1Chimpanzees modify intentional gestures to coordinate a search for hidden food

2Abstract

3Humans routinely communicate to coordinate their activities, persisting and elaborating 4signals to pursue goals that cannot be accomplished individually. Communicative persistence 5is associated with uniquely human cognitive skills such as intentionality, because interactants 6modify their communication in response to another's understanding of their meaning. Here 7were show that two language-trained chimpanzees effectively use intentional gestures to 8coordinate with an experimentally-naïve human to retrieve hidden food, providing some of 9the most compelling evidence to date for the role of communicative flexibility in successful 10coordination in nonhumans. Both chimpanzees (Panzee and Sherman) increase the rate of 11non-indicative gestures when the experimenter approaches the location of the hidden food. 12Panzee also elaborates her gestures in relation to the experimenter's pointing, which enables 13her to find food more effectively than Sherman. Communicative persistence facilitates 14effective communication during behavioural coordination and is likely to have been 15important in shaping language evolution.

16Introduction

17The ability to appreciate that others have comprehension states and that these states can affect 18their behaviour is hypothesised to underpin the emergence of complex forms of 19communication in human evolution1-3. In intentional communication, the signaller has a goal 20and influences the comprehension state of the recipient by flexibly modifying their 21communication 4-6. Communicative persistence is a key indicator of intentionality in humans 22and other primates and it precedes the transition to linguistically based communication in 23human infants7. There is growing evidence for intentionality and communicative persistence 24in great ape gestural signalling – defined as voluntary movements of arms, legs or bodily

25postures8. Communicative persistence can be evidenced by a signaller's repetition or

26elaboration of signals in relation to different comprehension states of the recipient, until their

27goal is obtained, or failure is clearly indicated[7,9,10]. However, understanding communicative

28persistence in non-verbal animals is not straight-forward; it is difficult to disentangle whether

29a signaller influences recipient's comprehension of the meaning of the signal or influences

30directly their behaviour (i.e. makes them do something without assessing any comprehension

31about the goal) [5,11]. Studying episodes of coordination, where individuals communicate with

32one another in turn-taking sequences to achieve a goal that could not be accomplished

33individually, enable the nature and complexity of communicative persistence to be

34determined12-14. Communicative persistence in these contexts requires coordination of

35attention and communication to a task, goal and to one another, providing evidence that

36signallers perceive others as entities with comprehension states about the goal15. For

37instance, if persistence reflects a particular internal state, contingent upon changes in the

38availability of the goal itself, then only repetitions of the original signals would be expected

39to occur. If, on the other hand, senders are aware of the impact that their signals will have on

40the recipient, then they should elaborate their signalling flexibly, contingent upon recipient's

41comprehension about the goal[9,16].

42In examining the ability of signallers to influence recipients, studying gestural

43communication is particularly useful because gestures are directional[17,18], meaningful[19,20] and

44can draw attention of the recipient to specific spatial locations in the environment[21]. These

45characteristics of gestural communication allow researchers to determine the signaller's goal

46in gesturing, in particular in relation to the meaning of elaborations, and to identify their role

47in effectively influencing the recipient. If communicative persistence is an unintentional

48expression of frustration at the goal itself, then diffuse, uninformative elaboration would be

49expected to occur[9]. If on the other hand, signallers perceive recipients as capable of

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50comprehension about the goal, then they should elaborate by the use of informative signals

51which refer to the role of the recipient in pursuit of the desired goal, i.e. inform the recipient

52what they want him to do[22]. For instance, when signallers direct their gestures to the recipient,

53but fail to achieve the desired response, they may direct the recipient's attention to the desired

54referent in the environment by the use of indicative gestures such as pointing. However, when

55recipients respond appropriately to the signal, signallers may use non-indicative gestures such

56as bobbing to affirm the recipient's comprehension about the goal.

