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Interpretation of human pointing by African elephants: generalisation and rationality

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Abstract Factors influencing the abilities of different animals to use cooperative social cues from humans are still unclear, in spite of long-standing interest in the topic. One of the few species that have been found successful at using human pointing is the African elephant (*Loxodonta africana*); despite few opportunities for learning about pointing, elephants follow a pointing gesture in an object-choice task, even when the pointing signal and experimenter's body position are in conflict, and when the gesture itself is visually subtle. Here, we show that the success of captive African elephants at using human pointing is not restricted to situations where the pointing signal is sustained until the time of choice: elephants followed human pointing even when the pointing gesture was withdrawn before they had responded to it. Furthermore, elephants rapidly generalised their response to a type of social cue they were unlikely to have seen before: pointing with the foot. However, unlike young children, they showed no sign of evaluating the 'rationality' of this novel pointing gesture according to its visual context: that is, whether the experimenter's hands were occupied or not.

Keywords Pointing · Social cues · Object-choice · Rationality · Communication

Introduction

The extent to which non-human animals understand and adapt their behaviour to human social signals is a question which has received much attention. The case of Clever Hans, the horse that seemed to be capable of counting and solving arithmetic problems, is one such early example where an animal perceived and responded to 'certain postures and movements of the questioner', signs which were 'given involuntarily by all the persons involved and without any knowledge on their part that they were giving any such signs' (Pfungst 1911, p. 88). Clever Hans has long served as a warning to researchers studying the cognition of non-human animals against underestimating or ignoring the potential impact of human signals, unconscious or otherwise, on animal behaviour. The systematic study of animals' use of human social signals has focused on what is thought to be a uniquely human gesture (Povinelli and Davis 1994; Tomasello et al. 2007): pointing with an extended arm and index finger. Human infants point and comprehend pointing by others from a young age (Behne et al. 2012). Although animals in captivity in some cases do point for humans (Leavens et al. 1996; Leavens and Hopkins 1999; Gómez 2007), even without explicit training to do so (Leavens and Hopkins 1998), there is little evidence that any species naturally uses an intentional pointing gesture to redirect the attention of others (but see Hobaiter et al. 2013 for possible whole-hand pointing by wild chimpanzees).

A typical context in which animals are tested for their ability to use human pointing is the 'object-choice task' (e.g. Anderson et al. 1995). The object-choice task requires the animal to choose between one of several containers, when an experimenter points to one of the containers where food is hidden. Using the object-choice task, it has been

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found that domestic animals including goats (Kaminski et al. 2005), cats (Miklósi et al. 2005), horses (Proops et al. 2010) and especially dogs (Miklósi et al. 1998; Hare and Tomasello 1999; Hare et al. 2002; Soproni et al. 2002; Miklósi et al. 2005) tend to be successful at using human pointing to find hidden food. Domestic animals' successful interpretation of pointing has led to the suggestion that the ability to respond to human social cues evolved during the process of domestication (Hare et al. 2002), possibly as a by-product of selection on systems mediating fear and aggression (Hare et al. 2005). Dogs have been found more skilful at interpreting human signals than are wolves (Hare et al. 2002; Miklósi et al. 2003), supporting the theory that the ability to read human social signals evolved during domestication. Non-human primates' use of human deictic signals in the object-choice task has produced conflicting results. In many instances, captive non-human primates have been found not to interpret pointing correctly when using only their pre-experimental knowledge (capuchin monkeys, Anderson et al. 1995; rhesus macaques, Anderson et al. 1996; cotton-top tamarins, Neiworth et al. 2002; chimpanzees, Hare et al. 2002; chimpanzees; and orang-utans, Tomasello et al. 1997). While there are individual apes of all species that have been found to successfully respond to human-given social cues in the object-choice task, these were predominantly individuals that had extensive experimental experience or had been raised in socio-communicatively rich environments (chimpanzees, Povinelli et al. 1990, 1992, 1999; Itakura and Tanaka 1998; Itakura et al. 1999; Mulcahy and Call 2009; Lyn et al. 2010; bonobos, Mulcahy and Call 2009; Lyn et al. 2010; gorillas, Peignot and Anderson 1999; and orang-utans, Call and Tomasello 1994; Tomasello et al. 1997; Itakura and Tanaka 1998). At the functional level, non-human apes' relatively poor performance is thought to be influenced by the inherently cooperative nature of this task, where food is helpfully pointed out to them: a situation which apes are unlikely to be familiar with from their own interactions with conspecifics (Hare 2001; Hare and Tomasello 2004), but inconsistencies in the methods used between species (reviewed in: Miklósi and Soproni 2006; Mulcahy and Hedge 2012) complicate interpretation of the mixed results. Nevertheless, the ability to follow human pointing is certainly not exclusive to domestic animals (e.g. seals, Scheumann and Call 2004; dolphins, Herman et al. 1999, Pack and Herman 2004; megachiropteran bats, Hall et al. 2011), and an alternative explanation has been proposed: that successful domestication was limited to species that naturally attended to and reacted appropriately to the cues that humans use to communicate, thus making them suitable for potential domestication (Smet and Byrne 2013). The latter theory was supported by the results from a study we carried out with African elephants (*Loxodonta africana*) (Smet and Byrne 2013).

