This is the accepted manuscript of a paper published as:

African elephants can use human pointing cues to find hidden food. Smet, A. F. & Byrne, R. W. 21 Oct 2013 In: Current Biology. 23, 20, p. 2033-2037

African elephants can use human pointing

cues to find hidden food

Authors: Anna F. Smet¹, Richard W. Byrne¹*

¹ Centre for Social Learning & Cognitive Evolution, School of Psychology and Neuroscience, University of St Andrews, St Andrews, Fife KY16 9JP, Scotland, UK

^{*}Correspondence: rwb@st-andrews.ac.uk, Tel. +44 (0) 1334 462051

2

Summary

How animals gain information from attending to the behaviour of others has been widely studied, driven partly by the importance of referential pointing in human cognitive development[1–4]: but species differences in reading human social cues remain unexplained. One explanation is that this capacity evolved during domestication[5, 6]; but it may be that only those animals able to interpret human-like social cues were successfully domesticated. Elephants are a critical taxon for this question: despite their longstanding use by humans they have never been domesticated[7]. Here we show that a group of 11 captive African elephants, 7 of them significantly as individuals, could interpret human pointing to find hidden food. We suggest that success was not due to prior training or extensive learning opportunities. Elephants successfully interpreted pointing when the experimenter's proximity to the hiding place was varied and when the ostensive pointing gesture was visually subtle, suggesting that they understood the experimenter's communicative intent. The elephant's native ability in interpreting social cues may have contributed to its long history of effective use by man.

Highlights

- African elephants can use human pointing cues to find hidden food
- Success is immediate, despite few prior learning opportunities
- Follow pointing correctly even when the human's body position conflicts with point direction
- With visually subtle forms of pointing, performance matches that of 2-year old children

Results and Discussion

For group-living animals, gaining information from conspecifics offers advantage: interpreting the behaviour of others in the social group, who may have privileged knowledge, can increase foraging success or early predator detection. The African elephant's (*Loxodonta africana*) complex society makes it a good candidate for using other's knowledge: its elaborate fission-fusion society is one of the most extensive of any mammal[8], and cognitive sophistication is known to correlate with the complexity of a species' social group ([9] for review).

The 'object-choice' task has been used with various species to test to what extent individuals can use information from social cues, something which human infants do successfully[2, 4]. A reward is hidden in one of several containers, and an experimenter signals which one by pointing. Results from the task have driven a controversy over two possible explanations for species variations in learning to interpret human social cues. One theory is that the ability to read human social-communicative signals evolved during domestication[5]. This is supported by the success of domestic animals including cats, goats, horses[10–12] and particularly dogs, which are substantially more skilful than wolves at this task[5] (but see[13]). Dogs' skill may represent a case of convergent evolution with humans[14], since non-

human primates without exceptional levels of prior experience with humans do not perform at a comparable level to that of dogs[15–19]. An alternative or complementary explanation is that those species that were successfully domesticated *already* attended and responded to human-like social cues, making them suitable for domestication. In this case, dogs' social skills may instead stem from canid ancestry: for group hunters, it pays to read social cues from group members and prey[20]. The question of why certain animals respond to human social cues remains unsettled.

The unique elephant-human relationship provides a singular opportunity to test whether an ability to respond to human social cues is a characteristic found in any wild animal which can form a close working relationship with humans. Tamed elephants have worked alongside humans since between 4000 and 8000 years ago[7]; elephants are taken from the wild, not domesticated, but readily form bonds with man. Elephants are thus an ideal study species to investigate whether responsiveness to human social cues is an essential enabling characteristic for close cooperation with humans, or whether this responsiveness is a secondary result of domestication. Surprisingly, Asian elephants have been found not to respond to human-given gestural cues, in spite of their being very suited to human work[21].

In two studies we tested a total of 11 captive African elephants, housed at an elephant-back safari operator, on their ability to use gestural cues ('pointing') given by a human experimenter (AFS, hereafter E). Since successive visual co-orienting between a social partner and a distant object of interest is a criterion for defining intentional communication in humans[22], every pointing cue included gaze alternation between the subject and the focus of the pointing signal. The studies were approved by the University of St Andrews' Animal Welfare & Ethics Committee (AWEC).

