each) in which to reach a criterion of 80% within a single set. All of the elephants reached this criterion.

For the Test Condition, subjects were given four sets of 15 trials, each comprising 12 test and three control trials. In each test trial, after the baited and empty buckets were positioned on the table, one of the two outer buckets was locked with its perforated lid while the other was locked with its solid lid. After the curtain was drawn the bucket with the solid lid was lifted off of the table (metal basket included) and set to rest on the stand directly behind its location on the table (Fig. 1c). This bucket would not be returned to its position on the table until after the 'investigation phase'. The procedure otherwise followed that of the Test Condition in experiment 2.

There were two types of test trials: 'baited trials' in which the subject was only permitted to investigate the 'baited bucket' and 'empty trials' in which the subject was only permitted to investigate the 'empty bucket'.

The procedure for control trials was identical to that within the Control Condition in experiment 2 except for an additional 5 s delay between the 'investigation phase' and the 'choice phase' to account for the additional time needed during test trials to replace onto the table the bucket that had been removed. The control trials were pseudorandomly interspersed between the last eight of the 12 test trials; the subjects were never run on two control trials consecutively.

For the Control Condition, subjects were subsequently run on a full 12-trial set, identical and in addition to the control trials interspersed within the Test Condition.

For all three conditions (Baseline, Test and Control), the location of the baited bucket was pseudorandomized (equal numbers in each location and no more than three consecutive occurrences of the same location). The sequence in which the cable ties were cut and the lids replaced no longer required pseudorandomization; the two experimenters operated in synchrony.

Analysis

Within each experiment, test and control data (see Table 2) were analysed using Wilcoxon signed-ranks tests, either one-sample (if compared to chance) or matched-pairs (if compared to each other). Prior to any corrections, the alpha level for all tests was set at $\alpha = 0.05$. In experiment 3, the three conditions were first analysed using a Friedman two-way analysis of variance by ranks, and then subjected to pairwise Wilcoxon comparisons (Siegel & Castellan,

Table 2
Raw count of correct choices for nine elephants across the different conditions

Subject	Acoustic Test	Acoustic Control	Olfaction Test	Olfaction Control	Exclusion E/B	Exclusion Control
Ploy	21(5.25)	5	29(7.25)	5	17/24	12
TangMo	24(6)	8	25(6.25)	2	—	—
Pepsi	29(7.25)	5	33(8.25)	4	19/21	14
Pleum	28(7)	7	33(8.25)	5	14/23	11
NamFon	17(4.25)	7	37(9.25)	7	—	—
Lanna	19(4.75)	8	30(7.5)	5	12/22	11
Poonlab	22(5.5)	7	29(7.25)	9	20/22	9
Phuki	—	—	36(9)	5	18/24	11
Bo	—	—	36(9)	6	13/23	11
Mean	22.9	6.7	32.0	5.3	16.1/22.7	11.3
Out of	48(12)	12	40(10)	10	24/24	24

Dashes (—) represent conditions in which the elephant did not participate. Numbers in parentheses represent the mean number of correct trials in each set. In the exclusion (E/B) condition (48 total trials), the two numbers represent number of trials with a correct choice in 'empty trials'/number of trials with a correct choice in 'baited trials'.

1988). The Bonferroni correction was applied to the P values of these pairwise comparisons to reduce the chance of type I errors.

RESULTS

Experiment 1: Acoustic Cuing

Across 48 test trials, the elephants did not select the baited bucket more often than would be predicted by chance (median = 22.0, Wilcoxon one-sample test: $T+ = 7.5$, $T- = 13.5$, $N = 6$, NS), nor was there any difference between their performance on control trials and chance (median = 7.0, $T+ = 22.0$, $T- = 6.0$, $N = 7$, NS). As these results suggest elephants did not use auditory cues in the two-way choice task, we did not proceed to test acoustic exclusion with the elephants.

Experiment 2: Olfactory Cuing

The first seven elephants tested with the same olfactory information (pineapple + sunflower seeds) chose the baited bucket significantly more often than was predicted by chance across 40 test trials (median = 30.0, $T+ = 28.0$, $T- = 0.00$, $N = 7$, $P = 0.016$), and these data remained significant when two additional elephants (which had only been given sunflower seeds as an olfactory cue) were added (median = 33.0, $T+ = 45.0$, $T- = 0.00$, $N = 9$, $P = 0.004$). There was no significant difference between their performance on control trials and chance (median = 5.0, $T+ = 9.5$, $T- = 5.5$, $N = 5$, NS).

