

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

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8 **Chimpanzees modify intentional gestures to coordinate a search for hidden food**

9 **Abstract**

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

23 **Introduction**

24 The ability to appreciate that others have comprehension states and that these states can affect
25 their behaviour is hypothesised to underpin the emergence of complex forms of
26 communication in human evolution¹⁻³. In intentional communication, the signaller has a goal
27 and influences the comprehension state of the recipient by flexibly modifying their
28 communication⁴⁻⁶. Communicative persistence is a key indicator of intentionality in humans
29 and other primates and it precedes the transition to linguistically based communication in
30 human infants⁷. There is growing evidence for intentionality and communicative persistence

31 in great ape gestural signalling – defined as voluntary movements of arms, legs or bodily
32 postures⁸. Communicative persistence can be evidenced by a signaller’s repetition or
33 elaboration of signals in relation to different comprehension states of the recipient, until their
34 goal is obtained, or failure is clearly indicated^{7,9,10}. However, understanding communicative
35 persistence in non-verbal animals is not straight-forward; it is difficult to disentangle whether
36 a signaller influences recipient’s comprehension of the meaning of the signal or influences
37 directly their behaviour (i.e. makes them do something without assessing any comprehension
38 about the goal) ^{5,11}. Studying episodes of coordination, where individuals communicate with
39 one another in turn-taking sequences to achieve a goal that could not be accomplished
40 individually, enable the nature and complexity of communicative persistence to be
41 determined¹²⁻¹⁴. Communicative persistence in these contexts requires coordination of
42 attention and communication to a task, goal and to one another, providing evidence that
43 signallers perceive others as entities with comprehension states about the goal¹⁵. For
44 instance, if persistence reflects a particular internal state, contingent upon changes in the
45 availability of the goal itself, then only repetitions of the original signals would be expected
46 to occur. If, on the other hand, senders are aware of the impact that their signals will have on
47 the recipient, then they should elaborate their signalling flexibly, contingent upon recipient’s
48 comprehension about the goal^{9,16}.

49 In examining the ability of signallers to influence recipients, studying gestural
50 communication is particularly useful because gestures are directional^{17,18}, meaningful^{19,20} and
51 can draw attention of the recipient to specific spatial locations in the environment²¹. These
52 characteristics of gestural communication allow researchers to determine the signaller’s goal
53 in gesturing, in particular in relation to the meaning of elaborations, and to identify their role
54 in effectively influencing the recipient. If communicative persistence is an unintentional
55 expression of frustration at the goal itself, then diffuse, uninformative elaboration would be

56 expected to occur⁹. If on the other hand, signallers perceive recipients as capable of
57 comprehension about the goal, then they should elaborate by the use of informative signals
58 which refer to the role of the recipient in pursuit of the desired goal, i.e. inform the recipient
59 what they want him to do²². For instance, when signallers direct their gestures to the
60 recipient, but fail to achieve the desired response, they may direct the recipient's attention to
61 the desired referent in the environment by the use of indicative gestures such as pointing.
62 However, when recipients respond appropriately to the signal, signallers may use non-
63 indicative gestures such as bobbing to affirm the recipient's comprehension about the goal.

64 Results from observational and experimental studies show some evidence for communicative
65 persistence in wild and captive apes. However these are restricted to less complex
66 experimental tasks or conspecific social interactions which did not require face to face
67 behavioural coordination from a distance through gestural signals, as in the present case, to
68 achieve a goal^{19,20,23-27}. For example, when presented with two food items (desirable and
69 undesirable), in close proximity and visible during a fixed delay interval, great apes persisted
70 with gesture production only following the (predetermined) delivery of the undesirable and
71 not the desirable food items^{6,28}. However, as the experimenter neither initiated nor responded
72 to the apes' communicative efforts prior to the food delivery, it is unclear whether the apes'
73 gestures following food delivery were in response to the experimenter's behaviour (delivery
74 of the undesirable food) or to the experimenter's apparent lack of comprehension of the apes'
75 gestures¹⁹. Moreover, recent research demonstrates that when two chimpanzees required help
76 of one another to retrieve a desirable food reward, they relied on a relatively simple leader-
77 follower strategy, rather than using a more elaborated form of communication to coordinate
78 food retrieval¹². Thus, the issue of whether great apes can flexibly persist in communication
79 to intentionally influence recipients remains unresolved².