The elephants could find food by following the direction of E's arm when E pointed from a position equidistant from the two possible hiding places with the whole ipsilateral arm and index finger aligned with the baited container (fig. 1). Elephants selected the indicated container significantly above chance: on average 67.5 % of the time (SD = 16.4; fig. 2, body-centred; individually, 5 out of 11 elephants chose the indicated container, table 1); for comparison, 12 month children reach 72.7% on this task[2]. We excluded the possibility that the elephants' success was due to some other factor, such as direct olfactory information or inadvertent cueing by the handlers, by including control trials where E did not point but looked straight ahead until the elephant chose. On these control trials, no elephant chose the baited container above chance; as a group they selected the baited container 46.7% of the time (SD = 13.8; fig. 2).

Any animal in captivity has ample opportunity for learning an association between humans and the food they provide; that some animals are extremely sensitive to human behaviour is well-demonstrated[23]. One way of solving the object-choice task is by approaching the experimenter, whose arm comes slightly closer to the baited container. Such performance biases have been found in pointing studies with other species (e.g. chimpanzees, which indiscriminately chose the container nearest to the experimenter[4]). To test whether elephants were choosing on the basis of a container's visual proximity to the experimenter's body, we varied E's position in trials interspersed with those where E stood centrally. If elephants were primarily relying on body location for their choices, we expected them to be systematically misled when E pointed from an asymmetric position, nearer to one container than the other. As expected, elephants correctly chose the baited container when E pointed to it from a position close to it (fig.2, asymmetric congruent; four elephants individually chose correctly significantly above chance, table 1). Crucially, however, when E stood near to the empty container but pointed to the further away baited container, elephants chose correctly significantly above chance

(fig.2, asymmetric incongruent; individually, one of the elephants chose the baited container significantly above chance, table 1).

Although elephants were able to use a communicative gesture to find hidden food, when E's position was in conflict with the direction of the pointing signal this reduced their ability to follow the direction of the point and gaze alternation (fig.2, ANOVA). Elephants were more likely to choose the baited container when E stood nearest to it and pointed to it ($M = 75.4 \, \%$, SD = 14.0) than when E pointed to the target container from beside the further away, empty container ($M = 59.8 \, \%$, SD = 12.8); and in control trials, where E did not point at any container but stood asymmetrically, elephants chose the baited container significantly more often when E stood near it ($M = 52.8 \, \%$, SD = 14.6) than further away ($M = 35.4 \, \%$, SD = 13.6). Elephants therefore did use E's body position to guide their choice when no communicative gesture was available, but when a communicative pointing signal was available they gave that greater weight. This suggests that elephants recognized the informational aspect of the gesture, rather than simply choosing by approaching the human body or outstretched arm.

Because the elephants were using something other than experimenter proximity, we next attempted to identify the visual features of a social cue necessary for elephants to interpret it as a location indicator. Features were systematically varied in order to identify whether elephants were choosing on the basis of: (1) E's head orientation when she looked back and forth from the elephant to the target container during pointing; (2) the side of E on which a limb protruded, as has been found to underlie the behaviour of domestic dogs and chimpanzees[4,24,25], or (3) the direction of the pointing gesture (fig. 3).

