

1  
2  
3  
4  
5  
6  
7  
8  
9

**Authors:** Anna F. Smet, Richard W. Byrne\*

**Title:** Interpretation of human pointing by African elephants: generalisation and rationality

**Affiliations:** Centre for Social Learning & Cognitive Evolution,  
School of Psychology and Neuroscience, University of St Andrews, Fife KY16 9JP, Scotland (UK)

**Corresponding author\*:** (RWB)

Email: [rwb@st-andrews.ac.uk](mailto:rwb@st-andrews.ac.uk), Tel. +44 (0) 1334 462051, Fax +44 (0) 1334 463042

10 **Abstract**

11

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19 gesture was withdrawn before they had responded to it.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

23

24 **Key words:** pointing, social cues, object-choice, rationality, communication

25

## 26 Introduction

27

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

42

43 A typical context in which animals are tested for their ability to use human pointing is the ‘object-choice task’  
44 (e.g. Anderson, Sallaberry, & Barbier, 1995). The object-choice task requires the animal to choose between one  
45 of several containers, when an experimenter points to one of the containers where food is hidden. Using the  
46 object-choice task, it has been found that domestic animals including goats (Kaminski et al. 2005), cats (Miklósi  
47 et al. 2005), horses (Proops et al. 2010) and especially dogs (Miklósi et al. 1998; Hare and Tomasello 1999;  
48 Hare et al. 2002; Soproni et al. 2002; Miklósi et al. 2005) tend to be successful at using human pointing to find  
49 hidden food. Domestic animals’ successful interpretation of pointing has led to the suggestion that the ability to  
50 respond to human social cues evolved during the process of domestication (Hare et al. 2002), possibly as a by-  
51 product of selection on systems mediating fear and aggression (Hare et al. 2005). Dogs have been found more  
52 skilful at interpreting human signals than are wolves (Hare et al., 2002; Miklósi et al., 2003), supporting the  
53 theory that the ability to read human social signals evolved during domestication. Non-human primates’ use of  
54 human deictic signals in the object-choice task has produced conflicting results. In many instances captive non-  
55 human primates have been found not to interpret pointing correctly when using only their pre-experimental

56 knowledge (capuchin monkeys, Anderson et al., 1995; rhesus macaques, Anderson, Montant, & Schmitt, 1996;  
57 cotton-top tamarins, Neiworth, Burman, Basile, & Lickteig, 2002; chimpanzees, Hare et al., 2002; chimpanzees,  
58 orangutans, Tomasello, Call, & Gluckman, 1997). While there are individual apes of all species that have been  
59 found to successfully respond to human-given social cues in the object-choice task, these were predominantly  
60 individuals that had extensive experimental experience or had been raised in socio-communicatively rich  
61 environments (chimpanzees, Povinelli et al. 1990; Povinelli et al. 1992; Itakura and Tanaka 1998; Povinelli et al.  
62 1999; Itakura et al. 1999; Mulcahy and Call 2009; Lyn et al. 2010; bonobos, Mulcahy and Call 2009; Lyn et al.  
63 2010; gorillas, Peignot and Anderson 1999; and orangutans, Call and Tomasello 1994; Tomasello et al. 1997;  
64 Itakura and Tanaka 1998). At the functional level, non-human apes' relatively poor performance is thought to be  
65 influenced by the inherently cooperative nature of this task, where food is helpfully pointed out to them: a  
66 situation which apes are unlikely to be familiar with from their own interactions with conspecifics (Hare 2001;  
67 Hare and Tomasello 2004); but inconsistencies in the methods used between species (reviewed in: Miklósi and  
68 Soproni 2006; Mulcahy and Hedge 2012) complicate interpretation of the mixed results. Nevertheless, the  
69 ability to follow human pointing is certainly not exclusive to domestic animals (e.g. seals, Scheumann & Call,  
70 2004; dolphins, Herman et al., 1999, Pack & Herman, 2004; megachiropteran bats, Hall, Udell, Dorey, Walsh, &  
71 Wynne, 2011), and an alternative explanation has been proposed: that successful domestication was limited to  
72 species that naturally attended to and reacted appropriately to the cues that humans use to communicate, thus  
73 making them suitable for potential domestication (Smet and Byrne 2013). The latter theory was supported by the  
74 results from a study we carried out with African elephants (*Loxodonta africana*) (Smet and Byrne 2013).