Elephants have never been domesticated, they are taken from the wild and tamed; yet these behaviourally and genetically wild animals have a long history of successful use by humans (Lair 1997), suggesting that they have desirable qualities for forming a working relationship with people. We found that African elephants correctly interpreted human pointing: including when the experimenter's body orientation gave a cue which conflicted with the direction of her pointing gesture, by standing beside the empty container in an object-choice task; as well as when pointing was visually subtle (Smet and Byrne 2013). However, all social cues were given continuously: the experimenter pointed in plain view of the subject and then maintained the pointing gesture until the subject had chosen one of the two containers, when the trial ended. Thus, in that study, elephants could solve the object-choice task by orienting to the baited container through constantly referring to the continuous vector provided by the experimenter's pointing arm. It has been argued (e.g. Miklósi and Soproni 2006) that leaving the arm extended in this way allows animals to rely on a quite different mechanism than deictic communication for success: the unchanging physical cues, such as an outstretched human hand, act as a guide to the location where food is likely to be found, because it is always found in that location in conjunction with that particular physical cue. In order to test animals in a situation which reflects real communication more closely, the signaller should produce a discrete gesture, which, having been perceived by the receiver at the time it is given then becomes unavailable to the receiver before they act upon it (Miklósi and Soproni 2006). In the object-choice task, this can be done by pointing only before the subject chooses a container. Dogs, cats (Miklósi et al. 2005), dolphins (Herman et al. 1999; Pack and Herman 2004) and a seal (Shapiro et al. 2003) show a small decrease or no decrease in their performance when a pointing signal is given only briefly compared with continuous presentation. When Asian elephants were tested on momentary pointing, where the pointing signal was given by a human experimenter for 5 s before being withdrawn, the elephants did not choose the indicated container above chance (Plotnik et al. 2013); however, 5 s may be insufficient for the elephant always to have registered the signal. In our first experiment, we test whether African elephants can follow a pointing cue even when it is not given continuously until the choice is made, to establish whether they need to continually refer to the pointing signal or whether they interpret its meaning and then respond to it, but we avoid the use of an arbitrary and brief presentation time.

While elephants appear to spontaneously interpret pointing by a human experimenter as an intentional signal, it is unclear whether they understand anything about the rationality of the experimenter's communicative action. Fourteen-month-old infants have been found capable of making judgements about the rationality of adult behaviour in the context of deciding which actions to imitate (Gergely et al. 2002). When infants watched an adult demonstrator switching on a lamp using her head, rather than hand, they were more likely to copy the demonstrator's method of switching on the lamp if she had her arms free when demonstrating the method, compared to when she demonstrated while her arms were occupied because she had wrapped a blanket around her body. Presumably, infants inferred some unknown reason for using the strange method when the demonstrator's hands were free during the demonstration, but when her hands were occupied then using an alternative method was obligatory, and infants did not judge that the unusual method was necessary to copy (Gergely et al. 2002). Enculturated chimpanzees were also found to imitate a human demonstrator operating an apparatus with an unusual body part (pressing it with his foot, forehead or sitting on it) more frequently when the demonstrator's hands were free during the demonstration, implying that the human chose the strange method freely compared to when his hands were occupied during the demonstration, implying that he was forced to use some alternative method because he was unable to use the preferred method (Buttelmann et al. 2007, but see also Buttelmann et al. 2008). In our second experiment, we test whether elephants can discern the intentions of a human experimenter, based on the rationality of her action. If elephants attend to the rationality of others' actions, they should be less likely to follow a novel referential signal that appears irrational, because they should interpret it as an arbitrary movement rather than an intentional signal.