Elephants failed to select the baited container based on E's head-and-eye gaze direction alone (M = 45.0 %, SD = 7.45, fig. 4, gaze alone). In contrast, they successfully interpreted pointing with the whole extended contralateral arm (M= 72.4 %, SD = 15.7, fig. 4: whole arm cross-body point; four elephants individually chose correctly above chance, table 1), and with the forward cross-body point, although E's arm did not protrude sideways of the periphery of her body (fig. 3; M= 58.0 %, SD = 8.94, fig. 4: forward cross-body point; individually, one elephant's performance was above chance, table 1). The main source of the elephants' information about the location of the food was evidently the pointing gesture itself: the forearm, hand and index-finger direction. Finally, we examined the case when E gestured with elbow protruding in the incorrect direction; in this situation, domestic dogs[24,25] and chimpanzees[4] use a rule of choosing the container on the side at which a limb protruded from the experimenter's outline, giving significantly below chance results. Elephants, however, responded at chance level (M=52.4%, SD = 11.8, fig. 4, elbow cross-body point); apparently they did not treat 'elbow cross-body pointing' as a communicative signal at all, just as is found with two year-old human infants[24]. Responses to subtle differences in pointing gestures have previously been trained in animals (e.g. in a seal [26], and to a lesser extent chimpanzees [4]; in both cases the subjects were extensively trained to follow a basic pointing gesture to a defined criterion before other variants were introduced). Here we found elephants capable of responding spontaneously to pointing gestures that require attention to subtle differences in the position of the forearm and hand.

Having found that elephants can indeed gain useful information from human pointing without prior training, we examined the data to determine whether our subjects had learned to follow the human gestures during the course of the experiment. We compared their performance on the first half of trials to that on the second half, for all conditions where elephants were successfully using social cues. In no case was any significant difference found between the proportions of correct trials in the first compared

to the second half of trials (fig. S1, S2). This suggests that elephants did not learn to solve the task with experience gained during the course of the experiment. More than half of the elephants found the food on the first trial of each trial type, except where gaze alone indicated the direction, and on control trials. All elephants (n = 9) found the food on the first whole arm cross-body point they were presented with (p = 0.004) (fig S1, S2).

All of these elephants have lived in captivity since infancy: they have had the opportunity to witness pointing used between humans. However, observing human interactions does not automatically translate into aptitude at interpretation of these interactions. Moreover, these elephants interact with numerous handlers, in a manner quite unlike the close, single, lifelong relationship between an Asian elephant and its mahout, or that of a dog and its master: handlers work with each elephant on a threeday rota before moving on to a different one. When not taking elephant-back rides, or participating in these experiments, elephants spend the daytime feeding in the African bush, where they are directed from a distance by vocal commands from handlers on foot who are often out of sight. These elephants' training is based exclusively on *vocal* commands, specifically so that they can be directed during elephant-back safaris and while feeding in the bush, without the need for close proximity to their handlers. During three months of interaction with the elephants and handlers, AFS never observed any of the handlers using pointing to direct any elephant. We concluded from this that the elephants had minimal opportunity for learning about pointing. Moreover, elephants' success on this task was not related to age, indicating that different amounts of experience with human handlers did not influence these elephants' abilities to solve the task (fig S1, S2). Future studies with younger elephants could test more precisely the role of experience in the development of elephants' ability to follow pointing.

Ç

Elephants rely primarily on their well-developed auditory and olfactory senses, as opposed to vision[27]; their retina has the same visual pigments as human 'colour-blind' deuteranopes[28], and initial findings suggest they have poor visual acuity[29]. Perhaps unsurprisingly, then, none of our elephants was able to use the experimenter's head-and-eye gaze direction alone to find the hidden food. Many other species similarly fail to use gaze direction to solve the object-choice task, including goats, pigs, wild boars, cotton-top tamarins, horses[11,12,19,30]; even domestic dogs are less adept at using gaze than pointing[5,31]. During interactions between elephants there are few, if any, advantages to attending to head orientation: the head orientation of elephants does not have the same range of motion separate from the torso as does that of primates. In this study we did not test whether the torso or body orientation of the experimenter influenced elephants' choices; however, since the elephants were proficient at understanding pointing, attending to torso orientation might have conferred little advantage. Regardless of any such limitations, the subjects in our study provide evidence that African elephants can use pointing to find hidden food, even when no limb protrudes in the direction of the target.