75

76 Elephants have never been domesticated, they are taken from the wild and tamed; yet these behaviourally and  
77 genetically wild animals have a long history of successful use by humans (Lair 1997), suggesting that they have  
78 desirable qualities for forming a working relationship with people. We found that African elephants correctly  
79 interpreted human pointing: including when the experimenter's body orientation gave a cue which conflicted  
80 with the direction of her pointing gesture, by standing beside the empty container in an object-choice task; as  
81 well as when pointing was visually subtle (Smet and Byrne 2013). However, all social cues were given  
82 continuously: the experimenter pointed in plain view of the subject and then maintained the pointing gesture  
83 until the subject had chosen one of the two containers, when the trial ended. Thus, in that study elephants could  
84 solve the object-choice task by orienting to the baited container through constantly referring to the continuous  
85 vector provided by the experimenter's pointing arm. It has been argued (e.g. Miklósi & Soproni, 2006) that

86 leaving the arm extended in this way allows animals to rely on a quite different mechanism than deictic  
87 communication for success: the unchanging physical cues, such as an outstretched human hand, act as a guide to  
88 the location where food is likely to be found, because it is always found in that location in conjunction with that  
89 particular physical cue. In order to test animals in a situation which reflects real communication more closely,  
90 the signaller should produce a discrete gesture, which, having been perceived by the receiver at the time it is  
91 given, then becomes unavailable to the receiver before they act upon it (Miklósi and Soproni 2006). In the  
92 object-choice task this can be done by pointing only before the subject chooses a container. Dogs, cats (Miklósi  
93 et al. 2005), dolphins (Herman et al. 1999; Pack and Herman 2004) and a seal (Shapiro et al. 2003) show a small  
94 decrease or no decrease in their performance when a pointing signal is given only briefly compared with  
95 continuous presentation. When Asian elephants were tested on momentary pointing, where the pointing signal  
96 was given by a human experimenter for 5s before being withdrawn, the elephants did not choose the indicated  
97 container above chance (Plotnik et al. 2013); however, 5s may be insufficient for the elephant always to have  
98 registered the signal. In our first experiment, we test whether African elephants can follow a pointing cue even  
99 when it is not given continuously until the choice is made, to establish whether they need to continually refer to  
100 the pointing signal or whether they interpret its meaning and then respond to it; but we avoid the use of an  
101 arbitrary and brief presentation time.

102

103 While elephants appear to spontaneously interpret pointing by a human experimenter as an intentional signal, it  
104 is unclear whether they understand anything about the rationality of the experimenter's communicative action.  
105 Fourteen-month-old infants have been found capable of making judgements about the rationality of adult  
106 behaviour in the context of deciding which actions to imitate (Gergely et al. 2002). When infants watched an  
107 adult demonstrator switching on a lamp using her head, rather than hand, they were more likely to copy the  
108 demonstrator's method of switching on the lamp if she had her arms free when demonstrating the method,  
109 compared to when she demonstrated while her arms were occupied because she had wrapped a blanket around  
110 her body. Presumably, infants inferred some unknown reason for using the strange method when the  
111 demonstrator's hands were free during the demonstration, but when her hands were occupied then using an  
112 alternative method was obligatory, and infants did not judge that the unusual method was necessary to copy  
113 (Gergely et al. 2002). Enculturated chimpanzees were also found to imitate a human demonstrator operating an  
114 apparatus with an unusual body part (pressing it with his foot, forehead, or sitting on it) more frequently when  
115 the demonstrator's hands were free during the demonstration, implying that the human chose the strange method

116 freely; compared to when his hands were occupied during the demonstration, implying that he was forced to use  
117 some alternative method because he was unable to use the preferred method (Buttelmann, Carpenter, Call, &  
118 Tomasello, 2007, but see also Buttelmann, Carpenter, Call, & Tomasello, 2008). In our second experiment, we  
119 test whether elephants can discern the intentions of a human experimenter, based on the rationality of her action.  
120 If elephants attend to the rationality of others' actions, they should be less likely to follow a novel referential  
121 signal that appears irrational, because they should interpret it as an arbitrary movement rather than an intentional  
122 signal.