57Results from observational and experimental studies show some evidence for communicative

58persistence in wild and captive apes. However these are restricted to less complex

59experimental tasks or conspecific social interactions which did not require face to face

60behavioural coordination from a distance through gestural signals, as in the present case, to

61achieve a goal[19,20,23-27]. For example, when presented with two food items (desirable and

62undesirable), in close proximity and visible during a fixed delay interval, great apes persisted

63with gesture production only following the (predetermined) delivery of the undesirable and

64not the desirable food items[6,28]. However, as the experimenter neither initiated nor responded

65to the apes' communicative efforts prior to the food delivery, it is unclear whether the apes'

66gestures following food delivery were in response to the experimenter's behaviour (delivery

67of the undesirable food) or to the experimenter's apparent lack of comprehension of the apes'

68gestures[19]. Moreover, recent research demonstrates that when two chimpanzees required help

69of one another to retrieve a desirable food reward, they relied on a relatively simple leader-

70follower strategy, rather than using a more elaborated form of communication to coordinate

71food retrieval[12]. Thus, the issue of whether great apes can flexibly persist in communication

72to intentionally influence recipients remains unresolved[2].

73In this study we examined communicative persistence in two language trained chimpanzees,

74using a spatial memory task that demanded simultaneous coordination between the

75chimpanzee and a human interactant to find hidden food[23,24]. Both chimpanzees (Panzee and

76Sherman) recruited and directed an experimenter to search for a food item, hidden at various

77distances and locations, with the experimenter unaware of the location of the food. The

78experimenter searched by repeatedly pointing towards potential target locations, watching the

79chimpanzee for feedback and, based on this feedback, varying the pointing direction, pointing

80distance, and his own distance to the target location.

81Here we show that both chimpanzees respond to experimenter's search efforts towards food

82by flexibly modifying their intentional gestures. Both increase the rate of non-indicative

83gestures when the experimenter approaches the location of the hidden food. Panzee also

84elaborates her gestures in relation to the experimenter's pointing and disambiguates the

85experimenter's understanding of her gestures about the location of hidden food. Panzee'

86strategy enables her to find food more effectively than Sherman. Communicative persistence

87facilitates effective communication and is likely to have underpinned language evolution.

88**Results**

89Communicative exchanges

90The chimpanzees used intentional gestures to coordinate search efforts with the experimenter

91(see also accompanying Supplementary Movie 1 of the task), for the food, hidden at various

92distances and locations (Supplementary Table S1), gesturing only when the experimenter was

93visually oriented towards them (Fig. 1a). These gestures were informative, goal-directed and

94either indicative (e.g. manual pointing) or non-indicative (manual shake and bobbing of the

95head or body)[1] in terms of their ability to draw the recipient's attention to specific spatial

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7[1] Note that bobbing gesture in chimpanzees is species-specific, for instance wild chimpanzees

8frequently direct the bobbing gesture towards conspecifics during reunion[18].

96locations(Supplementary Table S2)[6]. The experimenter and chimpanzee spontaneously 97influenced and shaped the directionality of each other's behavior by taking multiple turns in 98responding to indications of the location of food. On Panzee's trials, the mean (SD) number 99of turns prior to finding the hidden food per target location was 36.3 (30.57) as compared to 10043.5 (30.62) for Sherman. The majority of these turns involved intentional communication by 101the chimpanzees, the mean (SD) proportion for Panzee and Sherman were 0.76 (0.15) and 1020.81 (0.06) respectively (Supplementary Table S1), which was significantly higher than the 103proportion of turns lacking intentional communication for both Panzee (Wilcoxon signed 104ranks test; $n = 6$, t = 0, $p = 0.031$) and Sherman ($n = 6$, t = 0, $p = 0.031$). By alternating their 105communication in this manner, the chimpanzees and the experimenter were able to obtain the 106hidden food. Although the mean (SD) proportion of turns responded to with incorrect 107experimenter pointing directions was high for both Panzee: 0.74 (0.18) and Sherman: 0.78 108(0.17), most trials were successful (11 out of 12) and the food item was found quickly, within 109a large area of woodland. The mean (SD) duration of trials was 2.30 (1.8) minutes for Panzee 110and 3.02 (1.5) minutes for Sherman.