Our results show that elephants spontaneously attend to and correctly interpret human deictic gestures without extensive prior learning opportunities: the only non-human species so far to show this ability. The tendency to attend to human visual signals is likely to underlie elephants' successful use by humans, but their readiness to attend to human pointing and spontaneously interpret it as a communicative signal requires explanation. Asian elephants' failure to follow pointing in a similar task may have been due to procedural differences: in that study, the experimenter gave the visual signal for five seconds only, without gaze alternation, before a sliding table apparatus brought the containers within reach of the subjects[21]. We suggest that the most plausible account of our elephant's ability to interpret even subtle human pointing gestures as communicative is that human pointing, as we

10

presented it, taps into elephants' natural communication system. If so, then interpreting movements of other elephants as deictic communication must be a natural part of social interaction in wild herds; specifically, we suggest that the functional equivalent of pointing might take the form of referential indication with the trunk. A tendency to attribute communicative intentions is a favourable characteristic for an animal which works with a human handler and may explain why elephants have successfully been tamed for human work and have historically had a close bond with humans, in spite of being potentially dangerous and unmanageable due to their great size.

References

- 1. Leavens, D., A., and Hopkins, W. D. (1999). The whole-hand point: the structure and function of pointing from a comparative perspective. J. Comp. Psychol. *113*, 417–425.
- 2. Behne, T., Liszkowski, U., Carpenter, M., and Tomasello, M. (2012). Twelve-month-olds' comprehension and production of pointing. Br. J. Dev. Psychol. *30*, 359–75.
- 3. Behne, T., Carpenter, M., and Tomasello, M. (2005). One-year-olds comprehend the communicative intentions behind gestures in a hiding game. Dev. Sci. 8, 492–9.
- 4. Povinelli, D. J., Reaux, J. E., Bierschwale, D. T., Allain, A. D., and Simon, B. B. (1997). Exploitation of pointing as a referential gesture in young children, but not adolescent chimpanzees. Cogn. Dev. *12*, 423–461.
- 5. Hare, B., Brown, M., Williamson, C., and Tomasello, M. (2002). The domestication of social cognition in dogs. Science *298*, 1634–1636.
- 6. Hare, B., Rosati, A., Kaminski, J., Bräuer, J., Call, J., and 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, e1–e6.
- 7. Lair, R. C. (1997). Gone Astray The care and management of the Asian Elephant in domesticity (Rome: Food and Agriculture Organization of the United Nations, regional office for Asia and the Pacific).
- 8. Wittemyer, G., Douglas-Hamilton, I., and Getz, W. (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. Anim. Behav. *69*, 1357–1371.
- 9. Byrne, R. W., and Bates, L. A (2007). Sociality, evolution and cognition. Curr. Biol. *17*, R714–23.
- 10. Miklósi, A., Pongrácz, P., Lakatos, G., Topál, J., and Csányi, V. (2005). A comparative study of the use of visual communicative signals in interactions between dogs (Canis familiaris) and humans and cats (*Felis catus*) and humans. J. Comp. Psychol. *119*, 179–86.
- 11. Kaminski, J., Riedel, J., Call, J., and Tomasello, M. (2005). Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. Anim. Behav. *69*, 11–18.
- 12. Proops, L., Walton, M., and McComb, K. (2010). The use of human-given cues by domestic horses, *Equus caballus*, during an object choice task. Anim. Behav. *79*, 1205–1209.
- 13. Udell, Monique, A. R., Dorey, Nicole, R., Wynne, Clive, D. L., Udell, M. A. R., Dorey, N. R., and Wynne, C. D. L. (2008). Wolves outperform dogs in following human social cues. Anim. Behav. *76*, 1767–1773.