123

## 124 **General method**

125

### 126 **Subjects and housing**

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

137

### 138 **Materials**

139 We used two pink opaque plastic buckets (diameter 30 cm, height 45 cm) to hide the food. To conceal the  
140 baiting process from the subject, in Experiment 1 we used a large board (70 x 60 cm). The experimenter (AFS,  
141 hereafter referred to as E) stood at 3m distance and checked whether she could see into the buckets from an  
142 approximate 'elephant eye-level' of three metres, so we were confident the elephants could not see the baiting  
143 over the board. In Experiment 2 this board was replaced by a rectangular cloth to conceal the baiting process, as  
144 we were concerned that some of the elephants were reacting nervously to the board being pushed over, and two  
145 wooden trays (50 cm x 50 cm) were used to indicate more clearly where to put the buckets after baiting. We

146 used pieces of melon or orange of approximately 10 cm long as the food reward. A large brown blanket with a  
147 red and white stripe was used to occupy E's arms in Experiment 2.

148

149 Design

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

154

155 General procedure

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

176 allowed to consume its food reward before being instructed to return to the starting position. If it had chosen  
177 incorrectly then the handler instructed it to return to the starting position immediately (using the command ‘back  
178 up’). Trials were recorded using a Panasonic HDC-SD90 camcorder on a tripod. Elephants’ choices were noted  
179 after each trial and then checked against the video material.

180

181

182 Data analysis

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

186

187

### 188 **Experiment 1**

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

195

196 Method

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

199 The two different types of social cue were:

200 1. Whole-arm ipsilateral pointing - E used the whole, straight, extended ipsilateral arm and index finger to  
201 point to the baited container.

202 2. Whole-arm cross-body pointing - E used the whole, straight contralateral arm and extended index-

203 finger to point across the front of her body to the baited bucket, with the pointing hand stretching past

204 the periphery of her body to align the entire arm with the baited container.

205



206 Both types of social cue were already familiar to all the subjects from a previous experiment (Smet and Byrne  
207 2013) but the nature of presentation differed from what the subjects had experienced in that study: because here  
208 elephants were prevented from choosing one of the two buckets until their handlers thought they had seen the  
209 pointing signal, and they had also never before been presented with a pointing cue that was unsustained. The  
210 two different types of social cues were presented in each of the following ways:

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

217

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

224

## 225 Results

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

231

232 As a group, elephants chose the baited container significantly above chance in all of the four conditions (fig. 1)  
233 (one-sample t-tests: sustained whole-arm ipsilateral point,  $M = 0.80$ ,  $SE = 0.06$ ,  $t(7) = 5.06$ ,  $p = 0.001$ ,  
234 unsustained whole-arm ipsilateral point,  $M = 0.73$ ,  $SE = 0.05$ ,  $t(7) = 4.40$ ,  $p = 0.003$ , sustained whole-arm cross-  
235 body point,  $M = 0.79$ ,  $SE = 0.05$ ,  $t(7) = 5.61$ ,  $p = 0.001$ , unsustained whole-arm cross-body point,  $M = 0.67$ ,  $SE$

236 = 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  
237 social cue (whole-arm ipsilateral or cross-body pointing), the nature of its presentation (unsustained or sustained)  
238 and also whether there was any difference in subjects' performance in the first compared to the last half of trials  
239 in each condition. Only the nature of presentation had a significant effect on the proportion of correct trials ( $F(1,$   
240  $7) = 1.54$ ,  $p = 0.004$ ) with elephants choosing correctly significantly more often when pointing was sustained ( $M$   
241  $= 0.79$ ,  $SE = 0.05$ ) than when it was unsustained ( $M = 0.70$ ,  $SE = 0.06$ ). There was no significant main effect of  
242 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  
243 effects between type of point and nature of presentation ( $F(1, 7) = 0.36$ ,  $p = 0.57$ ), point type and half of trials  
244 ( $F(1,7) = 0.286$ ,  $p = 0.609$ ), nature of presentation and half of trials ( $F(1, 7) = 0.86$ ,  $p = 0.386$ ) or point type,  
245 nature of presentation and half of trials ( $F(1, 7) = 0.75$ ,  $p = 0.414$ ) (fig. 2).