Experiment 3: Olfactory Exclusion

The elephants' performance differed between 'empty trials' (median = 17/24 trials correct), 'baited trials' (median = 23/24 trials correct) and 'control trials' in which the subjects were not provided with information about either bucket (median = 11/24 trials correct; Friedman test $= \chi^2_2 = 14.0$, $N = 7$, $P = 0.001$; Fig. 2). The elephants performed significantly better in 'empty trials' than in 'control trials' (Wilcoxon matched-pairs signed-ranks test: $T+ = 28.0$, $T- = 0.00$, $N = 7$, $P = 0.016$), in 'baited trials' than in 'control trials' ($T+ = 28.0$, $T- = 0.00$, $N = 7$, $P = 0.016$), and in 'baited trials' than in 'empty trials' ($T+ = 28.0$, $T- = 0.00$, $N = 7$, $P = 0.016$). These results remained significant after a Bonferroni correction for multiple comparisons ($0.05/3 = \alpha = 0.017$). The elephants also did not show a significant learning effect between the first two and last two test sets in either 'baited' ($T+ = 13.0$, $T- = 8.0$, $N = 7$, NS) or 'empty' trials ($T+ = 8.0$, $T- = 2.0$, $N = 7$, NS), suggesting no significant change in their performance across trials.

DISCUSSION

Whereas the elephants did not follow acoustic cues in a two-way object choice task, they were able to use olfactory cues in the same task to locate food. In addition, the elephants effectively made choices by exclusion when given only olfactory information about the nonrewarding option.

The elephants did not demonstrate a capacity for locating food via acoustic signals derived directly from the food. In a previous object choice task (Plotnik et al., 2013), elephants successfully followed vocal cues to locate food. In that study, however, the elephants had received prior training with the cues. The vocal cues therefore probably served as directional commands rather than signals reliably associated with food. Although we did not counterbalance the auditory and olfactory conditions (because the former was a separate experiment completed before the latter was designed) the elephants had substantial experience with the apparatus before this study began (Plotnik et al., 2013). Thus, the negative outcome was not likely to be the result of the elephants' need to acclimate to a novel apparatus or condition. In addition, in informal replications of the auditory experiment (our unpublished data), the elephants did not score significantly above chance. We would not want to conduct formal replications of the auditory experiment with the same elephants as future success may be the result of learning, rather than a natural ability to use specific cues to find food, which was the main objective in this study.

Elephant ecology may account for this negative result in the auditory domain. While one might expect that elephants could be trained to recognize that acoustic cues derived from a food source are reliable indicators for the presence of food, there is no ecological validity to an elephant locating food resources spontaneously through audition. As such, the connection between the cue and the location of the food is arbitrary and thus might need to be learnt over time by the elephants. Object choice tasks using visual cues of a similarly arbitrary nature have also yielded negative results from elephants (Plotnik et al., 2013).

The elephants did demonstrate a capacity for locating food via direct olfactory investigation. When locating food in their environment, it is likely that elephants rely on their sense of olfaction and not vision or audition. Elephants may use olfactory cues (from food, water or conspecifics) when making migratory decisions, and thus may rely on their sense of smell when making specific decisions about their physical environment (e.g. Douglas-Hamilton & Douglas-Hamilton, 1975; Poole, 1996; Sukumar, 2003). Taken together, these findings also suggest that recognizing that differences in sensory perception exist between species and identifying such differences is fundamental for the appropriate design of future experiments. While primates and birds readily receive visual information about food rewards within experimental contexts (e.g. Call, 2004; Heimbauer, Antworth, & Owren, 2012; Hill, Collier-Baker, & Suddendorf, 2011; Mikolasch et al., 2012; Petit et al., 2005; Sabbatini & Visalberghi, 2008; Schloegl, 2011; Schloegl et al., 2009; Schmitt & Fischer, 2009; Shaw et al., 2013), assuming that other species that rely less on vision can similarly receive and interpret such information easily may put these species at a disadvantage as test subjects if the information is presented only in the form of visual cues.

