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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, 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19 gesture was withdrawn before they had responded to it.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

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397 **Ethical standards:** The experiments described in this paper comply with the current laws of the country in
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399

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- 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> =
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

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
	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
	<i>M</i>	0.63		0.69		0.75		0.53	
	<i>SE</i>	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