246

## 247 Discussion

248 The elephants in our study used two different types of human social cues to find hidden food. They were  
249 successful not only when the social cues were sustained by the human experimenter, thus replicating our  
250 previous findings (Smet and Byrne 2013), but also when the pointing signal was withdrawn before elephants  
251 had the opportunity to act on their interpretation of the signal. We found no evidence that elephants learnt to  
252 respond to this unsustained pointing during the course of the experiment, as their performance showed no  
253 improvement over time. Although elephants did not depend on continual reference to the pointing container for  
254 their successful use of pointing, their success was reduced when they had to remember the direction of the  
255 pointing signal, compared to when it was given continually, as has been found to a lesser extent in domestic cats  
256 and dogs (Miklósi et al. 2005). Since the direction of elephant visual attention was difficult to ascertain from  
257 head or eye-gaze direction, it may be that the handler's judgement of when a subject had seen the  
258 experimenter's pointing gesture was not always correct. If this were the case, in some of the unsustained  
259 pointing trials elephants may have been instructed to approach before actually having seen the pointing signal.  
260 This could explain the decrease in performance we found between sustained and unsustained pointing trials for  
261 each type of pointing cue. However, in many trials, it took longer than 5s for the handler to judge that the  
262 subject had seen the gesture (Online Resource 1), and on these trials elephants would most likely have failed to  
263 respond correctly if the pointing signal was always presented for 5s as it was in the study with Asian elephants,  
264 which failed at using a 5s point to find hidden food (Plotnik et al. 2013). It is premature to rule out a species  
265 difference between African and Asian elephants' abilities to follow human social cues, but our methodology may

266 have created a further advantage for our subjects. In our study there were also many trials where handlers  
267 judged that the subject had noticed the pointing gesture in less than 5 seconds, and especially in these trials it  
268 was likely to be advantageous to our subjects that they were able to approach immediately after having seen the  
269 pointing gesture, instead of waiting for the prescribed duration of the pointing to finish, during which time their  
270 attention may have become diverted from the task at hand.

271

## 272 **Experiment 2**

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

277

### 278 **Method**

279 Seven of the eight subjects that participated in this study had previously participated in Experiment 1; Malasha  
280 was unavailable for testing due to behavioural difficulties and was replaced. The new eighth subject (Izibulo)  
281 had participated in a study looking at his use of human social cues prior to this experiment (Smet and Byrne  
282 2013). After the pre-test, E baited the containers for each trial as previously described and then put each of the  
283 buckets onto one of the wooden trays which were positioned a metre apart to indicate more clearly to E where  
284 the buckets should be put after baiting. When each bucket was positioned in the centre of the trays, the distance  
285 between the buckets was still 1.5 metres.

286

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

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

304

### 305 Results

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

309

310 We found that elephants chose the correct container significantly more often than predicted by chance when E  
311 indicated it using a whole-arm ipsilateral point or a ‘rational’ leg point (fig. 3) (one-sample t-tests, respectively:  
312  $t(7) = 4.32, p = 0.003, t(7) = 3.97, p = 0.005$ ). When E indicated the baited container with her leg while her arms  
313 were free (‘irrational’ leg point), or did not signal at all (control), as a group the elephants chose the baited  
314 container at chance (one-sample t-tests, respectively:  $t(7) = 1.67, p = 0.138, t(7) = 0.40, p = 0.699$ ) (fig. 3).

315 However, when we compared performance at the group level across these conditions there was no significant  
316 effect of condition (repeated measures ANOVA:  $F(3, 21) = 2.56, p = 0.083$ ) and on the critical comparison  
317 between the ‘rational’ and ‘irrational’ leg point conditions, we found no significant differences between the two  
318 (post-hoc pairwise comparisons:  $p = 0.381$ ; table 2). As the results from the two conditions were not  
319 significantly different we pooled data from the two leg point conditions by dividing the total number of trials  
320 where each elephant chose correctly on either of the leg point conditions by 16, to obtain a total proportion of  
321 correct trials per subject. Using these pooled data, we found that subjects chose the baited bucket significantly  
322 above chance when E pointed to it with her leg (one-sample t-test,  $M = 0.66, SE = 0.05, t(7) = 2.958, p = 0.021$ ).