- 14. Hare, B., and Tomasello, M. (2005). Human-like social skills in dogs? Trends Cogn. Sci. 9, 439–44.
- 15. Itakura, S., and 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*, 119–26.
- 16. Peignot, P., and Anderson, J. R. (1999). Use of experimenter-given manual and facial cues by gorillas (*Gorilla gorilla*) in an object-choice task. J. Comp. Psychol. *113*, 253–260.
- 17. Anderson, J. R., Montant, M., and Schmitt, D. (1996). Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. Behav. Proc. *37*, 47–55.
- 18. Anderson, J. R., Sallaberry, P., and Barbier, H. (1995). Use of experimenter-given cues during object-choice tasks by capuchin monkeys. Anim. Behav. *49*, 201–208.
- 19. Neiworth, J. J., Burman, M. A., Basile, B. M., and Lickteig, M. T. (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.
- 20. Hare, B., and Tomasello, M. (1999). Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. J. Comp. Psychol. *113*, 173–177.
- 21. Plotnik, J. M., Pokorny, J., J., Keratimanochaya, T., Webb, C., Beronja, H., F., Hennessy, A., Hill, J., Hill, V., J., Kiss, R., Maguire, C., Melville, B., L., et al. (2013). Visual cues given by humans are not sufficient for Asian elephants (*Elephas maximus*) to find hidden food. PloS one 8, e61174.
- 22. Leavens, D. A., Russell, J. L., and Hopkins, W. D. (2005). Intentionality as Measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). Child Dev. 76, 291–306.
- 23. Pfungst, O. (1911). Clever Hans (The horse of Mr von Osten): A contribution to experimental animal and human psychology (New York: Henry Holt).
- 24. Lakatos, G., Soproni, K., Dóka, A., and Miklósi, A. (2009). A comparative approach to dogs' (*Canis familiaris*) and human infants' comprehension of various forms of pointing gestures. Anim. Cogn. *12*, 621–31.
- 25. Soproni, K., Miklósi, Á., Topál, J., and Csányi, V. (2002). Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. J. Comp. Psychol. *116*, 27–34.
- 26. Shapiro, A. D., Janik, V. M., and Slater, P. J. B. (2003). A gray seal's (*Halichoerus grypus*) responses to experimenter-given pointing and directional cues. J. Comp. Psychol. *117*, 355–62.
- 27. McComb, K., Reby, D., and Moss, C. (2011). Chapter 10: Vocal communication and social knowledge in African elephants. In The Amboseli Elephants. A long-term perspective on a long-

- lived mammal, C. J. Moss, H. Croze, and P. C. Lee, eds. (Chicago and London: The University of Chicago Press), pp. 162–175.
- 28. Yokoyama, S., Takenaka, N., Agnew, D. W., and Shoshani, J. (2005). Elephants and human color-blind deuteranopes have identical sets of visual pigments. Genetics *170*, 335–44.
- 29. Shyan-Norwalt, M. R., Peterson, J., Milankow King, B., Staggs, T. E., and Dale, R. H. I. (2010). Initial findings on visual acuity thresholds in an African elephant (*Loxodonta africana*). Zoo Biol. 29, 30–5.
- 30. Albiach-Serrano, A., Bräuer, J., Cacchione, T., Zickert, N., and Amici, F. (2012). The effect of domestication and ontogeny in swine cognition (*Sus scrofa scrofa and S. s. domestica*). App. Anim. Behav. Sci. *141*, 25–35.
- 31. Bräuer, J., Kaminski, J., Riedel, J., Call, J., and Tomasello, M. (2006). Making inferences about the location of hidden food: social dog, causal ape. J. Comp. Psychol. *120*, 38–47.

Acknowledgements We thank the School of Psychology and Neuroscience of the University of St Andrews for providing the funding for this research, and D. Perrett for advice in revising the manuscript. We are grateful to Wild Horizons and its board of directors in Victoria Falls for granting us permission to work with the elephants; Z. Sibanda and staff at Wild Horizons for advice and assistance with practical aspects of running the study; R. Parry and J. Dawson of the Victoria Falls Wildlife Trust for facilitation and logistical support on site; the team of elephant handlers who through their daily assistance made collecting the data possible; and R. Nicholas for assisting in the data collection.