80 In this study we examined communicative persistence in two language trained chimpanzees,
81 using a spatial memory task that demanded simultaneous coordination between the
82 chimpanzee and a human interactant to find hidden food^{23,24}. Both chimpanzees (Panzee and
83 Sherman) recruited and directed an experimenter to search for a food item, hidden at various
84 distances and locations, with the experimenter unaware of the location of the food. The
85 experimenter searched by repeatedly pointing towards potential target locations, watching the
86 chimpanzee for feedback and, based on this feedback, varying the pointing direction, pointing
87 distance, and his own distance to the target location.

88 Here we show that both chimpanzees respond to experimenter's search efforts towards food
89 by flexibly modifying their intentional gestures. Both increase the rate of non-indicative
90 gestures when the experimenter approaches the location of the hidden food. Panzee also
91 elaborates her gestures in relation to the experimenter's pointing and disambiguates the
92 experimenter's understanding of her gestures about the location of hidden food. Panzee's
93 strategy enables her to find food more effectively than Sherman. Communicative persistence
94 facilitates effective communication and is likely to have underpinned language evolution.

95 **Results**

96 **Communicative exchanges**

97 The chimpanzees used intentional gestures to coordinate search efforts with the experimenter
98 (see also accompanying Supplementary Movie 1 of the task), for the food, hidden at various
99 distances and locations (Supplementary Table S1), gesturing only when the experimenter was
100 visually oriented towards them (Fig. 1a). These gestures were informative, goal-directed and
101 either indicative (e.g. manual pointing) or non-indicative (manual shake and bobbing of the

102 head or body)¹ in terms of their ability to draw the recipient's attention to specific spatial
103 locations(Supplementary Table S2)⁶. The experimenter and chimpanzee spontaneously
104 influenced and shaped the directionality of each other's behavior by taking multiple turns in
105 responding to indications of the location of food. On Panzee's trials, the mean (SD) number
106 of turns prior to finding the hidden food per target location was 36.3 (30.57) as compared to
107 43.5 (30.62) for Sherman. The majority of these turns involved intentional communication by
108 the chimpanzees, the mean (SD) proportion for Panzee and Sherman were 0.76 (0.15) and
109 0.81 (0.06) respectively (Supplementary Table S1), which was significantly higher than the
110 proportion of turns lacking intentional communication for both Panzee (Wilcoxon signed
111 ranks test; $n = 6$, $t = 0$, $p = 0.031$) and Sherman ($n = 6$, $t = 0$, $p = 0.031$). By alternating their
112 communication in this manner, the chimpanzees and the experimenter were able to obtain the
113 hidden food. Although the mean (SD) proportion of turns responded to with incorrect
114 experimenter pointing directions was high for both Panzee: 0.74 (0.18) and Sherman: 0.78
115 (0.17), most trials were successful (11 out of 12) and the food item was found quickly, within
116 a large area of woodland. The mean (SD) duration of trials was 2.30 (1.8) minutes for Panzee
117 and 3.02 (1.5) minutes for Sherman.

118 Strategies of chimpanzees to lead experimenter to the food

119 By modifying their communication in response to changes in the experimenter's behaviour,
120 relative to the location of the hidden food, the chimpanzees were able to successfully retrieve
121 hidden food. The 'common strategy' was to modify their non-indicative gestures in relation

¹ Note that bobbing gesture in chimpanzees is species-specific, for instance wild chimpanzees frequently direct the bobbing gesture towards conspecifics during reunion¹⁸.

122 to the experimenter's spatial proximity to the target location. Both Panzee (Wilcoxon signed
123 ranks test; $n = 6$, $t = 0$, $p = 0.031$) and Sherman ($n = 6$, $t = 0$, $p = 0.031$) displayed a higher
124 rate of non-indicative gestures when the experimenter was near to the target location (within
125 0-4m), as compared to far from the target location (over 4m). Gesturing ceased as soon as
126 items were found by the experimenter (Fig. 1b), indicating that gesture production did not
127 simply reflect high arousal in anticipation of food delivery³¹. Instead, the chimpanzees
128 produced non-indicative gestures to provide positive feedback to the experimenter as he
129 approached the target location, and ceased once this goal had been met.