323

324 Finally, since the first trial data do not suggest that elephants spontaneously responded correctly to a ‘leg point’  
325 there was a possibility that the elephants learned to respond to this during the course of the study. We found that

326 for all our conditions subjects as a group performed slightly better on the second half of trials compared to the  
327 first ('rational' leg point: first half,  $M = 0.66$ ,  $SE = 0.07$ , second half,  $M = 0.72$ ,  $SE = 0.06$ ; 'irrational' leg point:  
328 first half,  $M = 0.56$ ,  $SE = 0.09$ , second half,  $M = 0.69$ ,  $SE = 0.09$ ; whole-arm ipsilateral point: first half,  $M = 0.63$ ,  
329  $SE = 0.11$ , second half,  $M = 0.88$ ,  $SE = 0.05$ , control: first half,  $M = 0.50$ ,  $SE = 0.11$ , second half,  $M = 0.56$ ,  $SE$   
330  $= 0.09$ ) but in no case was this difference significant (Wilcoxon's signed rank test: 'rational' leg point:  $T = 7$ ,  $p =$   
331  $0.688$ ; 'irrational' leg point:  $T = 5$ ,  $p = 0.344$ ; whole-arm ipsilateral point:  $T = 0$ ,  $p = 0.063$ ; repeated measures t-  
332 test: control:  $t(7) = -0.509$ ,  $p = 0.626$ ).

333

## 334 Discussion

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

355

356 General discussion

357

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

372

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

383

384 Elephants seem to utilise whatever social cues are available to them to infer the meaning of a gesture produced  
385 by a human. We suspect that this type of responsiveness to visual signals contributes to effective interpretation

386 of human communicative signals, which must always require considerable generalization from the natural  
387 signals used among elephants.

388

389

390 **Acknowledgements**

391 We are grateful to Wild Horizons and its board of directors in Victoria Falls for granting us permission to work  
392 with the elephants; Z. Sibanda and staff at Wild Horizons for advice and assistance with practical aspects of  
393 running the study and R. Parry and J. Dawson of the Victoria Falls Wildlife Trust for facilitation and logistical  
394 support on site. This research was carried out with funding from a departmental studentship from the School of  
395 Psychology and Neuroscience of the University of St Andrews, awarded to AFS.

396 **Author declaration:** The authors declare that they have no conflict of interest.

397 **Ethical standards:** The experiments described in this paper comply with the current laws of the country in  
398 which they were performed.

