Report

African Elephants Can Use Human Pointing Cues to Find Hidden Food

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Summary

How animals gain information from attending to the behavior 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 humanlike 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, seven 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.

Results and Discussion

For group-living animals, gaining information from conspecifics offers advantage: interpreting the behavior 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 others' 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 (see [9] for a review).

The "object-choice" task has been used with various species to test to what extent individuals can use information from social cues, something that 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 skillful than wolves at this task ([5], but see [13]). Dogs' skill may represent a case of convergent evolution with humans [14], since nonhuman primates

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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 that can form a close working relationship with humans. Tamed elephants have worked alongside humans since between 4,000 and 8,000 years ago [7]; elephants are taken from the wild, not domesticated, but they 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 (A.F.S., 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 and Ethics Committee.

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 (Figure 1). Elephants selected the indicated container significantly above chance—on average 67.5% of the time (SD = 16.4; Figure 2, body centered; individually, 5 out of 11 elephants chose the indicated container, Table 1); for comparison, 12-month-old 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 in which 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; Figure 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 behavior is well demonstrated [23]. One way of solving the objectchoice 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





Figure 1. Illustration of Experimental Setup

At the start of a session, the subject's handler (standing on the subject's left) led it to 3-4 m from the test location. Behind an opaque screen (70×60 cm), one of two opaque containers (buckets of diameter 30 cm, height 45 cm) was baited, and then E pushed the screen over and lifted the containers simultaneously outward, to positions approximately 1.5 m apart and in front of two wooden trays, and got the subject's attention. In experimental trials, E pointed toward 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-centered 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. See also the Supplemental Experimental Procedures and Movies S1. S2. and S3.

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 (Figure 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 (Figure 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

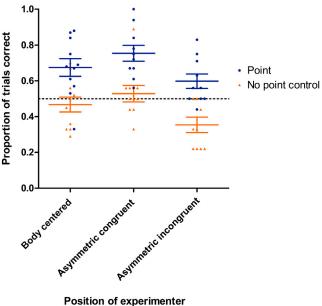


Figure 2. Proportion of Correct Trials for Each Elephant when E Pointed, Ipsilaterally with the Whole Arm, or Did Not Point, as in Control Trials

E stood in one of three different locations that 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-centered trials E stood equidistant from the two containers, and on asymmetric trials E stood closer to one of the containers. When body-centered, E's feet were approximately 75 cm from both containers; when asymmetric, E stood approximately 25 cm toward the midpoint from the nearest container. This figure shows the point and no point control conditions from the body-centered and asymmetric (congruent and incongruent) positions. Means ± 1 SE are indicated. All tests are two-tailed, with alpha 0.5. Results of a one-sample t test were as follows: body-centered whole-arm ipsilateral pointing [n = 11, t(10) = 3.533, p = 0.005], body-centered no point control [n = 11, t(10) = -0.787, p = 0.449], asymmetric congruent point [n = 10, mean = 75.4%, SD = 14.0, t(9) = 5.730, p < 0.001], and asymmetric incongruent point [n = 10, mean = 59.8%, SD = 12.8, t(9) = 2.424, p = 0.038]. Results of a 2 × 2 within-subjects ANOVA on the proportion of correct trials(n = 10) were as follows: 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. See also Figure S1.

with the direction of the pointing signal, this reduced their ability to follow the direction of the point (Figure 2, ANOVA). Elephants were more likely to choose the baited container when E stood nearest to it and pointed to it (mean = 75.4%, SD = 14.0) than when E pointed to the target container from beside the further away, empty container (mean = 59.8%, SD = 12.8), and in control trials, in which E did not point at any container but stood asymmetrically, elephants chose the baited container significantly more often when E stood near it (mean = 52.8%, SD = 14.6) than further away (mean = 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

	Number of Trials Correct/Number of Trials									
Subject	Body-Centered 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		No Point Control
Сосо	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
zibulo	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

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 lzibulo 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 were filmed using a Panasonic HDC-SD90 camcorder so that they could be verified from the video material. All elephants that performed significantly above chance in a condition, according to a two-tailed binomial test, are indicated by asterisks. p values were as follows: body-centered 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 incongruent point (Malasha, p = 0.008), whole-arm cross-body point (Emily, p = 0.039; Malasha, p = 0.031; Coco, p = 0.001; and Tendai, p = 0.001), and forward cross-body point (Coco, p = 0.031).

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 behavior of domestic dogs and chimpanzees [4, 24, 25]; or (3) the direction of the pointing gesture (Figure 3).

Elephants failed to select the baited container based on E's head-and-eye gaze direction alone (mean = 45.0%, SD = 7.45, Figure 4, gaze alone). In contrast, they successfully interpreted pointing with the whole extended contralateral arm (mean = 72.4%, SD = 15.7, Figure 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 (Figure 3; mean = 58.0%, SD = 8.94, Figure 4, forward crossbody 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 her 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 (mean = 52.4%, SD = 11.8, Figure 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 2-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 (Figures S1 and S2 available online). 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; Figures S1 and S2).

All of these elephants have lived in captivity since infancy: they have had the opportunity to witness pointing used between humans. However, observation of 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 3-day rotation 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 3 months of interaction with the elephants and

Table 1. Summary of Individual Results for All Conditions

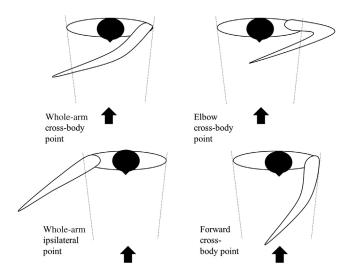


Figure 3. A Bird's-Eye View of the Visual Features of the Pointing Gestures Used in Experiment 2

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

handlers, A.F.S. 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 (Figures S1 and S2). Future studies with younger elephants could test more precisely the role of experience in the development of elephants' ability to follow pointing.

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 "color-blind" deuteranopes [28], and initial findings suggest that they have poor visual acuity [29]. Perhaps unsurprisingly, then, none of our elephants were 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, cottontop tamarins, and 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

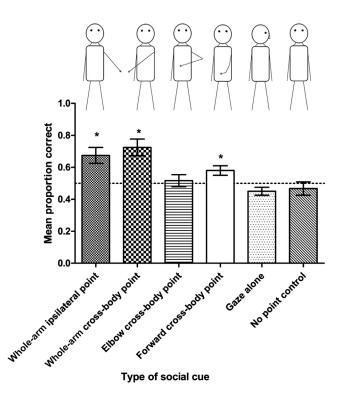


Figure 4. Mean Proportion of Correct Trials for Each Type of Social Cue All social cues here were given from a body-centered position between the two containers. In the graph, bars represent ± 1 SE. All tests are two-tailed, with alpha 0.5. Asterisks indicate that the proportion correct differs significantly from chance. Results of one-sample t tests were as follows: wholearm cross-body point [t(8) = 4.302, p = 0.003], forward cross-body point [t(8) = 2.683, p = 0.028], elbow cross-body point [t(8) = 0.623, p = 0.551], and gaze alone [t(8) = -2.013, p = 0.079]. See also Figure S2 and Movie S4.

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 nonhuman 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 5 s 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 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 favorable characteristic for an animal that 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.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, two figures, and four movies and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.08.037.

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