The elephants also made choices by exclusion to locate the food reward in trials in which only the empty bucket was presented for investigation. This capacity operates through at least one of two mechanisms: either the elephants excluded the nonrewarding bucket in 'empty trials' by avoiding an option identified as nonrewarding, or the elephants took an additional cognitive step and excluded the empty bucket by inferring that the alternative bucket must be baited (Mikolasch et al., 2012; Paukner et al., 2009; Penn &

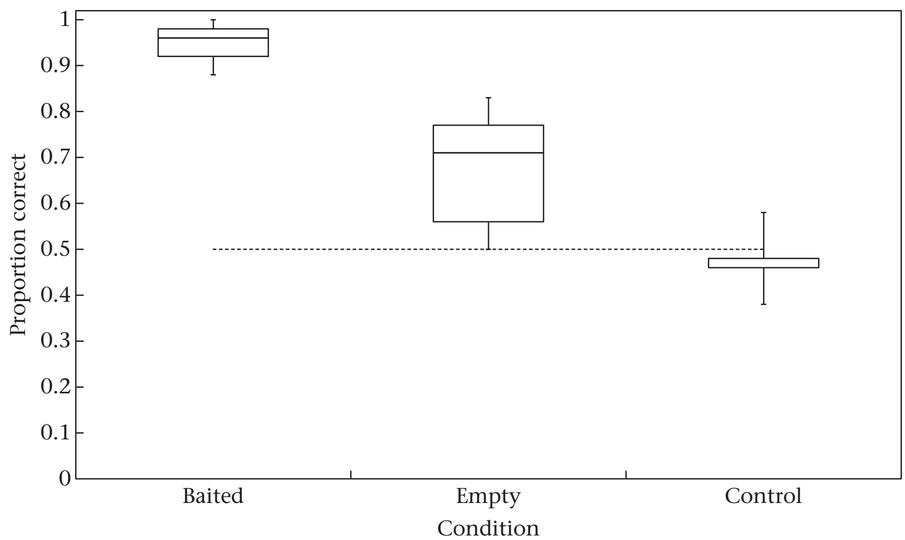

Figure 2. Box plot of olfactory exclusion data. The plot shows the proportion of trials within each condition (baited, empty, control) of experiment 3 in which the elephants correctly chose the bucket containing the food reward in the 'choice phase' (vertical bars show the range, while the box shows the median and interquartile range). The dashed line indicates chance performance.

Povinelli, 2007; Schloegl, 2011; Schloegl et al., 2009; Schmitt & Fischer, 2009; Shaw et al., 2013).

If the subject understands the rule that one container is always baited in each trial while the other remains empty, then the argument for inference is more plausible. After investigating the empty container, the subject would be able to form a mental representation of the contents within the alternative container in order to locate the food by inference (Shaw et al., 2013). If the subject fails to recognize this rule, it cannot mentally represent the contents of the baited bucket and the more likely explanation is that of avoidance. Given that the study subjects had participated in object choice tasks prior to the current study (Plotnik et al., 2013), they had substantial experience with and exposure to the apparatus. In all their contact with the apparatus, they were never presented with a trial in which both buckets were empty nor a trial in which both were baited. As such, based on the elephants' demonstrated success in the current study, it seems likely that they had an understanding that one and only one bucket was baited in each trial. Still, as there was no way to test empirically for an understanding of the rule in this experiment, we use the general, more ambiguous term 'exclusion'.

As elephants are a relatively new species in the study of convergent cognitive evolution (e.g. Byrne et al., 2009; Irie & Hasegawa, 2009; Plotnik, de Waal, & Reiss, 2006; Plotnik, Lair, Suphachoksahakun, & de Waal, 2011), it is difficult to design new, innovative approaches to understanding their intelligence without looking first to the previous literature, much of which has been focused on primates. Although this may help in the application of specific research questions to the study of elephant physical and social cognition, the present study suggests that careful attention to elephants', and other nonvisual cognitive animals', multimodal sensory capabilities will be important for deciding how to try to answer them.

Although previous studies have helped to explain how elephants use their auditory (Payne et al., 1986; Poole et al., 1988; McComb et al., 2000) and olfactory (Bagley et al., 2006; Bates et al., 2007; Bates et al., 2008; Buss et al., 1976; Poole et al., 1984; Rasmussen & Schulte, 1998; Vidya & Sukumar, 2005) senses in communicative social contexts, surprisingly little work has been devoted to understanding how elephants may use their senses to navigate their physical environment (Arvidsson et al., 2012; Plotnik et al., 2013). There has also been no direct investigation of how elephants use either visual or nonvisual senses in cognitively driven tasks. The results from this study add to the growing literature on exclusion and inferential reasoning and broaden our understanding of the physical contexts within which elephants rely on particular senses. More importantly, these results provide some of the first empirical evidence of elephants utilizing a mode of nonvisual sensory perception in a cognitive, physical task.