399

400 **References**

- 401 Anderson JR, Montant M, Schmitt D (1996) Rhesus monkeys fail to use gaze direction as an experimenter-  
402 given cue in an object-choice task. *Behav Processes* 37:47–55.
- 403 Anderson JR, Sallaberry P, Barbier H (1995) Use of experimenter-given cues during object-choice tasks by  
404 capuchin monkeys. *Anim Behav* 49:201–208. doi: 10.1016/0003-3472(95)80168-5
- 405 Behne T, Liszkowski U, Carpenter M, Tomasello M (2012) Twelve-month-olds' comprehension and production  
406 of pointing. *Br J Dev Psychol* 30:359–75. doi: 10.1111/j.2044-835X.2011.02043.x
- 407 Buttelmann D, Carpenter M, Call J, Tomasello M (2007) Enculturated chimpanzees imitate rationally. *Dev Sci*  
408 10:F31–8. doi: 10.1111/j.1467-7687.2007.00630.x
- 409 Buttelmann D, Carpenter M, Call J, Tomasello M (2008) Rational tool use and tool choice in human infants and  
410 great apes. *Child Dev* 79:609–26. doi: 10.1111/j.1467-8624.2008.01146.x
- 411 Call J, Tomasello M (1994) Production and comprehension of referential pointing by orangutans (*Pongo*  
412 *pygmaeus*). *J Comp Psychol* 108:307–17.
- 413 Gergely G, Bekkering H, Király I (2002) Rational imitation in preverbal infants. *Nature* 415:755. doi:  
414 10.1038/415755a
- 415 Gómez J-C (2007) Pointing behaviors in apes and human infants: a balanced interpretation. *Child Dev* 78:729–  
416 734.
- 417 Hall NJ, Udell MAR, Dorey NR, et al. (2011) Megachiropteran bats (*Pteropus*) utilize human referential stimuli  
418 to locate hidden food. *J Comp Psychol* 125:341–6. doi: 10.1037/a0023680
- 419 Hare B (2001) Can competitive paradigms increase the validity of experiments on primate social cognition?  
420 *Anim Cogn* 4:269–280. doi: 10.1007/s100710100084
- 421 Hare B, Brown M, Williamson C, Tomasello M (2002) The domestication of social cognition in dogs. *Science*  
422 (80- ) 298:1634–1636.
- 423 Hare B, Plyusnina I, Ignacio N, et al. (2005) Social cognitive evolution in captive foxes is a correlated by-  
424 product of experimental domestication. *Curr Biol* 15:226–230. doi: 10.1016/j
- 425 Hare B, Tomasello M (1999) Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate  
426 hidden food. *J Comp Psychol* 113:173–177. doi: 10.1037//0735-7036.113.2.173
- 427 Hare B, Tomasello M (2004) Chimpanzees are more skilful in competitive than in cooperative cognitive tasks.  
428 *Anim Behav* 68:571–581. doi: 10.1016/j.anbehav.2003.11.011
- 429 Herman LM, Abichandani SL, Elhadj AN, et al. (1999) Dolphins (*Tursiops truncatus*) comprehend the  
430 referential character of the human pointing gesture. *J Comp Psychol* 113:347–364.
- 431 Hobaiter C, Leavens DA, Byrne RW (2013) Deictic Gesturing in Wild Chimpanzees , (*Pan troglodytes*)? Some  
432 possible cases. *J Comp Psychol*. doi: 10.1037/a0033757
- 433 Itakura S, Agnetta B, Hare B, Tomasello M (1999) Chimpanzee use of human and conspecific social cues to  
434 locate hidden food. *Dev Sci* 2:448–456. doi: 10.1111/1467-7687.00089



- 435 Itakura S, Tanaka M (1998) Use of experimenter-given cues during object-choice tasks by chimpanzees (*Pan*  
436 *troglodytes*), an orangutan (*Pongo pygmaeus*), and human infants (*Homo sapiens*). *J Comp Psychol*  
437 112:119–26.
- 438 Kaminski J, Nitzschner M, Wobber V, et al. (2011) Do dogs distinguish rational from irrational acts? *Anim*  
439 *Behav* 81:195–203. doi: 10.1016/j.anbehav.2010.10.001
- 440 Kaminski J, Riedel J, Call J, Tomasello M (2005) Domestic goats, *Capra hircus*, follow gaze direction and use  
441 social cues in an object choice task. *Anim Behav* 69:11–18. doi: 10.1016/j.anbehav.2004.05.008
- 442 Lair RC (1997) *Gone astray - The care and management of the asian elephant in domesticity*. Food and  
443 Agriculture Organization of the United Nations, Regional Office for Asia and the Pacific, Rome
- 444 Leavens DA, Hopkins WD (1999) The whole-hand point: the structure and function of pointing from a  
445 comparative perspective. *J Comp Psychol* 113:417–425.
- 446 Leavens DA, Hopkins WD (1998) Intentional communication by chimpanzees: a cross-sectional study of the  
447 use of referential gestures. *Dev Psychol* 34:813–822.
- 448 Leavens DA, Hopkins WD, Bard KA (1996) Indexical and referential pointing in chimpanzees (*Pan*  
449 *troglodytes*). *J Comp Psychol* 110:346–53.
- 450 Lyn H, Russell JL, Hopkins WD (2010) The impact of environment on the comprehension of declarative  
451 communication in apes. *Psychol Sci* 21:360–5. doi: 10.1177/0956797610362218
- 452 Miklósi Á, Kubinyi E, Topál J, et al. (2003) A simple reason for a big difference: wolves do not look back at  
453 humans, but dogs do. *Curr Biol* 13:763–766. doi: 10.1016/S
- 454 Miklósi Á, Polgárdi R, Topál J, Csányi V (1998) Use of experimenter-given cues in dogs. *Anim Cogn* 1:113–  
455 121.
- 456 Miklósi Á, Pongrácz P, Lakatos G, et al. (2005) A comparative study of the use of visual communicative signals  
457 in interactions between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and humans. *J Comp*  
458 *Psychol* 119:179–86. doi: 10.1037/0735-7036.119.2.179
- 459 Miklósi Á, Soproni K (2006) A comparative analysis of animals' understanding of the human pointing gesture.  
460 *Anim Cogn* 9:81–93. doi: 10.1007/s10071-005-0008-1
- 461 Mulcahy NJ, Call J (2009) The performance of bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), and  
462 orangutans (*Pongo pygmaeus*) in two versions of an object-choice task. *J Comp Psychol* 123:304–309.  
463 doi: 10.1037/a0016222
- 464 Mulcahy NJ, Hedge V (2012) Are great apes tested with an object-choice task? *Anim Behav* 83:313–321.  
465 doi: 10.1016/j.anbehav.2011.11.019
- 466 Neiwirth JJ, Burman MA, Basile BM, Lickteig MT (2002) Use of experimenter-given cues in visual co-  
467 orienting and in an object-choice task by a New World monkey species, cotton top tamarins (*Saguinus*  
468 *oedipus*). *J Comp Psychol* 116:3–11. doi: 10.1037//0735-7036.116.1.3
- 469 Pack AA, Herman LM (2004) Bottlenosed dolphins (*Tursiops truncatus*) comprehend the referent of both static  
470 and dynamic human gazing and pointing in an object-choice task. *J Comp Psychol* 118:160–71. doi:  
471 10.1037/0735-7036.118.2.160
- 472 Peignot P, Anderson JR (1999) Use of experimenter-given manual and facial cues by gorillas (*Gorilla gorilla*)  
473 in an object-choice task. *J Comp Psychol* 113:253–260. doi: 10.1037//0735-7036.113.3.253