General method

Subjects and housing

A total of nine captive African savannah elephants participated in these experiments, $n = 8$ in each study with the eighth subject replaced for Experiment 2. The subjects were housed at an adventure-safari operator in Victoria Falls, Zimbabwe. The elephants had been trained to respond to verbal commands but not visual gestures, using only positive reinforcement. When these elephants are feeding in the bush, their handlers are often out of sight and so the use of verbal commands allows handlers to direct the elephants from a distance, as well as when they are on their backs during the elephant-back rides. Apart from participating in experiments, these elephants take tourists on elephant-back safaris; usually two rides per day. All nine of the elephants had previous experimental experience: some had participated in a relative quantity judgment study, and all had been tested on their use of a variety of human social signals (see Smet and Byrne 2013 for further details on their rearing histories and training experiences).

Materials

We used two pink opaque plastic buckets (diameter 30 cm, height 45 cm) to hide the food. To conceal the baiting process from the subject, in Experiment 1, we used a large board (70 × 60 cm). The experimenter (AFS, hereafter referred to as E) stood at 3 m distance and checked whether she could see into the buckets from an approximate 'elephant eye-level' of 3 m, so we were confident the elephants could not see the baiting over the board. In Experiment 2, this board was replaced by a rectangular cloth to conceal the baiting process, as we were concerned that some of the elephants were reacting nervously to the board being pushed over, and two wooden trays (50 cm × 50 cm) were used to indicate more clearly where to put the buckets after baiting. We used pieces of melon or orange of approximately 10 cm long as the food reward. A large brown blanket with a red and white stripe was used to occupy E's arms in Experiment 2.

Design

We used a within-subjects design where each elephant participated in trials of every treatment. Trials of the different treatments were presented in pseudo-randomised order, and for each condition, food placement was randomised and placed on each side an equal number of times. In every session, we used both types of fruit as a reward, changing randomly between the two to ensure the elephants were motivated.

General procedure

We will describe minor deviations from the general methods where they apply in each of our two experiments. At the start of a session, the subject was positioned 3–4 m away from where the buckets were placed, approximately 1.5 m apart. The subject's starting point was marked by two rocks, one on either side of the subject. Handlers always stood to the left of their elephants and prevented them from approaching too early. A pretest was run with each subject at the start of each experimental session, to ensure that subjects were motivated and to habituate them to the procedure where they would only be allowed to choose one of the containers per trial. In the pretest, E walked up centrally between the two buckets and dropped a piece of fruit into one of them in plain view of the subject. After the subject had chosen the container with the food in it three times in a row, it progressed to the test phase. In the test phase, the subject did not know the location of the food: baiting was done by E so that the subject could not see where the food was going, because of the position of the board (Experiment 1) or cloth (Experiment 2), which obscured the buckets when they were placed together during baiting. E always did the baiting in these two studies, by putting her two closed fists into each of the two buckets simultaneously, but leaving only one piece of food in one of the buckets. When baiting was complete, E pushed over the board or lifted the cloth, and put the buckets in their positions 1.5 m apart. She then walked up between the two containers and, standing just behind them, got the attention of the subject by calling its name or making some other sound and executed the social cue required for that trial. As in normal human pointing, E alternated the direction of her head- and eye-gaze by turning her head back and forth between the baited container and the subject for the entire duration that she was pointing on the test trials. The subject was instructed to approach by the handler (using the command ‘move up’) and the first bucket that it touched or that its trunk entered was coded as its choice and the other bucket then removed. If it had chosen correctly, it was allowed to consume its food reward before being instructed to return to the starting position. If it had chosen incorrectly, then the handler instructed it to return to the starting position immediately (using the command ‘back up’). Trials were recorded using a Panasonic HDC-SD90 camcorder on a tripod. Elephants’ choices were noted after each trial and then checked against the video material.