Figure legends

Fig. 1. Illustration of experimental set-up. At the start of a session the subject's handler (standing on the subject's left) led it to 3-4 metres from the test location. Behind an opaque screen (70 x 60 cm) one of two opaque containers (buckets of diameter 30 cm, height 45 cm) was baited, then E pushed the screen over and lifted the containers simultaneously outward, to positions approximately 1.5 metres apart and in front of two wooden trays, and got the subject's attention. In experimental trials, E pointed towards the baited container, while repeatedly turning her head to look back and forth between the elephant and the container. The handler instructed the subject to approach: E continued indicating until the elephant had chosen a container. In the figure E executes a whole arm ipsilateral point to the baited container from a body-centred position. In control trials E looked at the subject without pointing until it had chosen. When the subject touched or entered a container with its trunk this was coded as its choice. If it chose the baited container it was permitted to consume the food before being instructed to return to the starting position; if it did not, it was instructed to return immediately unrewarded. For all trials, E informed the handler of the food's location, but handlers were blind to the experimental hypothesis. Sessions were ended if the handler indicated that an elephant was unwilling, if an elephant left the testing area or if the elephants were called for the ride. Relates to Supplementary Experimental Procedures, and Movies S1-S3.

Fig. 2. Proportion of correct trials for each elephant when E pointed (whole arm ipsilateral pointing) or did not point (controls). E stood in one of three different locations which varied her proximity to the baited container; in all cases, pointing was done with a whole-arm action ipsilateral to the baited container. After baiting, E walked up to one of these three positions. On body-centred trials E stood equidistant from the two containers, and on asymmetric trials E stood closer to one of the

containers. When body-centred, E's feet were approximately 75 cm from both containers; when asymmetric, E stood approximately 25 cm towards the midpoint from the nearest container. This figure shows the point and no point control conditions from the body-centred and asymmetric (congruent and incongruent) positions. Means and standard error bars are indicated (+/- 1 SE). All tests are two-tailed, with alpha 0.5. Results of a one-sample t-test for: body-centred whole arm ipsilateral pointing (n = 11, t(10) = 3.533, p = 0.005), body-centred no point control (n = 11, t(10) = -0.787, p = 0.449), asymmetric congruent point (n = 10, M = 75.4%, SD = 14.0, t(9) = 5.730, p < 0.001), asymmetric incongruent point (n = 10, M = 59.8 %, SD = 12.8, t(9) = 2.424, p = 0.038). Results of a 2x2 within-subjects ANOVA on the proportion of correct trials, n = 10: main effect of experimenter's body position F(1,9) = 12.023, p = 0.007; main effect of pointing F(1,9) = 56.738, p < 0.001; no interaction F(1,9) = 0.083, p = 0.780. Relates to fig. S1.

Fig. 3. A bird's-eve view of the visual features of the pointing gestures used in Experiment 2.

Dotted lines indicate where the edge of the outline of E's body appears. The elephant faced in the direction of the arrow. For the whole arm cross-body point, E used the whole, straight contralateral arm and index-finger to point across the front of her body to the baited bucket, with the pointing hand stretching past the periphery of her body to align the whole arm with the baited bucket. For the elbow cross-body point E used the contralateral arm and index-finger to point at the baited bucket, but bent the arm so that the elbow protruded in the opposite direction of the baited bucket whereas the pointing hand was held in front of her torso. For the forward cross-body point E used the contralateral arm and index-finger to point at the baited bucket but with the entire gesture executed in front of her body, with her arm not protruding outwards to the side. We also included a condition of gaze alone, in which E looked back and forth between elephant and baited bucket, as in all other experimental trials, but did not point. These social cues were interspersed randomly with whole-arm ipsilateral pointing and

16

control trials. The cross-body pointing types were identical in shape to those used by Lakatos and colleagues[24].

Fig. 4. Mean proportion of correct trials for each type of social cue. All social cues here were given from a body-centred position between the two containers. Graph includes standard error bars (+/- 1 SE). All tests are two-tailed, with alpha 0.5. * indicates that the proportion correct differs significantly from chance. Results of one-sample t-tests: whole arm cross-body point (t(8) = 4.302, t(8) = 0.003), forward cross-body point (t(8) = 2.683, t(8) = 0.028), elbow cross-body point (t(8) = 0.623, t(8) = 0.0551), gaze alone (t(8) = -2.013, t(8) = 0.079). Relates to fig. S2 and movie S4.