- 474 Pfungst O (1911) *Clever Hans (The horse of Mr von Osten): A contribution to experimental animal and human*  
475 *psychology*. Henry Holt, New York
- 476 Plotnik JM, Pokorny JJ, Keratimanochaya, Titiporn Webb C, et al. (2013) Visual cues given by humans are not  
477 sufficient for Asian elephants (*Elephas maximus*) to find hidden food. *PLoS One* 8:e61174.
- 478 Poole JH, Granli PK (2009) *ElephantVoices Gestures Database*. <http://www.elephantvoices.org>.
- 479 Poole JH, Granli PK (2011) Signals, gestures and behavior of African elephants. In: Moss CJ, Croze H, Lee PC  
480 (eds) *Amboseli Elephants. A long-term Perspect. a long-lived mammal*. The University of Chicago Press,  
481 Chicago and London, pp 109–124
- 482 Povinelli DJ, Bierschwale DT, Cech CG (1999) Comprehension of seeing as a referential act in young children,  
483 but not juvenile chimpanzees. *Br J Dev Psychol* 17:37–60. doi: 10.1348/026151099165140
- 484 Povinelli DJ, Davis DR (1994) Differences between chimpanzees (*Pan troglodytes*) and humans (*Homo*  
485 *sapiens*) in the resting state of the index finger: implications for pointing. *J Comp Psychol* 108:134–9.
- 486 Povinelli DJ, Nelson KE, Boysen ST (1990) Inferences about guessing and knowing by chimpanzees (*Pan*  
487 *troglodytes*). *J Comp Psychol* 104:203–210.
- 488 Povinelli DJ, Nelson KE, Boysen ST (1992) Comprehension of role reversal in chimpanzees: evidence of  
489 empathy? 633–640.
- 490 Proops L, Walton M, McComb K (2010) The use of human-given cues by domestic horses, *Equus caballus*,  
491 during an object choice task. *Anim Behav* 79:1205–1209. doi: 10.1016/j.anbehav.2010.02.015
- 492 Scheumann M, Call J (2004) The use of experimenter-given cues by South African fur seals (*Arctocephalus*  
493 *pusillus*). *Anim Cogn* 7:224–30. doi: 10.1007/s10071-004-0216-0
- 494 Shapiro AD, Janik VM, Slater PJB (2003) A gray seal's (*Halichoerus grypus*) responses to experimenter-given  
495 pointing and directional cues. *J Comp Psychol* 117:355–62. doi: 10.1037/0735-7036.117.4.355
- 496 Smet AF, Byrne RW (2013) African elephants can use human pointing cues to find hidden food. *Curr Biol*  
497 23:2033–7. doi: 10.1016/j.cub.2013.08.037
- 498 Soproni K, Miklósi Á, Topál J, Csányi V (2002) Dogs' (*Canis familiaris*) responsiveness to human pointing  
499 gestures. *J Comp Psychol* 116:27–34. doi: 10.1037//0735-7036.116.1.27
- 500 Thorpe WH (1956) *Learning and instinct in animals*. Methuen, London
- 501 Tomasello M, Call J, Gluckman A (1997) Comprehension of novel communicative signs by apes and human  
502 children. *Child Dev* 68:1067–1080.
- 503 Tomasello M, Carpenter M, Liszkowski U (2007) A new look at infant pointing. *Child Dev* 78:705–22. doi:  
504 10.1111/j.1467-8624.2007.01025.x
- 505 Udell MAR, Dorey NR, Wynne CDL (2008) Wolves outperform dogs in following human social cues. *Anim*  
506 *Behav* 76:1767–1773. doi: 10.1016/j.anbehav.2008.07.028
- 507
- 508