Data analysis

We tested data for normality and used nonparametric tests if data deviated appreciably from normal. All *p* values are compared to an alpha-level of 0.05. Where Wilcoxon’s signed-rank test is used, we report exact significance values.

Experiment 1

In this study, we tested whether elephants could choose the indicated container without the experimenter pointing continually to it. The experimenter pointed to the baited container, and the subject’s handler made a decision about whether that elephant had seen the signal. When the handler decided the subject had seen the pointing signal (Online Resource 1), he instructed it to advance and in certain trials, E dropped her pointing arm to her side, so that the pointing signal was no longer visible as the subject approached the containers and touched one of the two.

Method

We presented eight elephants with a total of 80 trials each, consisting of two different types of social cue (40 trials each), each of two modes of presentation in randomised order (20 trials each for each type of pointing cue).

The two different types of social cue were as follows:

1. Whole-arm ipsilateral pointing—E used the whole, straight, extended ipsilateral arm and index finger to point to the baited container.
2. Whole-arm cross-body pointing—E used the whole, straight contralateral arm and extended 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 entire arm with the baited container.

Both types of social cue were already familiar to all the subjects from a previous experiment (Smet and Byrne 2013), but the nature of presentation differed from what the subjects had experienced in that study: because here elephants were prevented from choosing one of the two buckets until their handlers thought they had seen the pointing signal, and they had also never before been presented with a pointing cue that was unsustained. The two different types of social cues were presented in each of the following ways:

1. Sustained—Pointing was sustained by E while the subject chose one of the buckets, keeping the pointing arm in place and alternating head-gaze until the subject had touched one of the buckets (Online Resource 2).
2. Unsustained—E pointed while alternating head-gaze until the subject was instructed to approach. Then she stopped pointing and looked straight at the subject until it had touched one of the buckets (Online Resource 3).

Each type of social cue was presented as sustained and unsustained an equal number of times. For each condition, the reward was hidden equally often on the left and right side. All except one of the subjects completed all 80 trials. One that did not complete all 80 was excluded from further testing after handlers experienced behavioural difficulties with this elephant outside of the experimental context (Malasha); however, as the behavioural difficulties were unlikely to be connected to its performance in the study, its data were included for analysis.

Table 1 Individual number of trials correct for each point type and duration

Subjects	Whole-arm ipsilateral point				Whole-arm cross-body point			
	Sustained		Unsustained		Sustained		Unsustained	
	Correct/total	*p*	Correct/total	*p*	Correct/total	*p*	Correct/total	*p*
Coco	18/20	0.000*	15/20	0.041*	19/20	0.000*	14/20	0.115
Doji	16/20	0.012*	12/20	0.503	13/20	0.263	12/20	0.503
Jake	16/20	0.012*	12/20	0.503	11/20	0.824	10/20	1.000
Jock	9/20	0.824	10/20	1.000	15/20	0.041*	8/20	0.503
Jumbo	20/20	0.000*	17/20	0.003*	18/20	0.000*	19/20	0.000*
Malasha	13/14	0.002*	14/15	0.001*	14/16	0.004*	13/18	0.096
Tendai	17/20	0.003*	16/20	0.012*	18/20	0.000*	17/20	0.003*
Tembi	14/20	0.115	16/20	0.012*	14/20	0.115	12/20	0.503

This table gives the number of trials in which each subject chose the baited container, compared to the total number of trials. The *p* values given are for binomial tests. *p* values that are significant compared to an alpha-level of 0.05 are indicated with an asterisk (*). See also Online Resource 1 for comparisons between first and last trials

Results

We found that elephants chose the baited container significantly above chance in all conditions. At the individual level, 6/8 elephants chose correctly when sustained whole-arm ipsilateral pointing indicated the baited container; 5/8 elephants when sustained whole-arm cross-body pointing was used; 5/8 elephants when unsustained whole-arm ipsilateral pointing was used; and 2/8 elephants when unsustained whole-arm cross-body pointing indicated the baited container (Table 1).