111Strategies of chimpanzees to lead experimenter to the food

112By modifying their communication in response to changes in the experimenter's behaviour, 113relative to the location of the hidden food, the chimpanzees were able to successfully retrieve 114hidden food. The 'common strategy' was to modify their non-indicative gestures in relation 115to the experimenter's spatial proximity to the target location. Both Panzee (Wilcoxon signed 116ranks test; $n = 6$, t = 0, $p = 0.031$) and Sherman ($n = 6$, t = 0, $p = 0.031$) displayed a higher 117rate of non-indicative gestures when the experimenter was near to the target location (within 1180-4m), as compared to far from the target location (over 4m). Gesturing ceased as soon as 119items were found by the experimenter (Fig. 1b), indicating that gesture production did not 120simply reflect high arousal in anticipation of food delivery[31]. Instead, the chimpanzees

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121produced non-indicative gestures to provide positive feedback to the experimenter as he

122approached the target location, and ceased once this goal had been met.

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124In addition to this common strategy, Panzee elaborated her gestural exchanges in relation to

125the accuracy of the experimenter's pointing gestures. Panzee produced a higher rate of non-

126indicative gestures when the experimenter pointed toward the food rather than elsewhere

127(Wilcoxon signed ranks test; $n = 6$, $t = 0$, $p = 0.031$, Fig. 2). Panzee thus 'shaped' the

128experimenter's understanding of direction by observing his directional points and giving him

129a 'push' in the right direction, at just the right moment. In contrast, incongruent experimenter

130responses led to a higher rate of indicative gestures. When the experimenter was far from the

131target location (Wilcoxon signed ranks test; $n = 6$, t = 0, p = 0.031) or when his pointing was

132not directed toward the hidden food (Wilcoxon signed ranks test; $n = 6$, t = 0, p = 0.031, Fig.

1332), Panzee increased her pointing rate. Further, Panzee would raise her pointing hand high if

134the experimenter pointed too close (Wilcoxon signed ranks test; $n = 6$, t = 0, p = 0.031), but

135lower her hand downwards when pointing was at the correct distance or beyond the target

136location ($n = 6$, t = 0, p = 0.031, Fig. 3). Panzee's pointing gestures were directed towards the

137hidden object more often than elsewhere (Wilcoxon signed ranks test; $n = 6$, t = 0, p = 0.031).

138Panzee thus used pointing to influence the experimenter's understanding of what was "off

139track" and what was "on track", whilst simultaneously indicating the precise location of the

140hidden food.

141In contrast, Sherman only responded to the overall proximity of the experimenter to the target

142location with manual shaking and bobbing (Table 1) and Panzee's method increased the

143efficacy of the experimenter's search on this task[30]. There were no significant differences

144between the chimpanzees in the experimenter or in the chimpanzee distance to the target at

145the start of the trials, or trial duration (Supplementary Table S1) but the distance covered by

146the experimenter during their search, corrected for chimpanzee communicative effort

147(duration of responses), was significantly greater for Panzee's than Sherman's trials (Mann –

148Whitney test, $n = 12$, $t = 26$, $p = 0.041$). This shows that Panzee's skills at communication

149were more efficient at directing the experimenter to the food and the success of the task was

150influenced by the ability of chimpanzees to communicate its location[30]. Additionally, when

151comparing performance by experimenters who were familiar and unfamiliar with the

152chimpanzees' behaviour on this particular task, the success rate of the inexperienced

153experimenter was also high (5/6 trials were successful) and the trial duration did not differ

154between experimenters across trials matched for distance to hidden food (Mann – Whitney

155test, $n = 12$, $t = 37$, $p = 0.818$; Supplementary Table S3). This indicates that success was not

156solely determined by the experimenter's experience on this particular task, but was instead

157the result of intentional communication between the chimpanzees and experimenters.