130

131 In addition to this common strategy, Panzee elaborated her gestural exchanges in relation to
132 the accuracy of the experimenter's pointing gestures. Panzee produced a higher rate of non-
133 indicative gestures when the experimenter pointed toward the food rather than elsewhere
134 (Wilcoxon signed ranks test; $n = 6$, $t = 0$, $p = 0.031$, Fig. 2). Panzee thus 'shaped' the
135 experimenter's understanding of direction by observing his directional points and giving him
136 a 'push' in the right direction, at just the right moment. In contrast, incongruent experimenter
137 responses led to a higher rate of indicative gestures. When the experimenter was far from the
138 target location (Wilcoxon signed ranks test; $n = 6$, $t = 0$, $p = 0.031$) or when his pointing was
139 not directed toward the hidden food (Wilcoxon signed ranks test; $n = 6$, $t = 0$, $p = 0.031$, Fig.
140 2), Panzee increased her pointing rate. Further, Panzee would raise her pointing hand high if
141 the experimenter pointed too close (Wilcoxon signed ranks test; $n = 6$, $t = 0$, $p = 0.031$), but
142 lower her hand downwards when pointing was at the correct distance or beyond the target
143 location ($n = 6$, $t = 0$, $p = 0.031$, Fig. 3). Panzee's pointing gestures were directed towards the
144 hidden object more often than elsewhere (Wilcoxon signed ranks test; $n = 6$, $t = 0$, $p = 0.031$).
145 Panzee thus used pointing to influence the experimenter's understanding of what was "off

146 track” and what was “on track”, whilst simultaneously indicating the precise location of the
147 hidden food.

148 In contrast, Sherman only responded to the overall proximity of the experimenter to the target
149 location with manual shaking and bobbing (Table 1) and Panzee’s method increased the
150 efficacy of the experimenter’s search on this task³⁰. There were no significant differences
151 between the chimpanzees in the experimenter or in the chimpanzee distance to the target at
152 the start of the trials, or trial duration (Supplementary Table S1) but the distance covered by
153 the experimenter during their search, corrected for chimpanzee communicative effort
154 (duration of responses), was significantly greater for Panzee’s than Sherman’s trials (Mann –
155 Whitney test, $n = 12$, $t = 26$, $p = 0.041$). This shows that Panzee’s skills at communication
156 were more efficient at directing the experimenter to the food and the success of the task was
157 influenced by the ability of chimpanzees to communicate its location³⁰. Additionally, when
158 comparing performance by experimenters who were familiar and unfamiliar with the
159 chimpanzees’ behaviour on this particular task, the success rate of the inexperienced
160 experimenter was also high (5/6 trials were successful) and the trial duration did not differ
161 between experimenters across trials matched for distance to hidden food (Mann – Whitney
162 test, $n = 12$, $t = 37$, $p = 0.818$; Supplementary Table S3). This indicates that success was not
163 solely determined by the experimenter’s experience on this particular task, but was instead
164 the result of intentional communication between the chimpanzees and experimenters.

165 **Discussion**

166 The communicative flexibility reported in this paradigm^{29,30,32,33} goes far beyond that
167 reported in previous studies, where apes were faced with an unresponsive experimenter^{6,28} or
168 where conspecific social interactions did not require face to face behavioural coordination
169 though intentional gestural signals to achieve the desired goal^{19,20,23-27}. Here, chimpanzees

170 dynamically and flexibly modified their intentional gestures in relation to the naïve
171 experimenter's search efforts towards the hidden food, to successfully guide the experimenter
172 to the food item. Such communicative persistence, particularly in turn-taking episodes of
173 communication where individuals respond communicatively to one another, is a key marker
174 of intentional communication in humans and primates^{7,11}. This study therefore provides some
175 of the clearest evidence to date for such communicative persistence, and thus intentional
176 communication, in chimpanzees.

177 Both chimpanzees showed communicative persistence, and used intentional gestural
178 communication to guide the experimenter to a hidden food item. One interpretation could be
179 that chimpanzees did not communicate to influence the experimenter to find hidden food, but
180 simply adhered to behaviour of experimenter, allowing him to regulate the search for hidden
181 food, while they communicated, regardless of experimenter search²². In this case, success of
182 chimpanzees in the current task would be due to the experimenter's ability to read and
183 interpret the chimpanzee's behaviour, rather than chimpanzees' skill at communicating.
184 However, the success rate of the inexperienced experimenter was high, he found food
185 relatively quickly and there was no significant difference in trial duration between the
186 experienced and inexperienced experimenters. In previous experiments, uncued control
187 objects (that are not shown to the chimpanzees) were very rarely found³⁰. Further, as both
188 experimenters were naive to the location of the food, hidden in a different location (with a
189 varying angle and distance) on each trial, in the large woodland area and care was taken to
190 fully conceal the hiding place³⁰, it is clear that the search behaviour of the experimenters, and
191 their success in finding the hidden food, was shaped by communication with the
192 chimpanzees.