As a group, elephants chose the baited container significantly above chance in all of the four conditions (Fig. 1) (one-sample *t* tests: sustained whole-arm ipsilateral point, $M = 0.80$, $SE = 0.06$, $t(7) = 5.06$, $p = 0.001$, unsustained whole-arm ipsilateral point, $M = 0.73$, $SE = 0.05$, $t(7) = 4.40$, $p = 0.003$, sustained whole-arm cross-body point, $M = 0.79$, $SE = 0.05$, $t(7) = 5.61$, $p = 0.001$, unsustained whole-arm cross-body point, $M = 0.67$, $SE = 0.06$, $t(7) = 2.60$, $p = 0.035$). We used a 3-way repeated-measures ANOVA to test for the effects of the type of social cue (whole-arm ipsilateral or cross-body pointing), the nature of its presentation (unsustained or sustained) and also whether there was any difference in subjects' performance in the first compared to the last half of trials in each condition. Only the nature of presentation had a significant effect on the proportion of correct trials [$F(1, 7) = 1.54$, $p = 0.004$] with elephants choosing correctly significantly more often when pointing was sustained ($M = 0.79$, $SE = 0.05$) than when it was unsustained ($M = 0.70$, $SE = 0.06$). There was no significant main effect of point type [$F(1,7) = 1.54$, $p = 0.255$], or of the half of trials [$F(1, 7) = 0.10$, $p = 0.764$], nor any interaction effects between type of point and nature of presentation [$F(1, 7) = 0.36$, $p = 0.57$], point type and half of trials [$F(1,7) = 0.286$, $p = 0.609$], nature of presentation and half of trials [$F(1, 7) = 0.86$, $p = 0.386$] or point type, nature of presentation and half of trials [$F(1, 7) = 0.75$, $p = 0.414$] (Fig. 2).

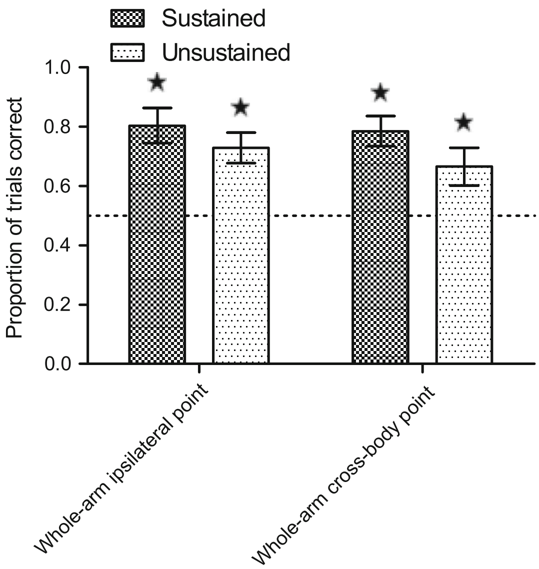

Fig. 1 Graph showing the mean proportion of correct trials for each condition. As a group, subjects chose correctly significantly above chance on all conditions. *Note* Figures created in GraphPad Prism 5

Discussion

The elephants in our study used two different types of human social cues to find hidden food. They were successful not only when the social cues were sustained by the human experimenter, thus replicating our previous findings (Smet and Byrne 2013), but also when the pointing signal was withdrawn before elephants had the opportunity to act

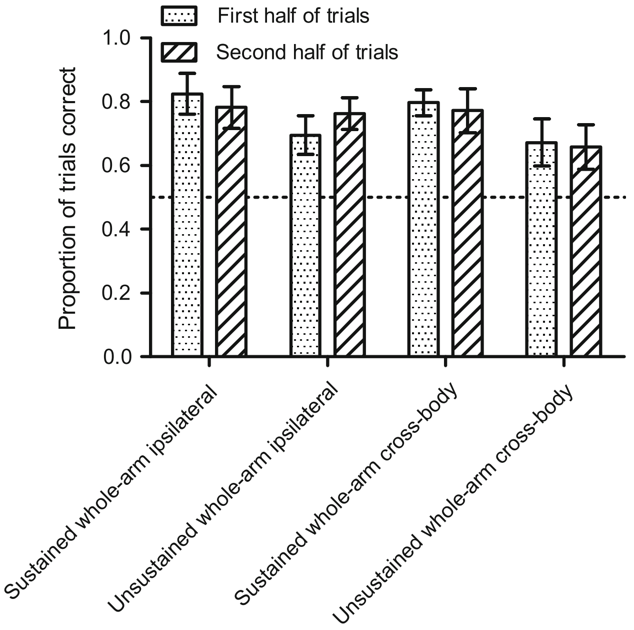

Fig. 2 Graph showing the mean proportion of correct trials for the two types of social cue, and the durations of presentation, divided according to the first and second half of trials