158**Discussion**

159The communicative flexibility reported in this paradigm[29,30,32,33] goes far beyond that reported

160in previous studies, where apes were faced with an unresponsive experimenter[6,28] or where

161conspecific social interactions did not require face to face behavioural coordination though

162intentional gestural signals to achieve the desired goal[19,20,23-27]. Here, chimpanzees

163dynamically and flexibly modified their intentional gestures in relation to the naïve

164experimenter's search efforts towards the hidden food, to successfully guide the experimenter

165to the food item. Such communicative persistence, particularly in turn-taking episodes of

166communication where individuals respond communicatively to one another, is a key marker

167of intentional communication in humans and primates[7,11]. This study therefore provides some

168of the clearest evidence to date for such communicative persistence, and thus intentional

169communication, in chimpanzees.

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170Both chimpanzees showed communicative persistence, and used intentional gestural 171communication to guide the experimenter to a hidden food item. One interpretation could be 172that chimpanzees did not communicate to influence the experimenter to find hidden food, but 173simply adhered to behaviour of experimenter, allowing him to regulate the search for hidden 174food, while they communicated, regardless of experimenter search[22]. In this case, success of 175chimpanzees in the current task would be due to the experimenter's ability to read and 176interpret the chimpanzee's behaviour, rather than chimpanzees' skill at communicating. 177However, the success rate of the inexperienced experimenter was high, he found food 178relatively quickly and there was no significant difference in trial duration between the 179experienced and inexperienced experimenters. In previous experiments, uncued control 180objects (that are not shown to the chimpanzees) were very rarely found[30]. Further, as both 181experimenters were naive to the location of the food, hidden in a different location (with a 182varying angle and distance) on each trial, in the large woodland area and care was taken to 183fully conceal the hiding place[30], it is clear that the search behaviour of the experimenters, and 184their success in finding the hidden food, was shaped by communication with the 185chimpanzees.

186Moreover, the chimpanzee reactions to the experimenter's behaviour towards the food further 187clarifies whether chimpanzees communicated with regard for the experimenter. If 188chimpanzees simply learned the appropriate individual behaviours to get the food without 189perceiving the role of the experimenter in finding food, they should simply continue repeating 190the same movement sequences and communicative strategy, rather than modifying their 191behaviour in relation to experimenter's behaviour towards the food[22]. However, chimpanzees 192used communicative means which referred to the role of the experimenter, i.e. Panzee and 193Sherman used manual shaking and bobbing to signal that the experimenter was close to the 194food. Panzee also pointed higher to indicate experimenter's pointing was too close or pointed

195lower to indicate that experimenter's pointing was too far. This ability to make distinctions

196such as 'near' and 'far', is similar to some human pointing gestures[34], and reveals a

197sophistication comparable to the usage of some deictic words in human language. These

198strategies can be seen as evidence that chimpanzees understood their own and the

199experimenters' actions as interdependent of one another to find hidden food.

200Additionally, it could be claimed that the communicative strategies employed by the

201chimpanzees were shaped by the experimenter in repeated sessions of this task, or on similar

202tasks, ritualising the interactions[35]. In captivity, chimpanzees can point to food locations

203outside their reach[36-38], and some language-trained apes are more likely to use their index

204finger than whole hand to point, indicating that gesture use and morphology are influenced by

205experience[37]. However, communicative persistence more broadly is also evident in wild

206chimpanzee gestural communication, indicating that the capacity is not unique to enculturated

207individuals[18-20]. Nonetheless, in this experiment the pointing by Panzee was more elaborate,

208producing tactics that resemble those evident in human communication[34]. By raising her arm

209higher when the experimenter incorrectly pointed lower, and lowering her arm when

210experimenter incorrectly pointed higher, Panzee associated her own behaviour with

211experimenter's change in pointing height. As Panzee modified her pointing in relation to

212changes of height of experimenter's pointing relative to location of the food, and not the

213experimenter's pointing height itself, the specific communicative tactics used indicate

214considerable flexibility in intentional communication in chimpanzees[39].