Tables

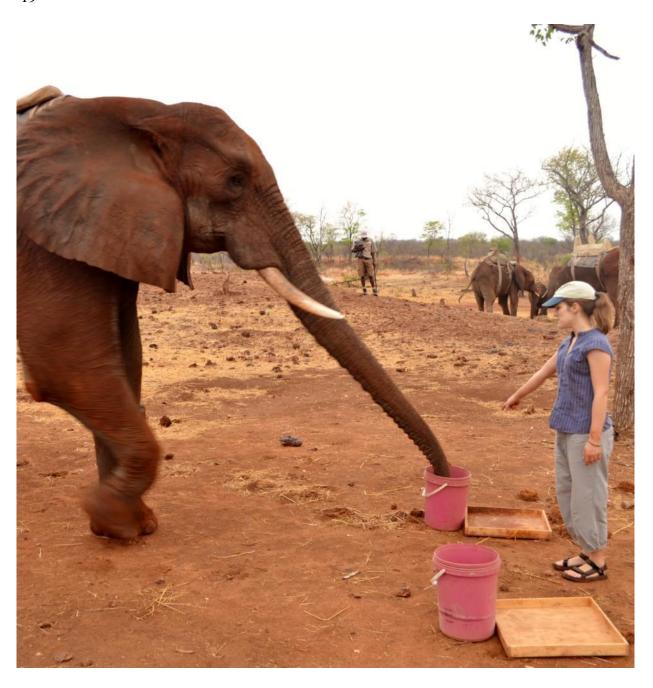
Summary of individual results for all condition

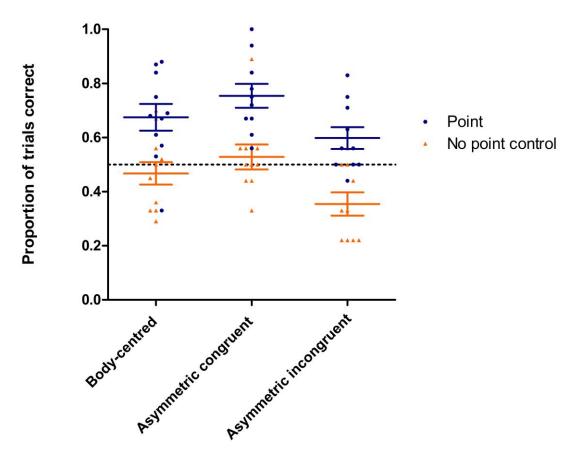
Subject	Number of trials correct/Number of trials									
	Body- centred whole arm ipsilateral point	Asymmetric congruent whole arm ipsilateral point	Asymmetric congruent no point control	Asymmetric incongruent whole arm ipsilateral point	Asymmetric incongruent no point control	Whole arm cross- body point	Forward cross- body point	Elbow cross- body point	Gaze alone	No point control
Coco	46/52 *	17/18 *	8/9*	12/17	2/9	15/18 *	14/18 *	14/20	9/18	10/28
Jock	34/50 *	12/18	3/9	9/18	2/9	12/18	10/18	7/20	7/18	9/27
Jumbo	38/55 *	13/18	5/9	10/18	4/9	13/18	10/18	8/20	8/18	13/30
Malasha	46/53 *	14/18 *	5/9	15/18*	5/9	14/18 *	11/18	11/20	10/18	16/32
Tendai	43/51 *	17/17 *	5/10	9/18	3/9	16/18 *	10/18	10/19	8/17	19/27
Jake	31/51	10/18	4/9	9/18	3/9	10/17	8/17	10/18	9/17	14/31
Doji	12/18	-	-	-	-	4/10	6/11	4/10	5/11	2/7
Tembi	20/35	16/19*	4/9	12/19	2/9	6/8	5/8	6/10	3/9	11/21
Emily	19/36	11/18	5/9	8/18	2/9	8/9 *	4/8	5/8	3/8	10/18
Izibulo	6/18	12/18	5/10	10/18	4/8	-	-	-	-	10/15
Janet	9/12	9/12	3/6	9/12	3/6	-	-	-	-	2/6