on their interpretation of the signal. We found no evidence that elephants learnt to respond to this unsustained pointing during the course of the experiment, as their performance showed no improvement over time. Although elephants did not depend on continual reference to the pointing container for their successful use of pointing, their success was reduced when they had to remember the direction of the pointing signal, compared to when it was given continually, as has been found to a lesser extent in domestic cats and dogs (Miklósi et al. 2005). Since the direction of elephant visual attention was difficult to ascertain from head or eye-gaze direction, it may be that the handler's judgement of when a subject had seen the experimenter's pointing gesture was not always correct. If this were the case, in some of the unsustained pointing trials, elephants may have been instructed to approach before actually having seen the pointing signal. This could explain the decrease in performance we found between sustained and unsustained pointing trials for each type of pointing cue. However, in many trials, it took longer than 5 s for the handler to judge that the subject had seen the gesture (Online Resource 1), and on these trials, elephants would most likely have failed to respond correctly if the pointing signal was always presented for 5 s as it was in the study with Asian elephants, which failed at using a 5 s point to find hidden food (Plotnik et al. 2013). It is premature to rule out a species difference between African and Asian elephants' abilities to follow human social cues, but our methodology may have created a further advantage for our subjects. In our study, there were also many trials where handlers judged that the subject had noticed the pointing gesture in less than 5 s, and especially in these trials, it was likely to be advantageous to our subjects that they were able to approach immediately after having seen the pointing gesture, instead of waiting for the prescribed duration of the pointing to finish, during which time their attention may have become diverted from the task at hand.

Experiment 2

In this study, we tested whether elephants would generalise from their understanding of human pointing to a human social signal given in a novel way: pointing with the leg. Our method was also designed to test whether elephants would discriminate the rationality of an experimenter's choice of directional gesture when responding to this novel visual signal.

Method

Seven of the eight subjects that participated in this study had previously participated in Experiment 1; Malasha was unavailable for testing due to behavioural difficulties and was replaced. The new eighth subject (Izibulo) had participated in a study looking at his use of human social cues prior to this experiment (Smet and Byrne 2013). After the pretest, E baited the containers for each trial as previously described and then put each of the buckets onto one of the wooden trays which were positioned a metre apart to indicate more clearly to E where the buckets should be put after baiting. When each bucket was positioned in the centre of the trays, the distance between the buckets was still 1.5 m.

We presented each subject with a total of 32 trials: eight trials for each of the four different conditions in a pseudorandomised order, with food being placed equally often on the left and the right for each condition. We used a small number of trials per condition as we were especially interested in the elephants' first trial responses to the experimental treatments. E selected a different starting point from the list of trials for each subject, which were in a random order. In addition to the familiar whole-arm ipsilateral point condition were two novel test conditions: the 'rational' leg point (Online Resource 4) and 'irrational' leg point (Online Resource 5). For both of these, instead of using her arm to point, E stretched the leg closest to the baited container outwards in the container's direction, with only the toe-end of the shoe on that foot touching the ground. The difference between the 'irrational' and 'rational' conditions was that in 'rational' leg pointing trials E had her arms occupied because she was holding

Table 2 Individual and first trial performance per condition

Subject	'Irrational' leg point		'Rational' leg point		Whole-arm ipsilateral point		Control	
	Trials correct out of 8	First trial	Trials correct out of 8	First trial	Trials correct out of 8	First trial	Trials correct out of 8	First trial
Coco	7	Correct	7	Correct	8	Correct	5	Incorrect
Doji	5	Correct	5	Incorrect	6	Correct	7	Correct
Emily	6	Correct	7	Incorrect	5	Incorrect	3	Correct
Izibulo	5	Incorrect	5	Incorrect	6	Correct	4	Incorrect
Jake	4	Incorrect	6	Correct	4	Incorrect	4	Correct
Jock	2	Incorrect	5	Correct	5	Correct	5	Correct
Tembi	4	Incorrect	4	Incorrect	7	Incorrect	1	Incorrect
Tendai	7	Correct	5	Correct	7	Correct	5	Correct
M	0.63		0.69		0.75		0.53	
SE	0.07		0.05		0.06		0.08	