215The specific and individual strategies employed in response to the experimenter's search

216behaviour differed between Panzee and Sherman. Sherman's understanding of how to use

217gestures to guide the experimenters' search actions was more limited, in that he simply

218responded to the overall proximity of the experimenter to the target location with manual

219shaking and bobbing. Sherman displayed a low frequency of points, and did not use or

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220modify morphology (height) of his pointing to indicate the location of the food, suggesting

221that Sherman did not understand as well as Panzee did the communicative potential of

222pointing to guide the experimenter's understanding in this task. Thus in Sherman's case, the

223search may have been driven mainly by the experimenter's interpretation of these non-

224indicative gestures. In contrast, Panzee clearly used directional pointing to guide the

225experimenter's search behaviour. While Sherman understood the experimenter's behaviour in

226relation to the food location, Panzee appears to have understood the experimenter's

227comprehension of her communicative gestures about the location of the hidden food. By

228tailoring her communicative signals to accommodate the experimenter's level of

229comprehension, Panzee was significantly more effective than Sherman at directing the

230experimenter to the food.

231The different strategies used by Panzee and Sherman reveal the importance of intentional

232communication in effectively coordinating behaviour[9]. Both Panzee and Sherman responded

233to the overall proximity of the experimenter to the target location, but also Panzee responded

234to the experimenter's understanding of her gestures by confirming accurate searches and

235correcting the experimenter's inaccurate searches. When the experimenter pointed to

236different referents in the environment, Panzee agreed or disagreed with experimenter's

237interpretation and was able to achieve the goal of finding food much faster than Sherman,

238showing that intentional communication can increase the efficiency of attaining goals.

239Chimpanzees' abilities to intentionally coordinate to obtain desired goals thus appears more

240sophisticated than previously demonstrated, and this level of skilled communication would

241have been available in early humans. It potentially could have been involved as a part of the

242general cognitive and communicative background in the evolution of language. In one

243scenario for the evolution of language, selection for enhanced communication took place in

244the context of coordinating social foraging of complex resources such as large game and

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245underground storage organs of plants[3,40-42]. The communicative strategies employed by
246chimpanzees in our study suggest that intentionally coordinating to obtain desired goals may
247have been an important aspect of social behaviour and foraging in early humans. By
248reformulating the understanding of the location of the resource by communicative signals,
249and confirming and disconfirming this understanding, two or more interactants would have
250increased their efficiency in foraging, hunting or other joint activities. In absence of language,
251gesturing to different referents in environment may have acted as a translation of another's
252intent into communicative signals, thus assisting interactants in making the mapping between
253communicative signals and real world events.

254The use of hand signals to coordinate joint activities in hunter-gatherer groups can provide
255insights into how this process may have worked, as the hunter-gatherer lifestyle was the
256dominant one for the vast majority of human evolution[43]. When hunting, many different
257hunter-gatherer groups use an extensive range of hand signals to coordinate joint activity –
258these include Congo Pygmies [44], Aboriginal Australians [45]and two Kalahari Khoe speaking
259groups [46]. Further, a cross-cultural comparison of hunter-gatherer groups demonstrated that
260hand signals occur more frequently in societies that have a higher dependence on hunting for
261subsistence [47]. Thus use of hand signals appears to be important in coordinating joint
262activities across groups of hunter-gatherers.

263The context of joint activity may have provided a training arena for the acquisition of
264linguistically based communication from learnt, ritualised signals in our hominin ancestors[9].
265The intentionality in gestural communication suggests that language evolution may have
266occurred primarily in gestural domain. However, gestures frequently co-occur with
267vocalisations; whereby gestures intentionally convey meaning to recipients, vocalisations are
268unintentional from signaller's perspective[5,18-20]. The scaffolding of vocalisations by intentional
269gestures may have enabled an attribution of meaning to vocalisations and a gradual move

270towards intentional communication in the vocal domain[17,48,49]. Studying the processes of vocal 271and gestural intentional communication in both humans and non-human primates in the 272context of coordinating joint activity may thus provide important insights into language 273evolution[23-25].