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Appendix

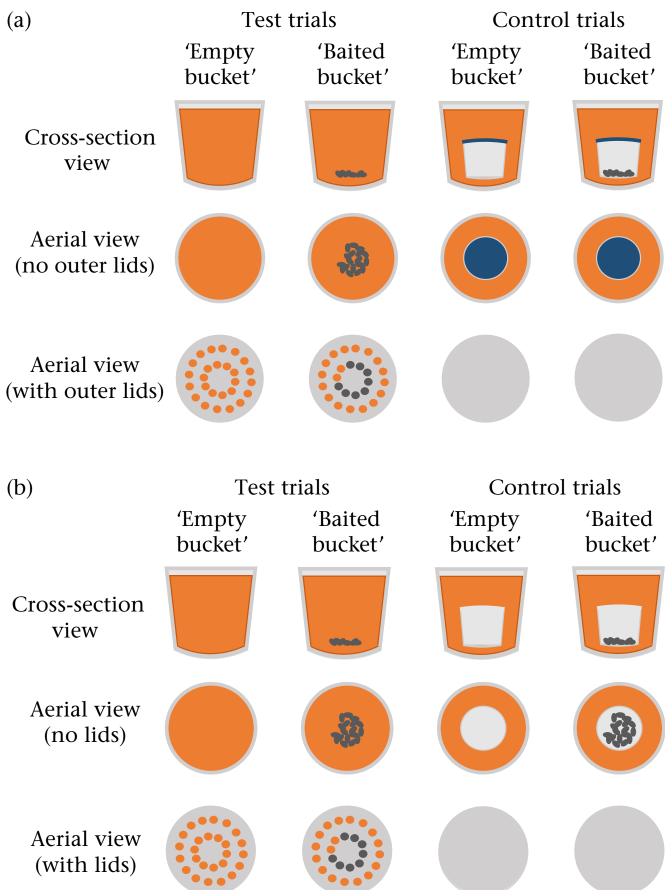

Figure A1. Bucket, lid and food arrangements for (a) the 'investigation phase' and (b) the 'choice phase' of test trials and control trials in experiment 2, as described in the Methods.

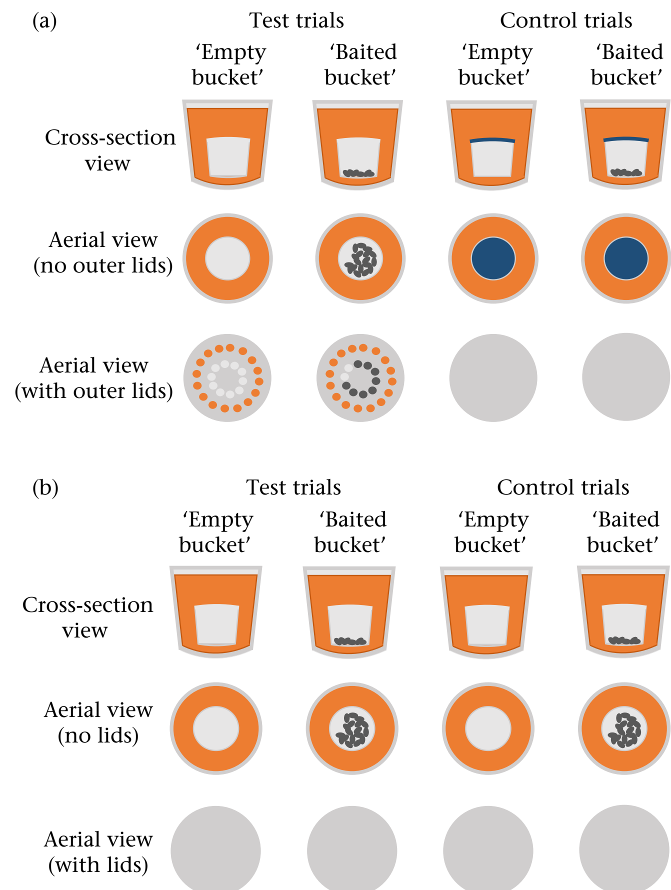

Figure A2. Bucket, lid and food arrangements for (a) the 'investigation phase' and (b) the 'choice phase' of test trials and control trials in experiment 3, as described in the Methods.