Table 1. This table shows the number of correct trials given out of the total number of trials for a condition per elephant. Subjects were individually tested, and elephants participated in trials of each treatment (within-subjects design). Subjects were selected based on elephant willingness to participate and availability of the elephant and its handler on that day. Doji did not participate in Experiment 1 due to injury, while Izibulo and Janet did not participate in Experiment 2 due to lack of handler availability and unwillingness to participate (no data indicated by '-'). Subjects' choices were scored at the time of choice, and filmed using a Panasonic HDC-SD90 camcorder so that they could be verified from the

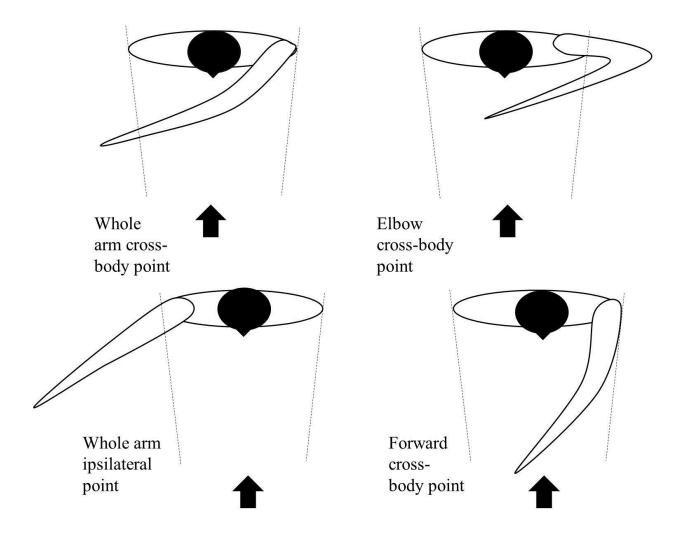
18

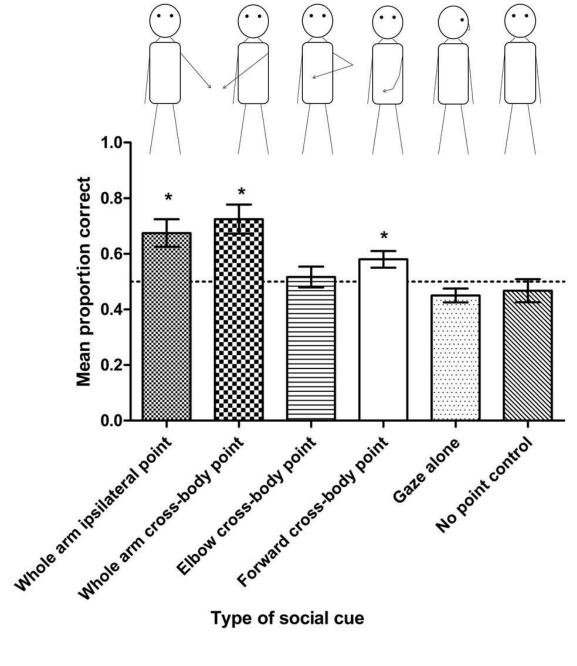
video material. All elephants that performed significantly above chance in a condition, according to a two-tailed binomial test, are indicated by *. Body-centred whole arm ipsilateral point (Jock: p=0.013, Jumbo: p=0.006, Coco: p<0.001, Malasha: p<0.001 and Tendai: p<0.001), asymmetric congruent point (Malasha: p=0.031, Tembi: p=0.004, Coco, Tendai: p<0.001), asymmetric incongruent point (Malasha: p=0.008), whole arm cross-body point (Emily: p=0.039, Malasha: p=0.031, Coco: p=0.008, Tendai: p=0.001), forward cross-body point (Coco: p=0.031).





Position of experimenter





Type of social cue