274**Methods**

275**Subjects**

276 The subjects were two chimpanzees (*Pan troglodytes)* - Panzee (female, 18 years old) 277and Sherman (male, 30 years old). Both chimpanzees had been reared from an early age by 278human caregivers and given extensive exposure to lexigrams. For details of their rearing and 279experimental histories, see[29]. The current task has been used to examine recall memory, 280performance in simulated foraging problems, and use of the lexigram keyboard, but the 281communication strategies used have not previously been systematically examined through 282video analysis. For full details of the task and the enclosures, see[29,30,33]. The experiments 283complied with ethical regulations and approved by the committee

284**Design and Procedure**

285 Each chimpanzee was tested individually in the outdoor enclosure, taking part in 6 286trials. In each trial, Experimenter 1 hid a food item 3-45 m from the outdoor enclosure under 287natural cover (e.g. log, soil, leaves, branches) in a trial-unique location in the surrounding 288woodland, whilst the chimpanzee was watching (Supplementary Table S1), concealing any 289signs of hiding place (e.g. breaking up of soil). The chimpanzee could not enter the woodland 290itself. In order to retrieve the food, the chimpanzee had to recruit the assistance of an 291uninformed person (Experimenter 2) and direct him to the food item. Experimenter 2 was a 292keeper, familiar to the chimpanzees, and experienced in conducting the experiment.

293Additionally, three trials for each chimpanzee were conducted with a keeper familiar to the

294chimpanzees but naive to this experimental task.

295　　　Experimenter 2 started near the outdoor enclosure and watched for the chimpanzee's

296initial directional gesture, then walked in that direction, and stopped to take further directions.

297Experimenter 2 also would face and "query" the chimpanzee periodically by pointing (with a

2981.5m stick) in various directions of possible travel, by noting which of these directions

299evoked immediate bobbing/shaking responses by the chimpanzee (rather than continued

300pointing), and by moving further in that direction, iterating the process.　If the food was

301found, it was offered to the chimpanzee. During the trials, both the chimpanzees and the

302experimenter's behaviour were videotaped.

303**Behavioural Coding**

304　**Chimpanzee behaviour**

305Behavioural responses of the chimpanzee to the experimenter's pointing gestures were coded.

306A response started immediately after the pointing gesture of the experimenter was made and

307ended when the experimenter made another pointing gesture, started walking, or searched

308through the groundcover with the stick. *Indicative gestures* made by the chimpanzees that

309were coded included any movement which appeared to be aimed at specific distal target or a

310lexigram keyboard, using both extended index finger and open hand. The morphology of

311indicative gestures towards the hidden object was described in terms of the arm, forearm and

312finger positions and classified into: indicate up (arm, forearm and finger directed vertically

313up) or indicate down (arm, forearm and finger directed horizontally or down). Additionally,

314the direction of gesturing was recorded using the following categories: object (pointing in the

315direction of the object), other direction.

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316*Non-indicative gestures* coded included armshake, defined as any shaking or swinging of one

317or both hands or arms repeatedly; bobbing (subject bobs and weaves with head or whole body

318in bowing position upwards or forwards) and rocking (subject stands or sits and rocks its

319body from side to side or from forwards to backwards). Two additional behavioural responses

320recorded were scratching and vocalisations (for full descriptions of categories coded see

321Supplementary Table S2).

322**Experimenter behaviour**

323   The trial started when Experimenter 2 arrived outdoors and began to interact with the

324chimpanzee (as opposed to when they interacted indoors), and the end of the trial was the

325moment the food item was found and removed from its location. The experimenter's search

326behaviour (pointing with the stick) was recorded when the experimenter was standing in one

327place. All potential pointing gestures made by the experimenter whilst walking were

328excluded because they were not responded to by the chimpanzees and it was not always

329possible to reliably determine the accuracy of these pointing gestures relative to the food

330location. Each time the experimenter made a pointing gesture, the following three pieces of

331information were recorded. First, the distance of the experimenter to the hidden object,

332determined from a map of the area of woodland, were categorised as close (0 – 4 m between

333experimenter and the object) and far (above 4m). Second, the direction of the experimenter's

334pointing gestures was coded as: point towards the object (experimenter pointing in the

335direction of a hidden object, the location of which is within the experimenter's field of vision)

336or point elsewhere (experimenter pointing in a direction other than towards the hidden

337object). Third, the experimenter's accuracy at indicating distance to the object was recorded,

338as evidenced by the height at which experimenter held the end of pointing stick relative to the

339object's location. This was scored as correct, too far or too close, by assessing whether

340hidden object fell inside, outside or on the circle visually drawn by the end of line extended

341from the end of the stick held by the experimenter.