509

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

510

511 **Table 1 Individual number of trials correct for each point type and duration** The table gives the number of  
512 trials in which each subject chose the baited container, compared to the total number of trials. The *p*-values  
513 given are for binomial tests. *P*-values that are significant compared to an alpha-level of .05 are indicated with an  
514 asterisk (\*). See also Online Resource 1 for comparisons between first and last trials.

515

516

		'Irrational' leg point		'Rational' leg point		Whole-arm ipsilateral point		Control	
	Subject	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
	<b>Coco</b>	7	Correct	7	Correct	8	Correct	5	Incorrect
	<b>Doji</b>	5	Correct	5	Incorrect	6	Correct	7	Correct
	<b>Emily</b>	6	Correct	7	Incorrect	5	Incorrect	3	Correct
	<b>Izibulo</b>	5	Incorrect	5	Incorrect	6	Correct	4	Incorrect
	<b>Jake</b>	4	Incorrect	6	Correct	4	Incorrect	4	Correct
	<b>Jock</b>	2	Incorrect	5	Correct	5	Correct	5	Correct
	<b>Tembi</b>	4	Incorrect	4	Incorrect	7	Incorrect	1	Incorrect
	<b>Tendai</b>	7	Correct	5	Correct	7	Correct	5	Correct
	<b><i>M</i></b>	0.63		0.69		0.75		0.53	
	<b><i>SE</i></b>	0.07		0.05		0.06		0.08	

517

518 **Table 2 Individual and first trial performance per condition** This table shows the number of trials where  
519 each elephant chose the baited container correctly on each condition, and whether they chose correctly on the  
520 first trial of a particular condition. See also Online Resource 1 for comparisons between first and last trials. The  
521 table includes the mean (*M*) and standard error (*SE*) values for each condition

522

523 Note: figures created in GraphPad Prism 5.

524

525 **Fig. 1 Graph showing the mean proportion of correct trials for each condition** As a group, subjects chose  
526 correctly significantly above chance on all conditions.

527

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

530

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

533

534 Supplementary materials: Captions

535

536 **Online Resource 1** Supplementary results and figures. Supplementary fig. 1. Shows the mean duration of the  
537 unsustained pointing cue in Experiment 1. Supplementary fig. 2. The number of elephants that chose correctly  
538 on the first and last trials of each condition in Experiment 1. Supplementary fig. 3. The number of elephants that  
539 chose correctly on the first and last trials of each condition in Experiment 2.

540 **Online Resource 2** Video clip from Experiment 1 showing a sustained whole-arm ipsilateral pointing trial

541 **Online Resource 3** Video clip from Experiment 1 showing an unsustained whole-arm ipsilateral pointing trial

542 **Online Resource 4** Video clip from Experiment 2 showing a 'rational' leg point trial

543 **Online Resource 5** Video clip from Experiment 2 showing an 'irrational' leg point trial

544