This table shows the number of trials where each elephant chose the baited container correctly on each condition, and whether they chose correctly on the first trial of a particular condition. See also Online Resource 1 for comparisons between first and last trials. The table includes the mean (*M*) and standard error (SE) values for each condition

closed a blanket which she wrapped around her entire upper body including her arms, while in the 'irrational' pointing trials, the blanket was draped over her left shoulder and both her arms were visibly unoccupied. Note that here E always sustained the pointing cue until subjects had chosen one of the buckets. The fourth condition was a control: in control trials, E did not indicate where the food was hidden but instead stood and watched the elephant until it made its choice. In these control trials, E informed the handler where the food was hidden before the subject was allowed to approach, in order to test whether elephants' choices were based on unconscious cues by handlers or the experimenter, or if they were able to smell where the food was hidden.

Results

Elephants chose the baited container above half the time on all experimental conditions (Table 2). Because of the small number of trials for each condition, we did not conduct tests for differences from chance for individual elephants.

We found that elephants chose the correct container significantly more often than predicted by chance when E indicated it using a whole-arm ipsilateral point or a 'rational' leg point (Fig. 3) [one-sample *t* tests, respectively: $t(7) = 4.32$, $p = 0.003$, $t(7) = 3.97$, $p = 0.005$]. When E indicated the baited container with her leg while her arms were free ('irrational' leg point), or did not signal at all (control), as a group the elephants chose the baited container at chance [one-sample *t* tests, respectively: $t(7) = 1.67$, $p = 0.138$, $t(7) = 0.40$, $p = 0.699$] (Fig. 3). However, when we compared performance at the group level across these conditions, there was no significant effect of condition [repeated-measures ANOVA: $F(3, 21) = 2.56$, $p = 0.083$] and on the critical comparison between the 'rational' and 'irrational' leg point conditions, we found no significant differences between the two (post hoc pairwise comparisons: $p = 0.381$; Table 2). As the results from the two conditions were not significantly different, we pooled data from the two leg point conditions by dividing the total number of trials where each elephant chose correctly on either of the leg point conditions by 16, to obtain a total proportion of correct trials per subject. Using these pooled data, we found that subjects chose the baited bucket significantly above chance when E pointed to it with her leg [one-sample *t* test, $M = 0.66$, $SE = 0.05$, $t(7) = 2.958$, $p = 0.021$].

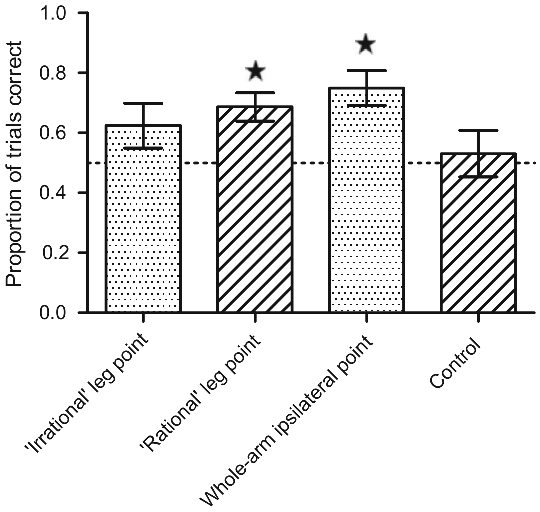

Fig. 3 Proportion of trials correct per condition. Elephants chose the baited container significantly more often than predicted by chance when E pointed with a whole-arm ipsilateral point and a 'rational' leg point

Finally, since the first trial data do not suggest that elephants spontaneously responded correctly to a 'leg point', there was a possibility that the elephants learned to respond to this during the course of the study. We found that for all our conditions, subjects as a group performed slightly better on the second half of trials compared to the first ('rational' leg point: first half, $M = 0.66$, $SE = 0.07$, second half, $M = 0.72$, $SE = 0.06$; 'irrational' leg point: first half, $M = 0.56$, $SE = 0.09$, second half, $M = 0.69$, $SE = 0.09$; whole-arm ipsilateral point: first half, $M = 0.63$, $SE = 0.11$, second half, $M = 0.88$, $SE = 0.05$; control: first half, $M = 0.50$, $SE = 0.11$, second half, $M = 0.56$, $SE = 0.09$) but in no case was this difference significant (Wilcoxon's signed-rank test: 'rational' leg point: $T = 7$, $p = 0.688$; 'irrational' leg point: $T = 5$, $p = 0.344$; whole-arm ipsilateral point: $T = 0$, $p = 0.063$; repeated-measures t test: control: $t(7) = -0.509$, $p = 0.626$).