342Finally, the visual attention of the experimenter to the chimpanzee was recorded as attention

343present (experimenter looking at the chimpanzee, as judged from the direction of his head) or

344absent (any other direction). The presence of the object was coded as object absent (object

345hidden) or object found (object located and removed from the hiding place by the

346experimenter); for these analyses, the behavioural responses of the chimpanzees were

347recorded when the experimenter was either locomoting or standing and pointing in a direction

348or inspecting the surface of the ground. A trial ended when the experimenter disengaged from

349the chimpanzee and left the area.

350**Analyses**

351For the main analyses of chimpanzee behaviour during trials with the experienced

352experimenter, each subject was analysed individually. For each subject, data from all six

353trials were pooled for analyses, with paired comparisons used to analyse behaviour patterns.

354As trials varied in length, all behaviours were either converted to rates per minute or

355proportions of all points. Distance per minute of response was calculated by dividing the

356distance of the experimenter from the target at the beginning of the trial by the total

357chimpanzee response duration to the experimenter's pointing gestures during that trial. The

358additional trials with an inexperienced experimenter, to examine if experience of the

359experimenter affected the success in finding food, were pooled for both chimpanzees,

360matching trials in terms of the chimpanzee taking part in the trial and the distance to the food

361hidden. Non-parametric statistics were used with the alpha level set at 0.05 and all tests were

362two-tailed. One trial for each chimpanzee was coded by a second observer and agreement

363(Cohen's Kappa) was good to excellent for both experimenter and chimpanzee behaviour

364ranging from 0.71 to 0.83.

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489 **Tables and Figures**

490Fig. 1 Chimpanzee behavioural responses to experimenter pointing gestures according to a)

491experimenter visual attention towards chimpanzee; b) object presence.

492Fig. 2 Influence of experimenter comprehension of object location (as indicated by accuracy

493of his pointing) on chimpanzee production of indicative and non-indicative gestures

494Fig. 3 Influence of experimenter comprehension of distance to hidden food (as indicated by

495the height of his pointing) on Panzee's production of upward and downward pointing

496Table 1. Results of statistical tests of Sherman's responses to experimenter's pointing

497gestures

498**Figure legends**

499Fig. 1 The voluntary control of each behavioural response of the chimpanzees was examined.

500Responses of the chimpanzees were categorised as intentional (as opposed to non-intentional)

501only when the production was significantly higher when visual attention of the experimenter

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502was present versus absent and the object was hidden versus found. The tests results for each

503behavioural response type were following: Influence of experimenter's visual attention:

504Panzee: Point ($p = 0.031$), Manual shake ($p = 0.031$), Bob ($p = 0.031$), Rock ($p = 0.063$),

505Scratch ($p = 0.063$), Vocalisation ($p = 0.5$), Sherman: Point ($p = 0.031$), Manual shake ($p =$

5060.031), Bob ($p = 0.031$), Rock ($p = 0.063$), Scratch ($p = 0.250$), Vocalisation ($p = 0.250$);

507Influence of object hidden versus found: Panzee: Point ($p = 0.031$), Manual shake ($p =$

5080.031), Bob ($p = 0.031$), Rock ($p = 0.438$), Scratch ($p = 0.313$), Vocalisation ($p = 1$);

509Sherman: Point ($p = 0.031$), Manual shake ($p = 0.031$), Bob ($p = 0.031$), Rock ($p = 0.438$),

510Scratch ($p = 0.313$), Vocalisation ($p = 1$). Only those behavioural response types classified as

511intentional were considered in further analyses. All statistical tests were performed using

512Wilcoxon signed-ranks test, two-tailed, with exact probabilities used, $n = 6$ trials for each

513individual.

514**Supplementary Information** is linked to the online version of the paper at www.nature.com/

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522**Author contributions** A.I.R. designed the study, coding scheme, coded the footage, analysed

523the data and wrote up the paper

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