Discussion

African elephants rapidly generalise to an entirely novel kind of pointing: pointing with the foot. However, it would seem that in this context, elephants do not differentiate between an intentional communicative signal given in a novel way but with an obvious visual explanation for the strange new action, and the same action when there is no obvious reason for why it is performed in this particular way. Although we are confident that elephants in this study were familiar with the physical properties of the blanket that was used, as similar blankets were carried by handlers, often over a shoulder or wrapped around them in the mornings in cold weather, it may be that the elephants simply did not recognise that the experimenter's hands were occupied when she wrapped the blanket around herself. Furthermore, they may not have interpreted this as a piece of contextually relevant information in deciding to interpret the leg 'point' as communicative. Our results are similar to what has been found in domestic dogs, which also did not discriminate between a pointing cue given with the leg when the experimenter's hands were unoccupied, compared to when she carried a book which occupied her hands (Kaminski et al. 2011). It may be that, as thought to be the case for the domestic dogs in that study, our elephants may be so motivated to follow the human's cues that the manner in which the human communicates is simply irrelevant (Kaminski et al. 2011). Given the large number of trials that these elephants have already been exposed to in previous studies where humans pointed to hidden food in various ways, they may have adopted the strategy of always choosing the container which is indicated by the human in some way. Since there was an extremely limited cost to choosing incorrectly, elephants would not suffer from following this strategy. Thus, elephants might have come to follow social cues given by a human even if the cue is completely arbitrary, regardless of whether there is a visual reason for why a cue is given in a strange or novel manner: we therefore cannot rule out the possibility that they distinguish these reasons.

General discussion

Elephants do not need continual reference to one of the containers in the object-choice task in the form of a sustained pointing gesture in order to follow a human pointing signal. They will respond correctly following a pointing signal that is given before the time that they are able to choose one of the two containers. This shows that their success at using human pointing signals is not simply because they are led to the baited container by constantly referring to the experimenter's pointing arm as a cue to one of the two buckets. Instead, with unsustained pointing, comparable to 'real' communication (Miklósi and Soproni 2006), the elephants' success suggests they interpret the human's signal when they see it and then respond to it. Their decline in performance, when pointing was terminated before they approached to choose, may be due to the memory load that this requires for success, in contrast to sustained pointing where there is a constant visual reminder of the direction of the signal, or may be an artefact of human error in deciding when an elephant has actually seen the signal. There is as yet no evidence that wild elephants can use the visual communicative signals of others, although elephant visual signals and gestures are well-documented (Poole and Granli 2009, 2011). However, the ability to respond to the discrete communicative signals of others is likely to play an important part in elephant communication in the wild.

The elephants in this study readily followed human pointing when it was presented in a novel way that they were unlikely to have seen before. However, we did not find evidence that elephants took into account the rationality of a novel gesture in their interpretation of its meaning. A possible explanation is that elephants are so motivated to follow human social signals that they always interpret human signals as communicative and may have been further encouraged by the fact that the leg pointing signal was always accompanied by head-gaze alternation. As the possible range of responses available to the elephants in this context was limited, it is also possible that the leg point resulted in local enhancement (Thorpe 1956) to the area in space where it was carried out, rather than acting as deictic communication. If this is the case, one would predict that all animals capable of responding to local enhancement (including, for example, greylag geese, and bumblebees, reviewed in Hoppitt and Laland 2013) will prove to be successful at using leg 'pointing'.

Elephants seem to utilise whatever social cues are available to them to infer the meaning of a gesture produced by a human. We suspect that this type of responsiveness to visual signals contributes to effective interpretation of human communicative signals, which must always require considerable generalisation from the natural signals used among elephants.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical standard The experiments described in this paper comply with the current laws of the country in which they were performed.

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