193 Moreover, the chimpanzee reactions to the experimenter's behaviour towards the food further
194 clarifies whether chimpanzees communicated with regard for the experimenter. If
195 chimpanzees simply learned the appropriate individual behaviours to get the food without
196 perceiving the role of the experimenter in finding food, they should simply continue repeating
197 the same movement sequences and communicative strategy, rather than modifying their
198 behaviour in relation to experimenter's behaviour towards the food²². However, chimpanzees
199 used communicative means which referred to the role of the experimenter, i.e. Panzee and
200 Sherman used manual shaking and bobbing to signal that the experimenter was close to the
201 food. Panzee also pointed higher to indicate experimenter's pointing was too close or pointed
202 lower to indicate that experimenter's pointing was too far. This ability to make distinctions
203 such as 'near' and 'far', is similar to some human pointing gestures³⁴, and reveals a
204 sophistication comparable to the usage of some deictic words in human language. These
205 strategies can be seen as evidence that chimpanzees understood their own and the
206 experimenters' actions as interdependent of one another to find hidden food.

207 Additionally, it could be claimed that the communicative strategies employed by the
208 chimpanzees were shaped by the experimenter in repeated sessions of this task, or on similar
209 tasks, ritualising the interactions³⁵. In captivity, chimpanzees can point to food locations
210 outside their reach³⁶⁻³⁸, and some language-trained apes are more likely to use their index
211 finger than whole hand to point, indicating that gesture use and morphology are influenced by
212 experience³⁷. However, communicative persistence more broadly is also evident in wild
213 chimpanzee gestural communication, indicating that the capacity is not unique to enculturated
214 individuals¹⁸⁻²⁰. Nonetheless, in this experiment the pointing by Panzee was more elaborate,
215 producing tactics that resemble those evident in human communication³⁴. By raising her arm
216 higher when the experimenter incorrectly pointed lower, and lowering her arm when
217 experimenter incorrectly pointed higher, Panzee associated her own behaviour with

218 experimenter's change in pointing height. As Panzee modified her pointing in relation to
219 changes of height of experimenter's pointing relative to location of the food, and not the
220 experimenter's pointing height itself, the specific communicative tactics used indicate
221 considerable flexibility in intentional communication in chimpanzees³⁹.

222 The specific and individual strategies employed in response to the experimenter's search
223 behaviour differed between Panzee and Sherman. Sherman's understanding of how to use
224 gestures to guide the experimenters' search actions was more limited, in that he simply
225 responded to the overall proximity of the experimenter to the target location with manual
226 shaking and bobbing. Sherman displayed a low frequency of points, and did not use or
227 modify morphology (height) of his pointing to indicate the location of the food, suggesting
228 that Sherman did not understand as well as Panzee did the communicative potential of
229 pointing to guide the experimenter's understanding in this task. Thus in Sherman's case, the
230 search may have been driven mainly by the experimenter's interpretation of these non-
231 indicative gestures. In contrast, Panzee clearly used directional pointing to guide the
232 experimenter's search behaviour. While Sherman understood the experimenter's behaviour in
233 relation to the food location, Panzee appears to have understood the experimenter's
234 comprehension of her communicative gestures about the location of the hidden food. By
235 tailoring her communicative signals to accommodate the experimenter's level of
236 comprehension, Panzee was significantly more effective than Sherman at directing the
237 experimenter to the food.

238 The different strategies used by Panzee and Sherman reveal the importance of intentional
239 communication in effectively coordinating behaviour⁹. Both Panzee and Sherman responded
240 to the overall proximity of the experimenter to the target location, but also Panzee responded
241 to the experimenter's understanding of her gestures by confirming accurate searches and

242 correcting the experimenter's inaccurate searches. When the experimenter pointed to
243 different referents in the environment, Panzee agreed or disagreed with experimenter's
244 interpretation and was able to achieve the goal of finding food much faster than Sherman,
245 showing that intentional communication can increase the efficiency of attaining goals.

246 Chimpanzees' abilities to intentionally coordinate to obtain desired goals thus appears more
247 sophisticated than previously demonstrated, and this level of skilled communication would
248 have been available in early humans. It potentially could have been involved as a part of the
249 general cognitive and communicative background in the evolution of language. In one
250 scenario for the evolution of language, selection for enhanced communication took place in
251 the context of coordinating social foraging of complex resources such as large game and
252 underground storage organs of plants^{3,40-42}. The communicative strategies employed by
253 chimpanzees in our study suggest that intentionally coordinating to obtain desired goals may
254 have been an important aspect of social behaviour and foraging in early humans. By
255 reformulating the understanding of the location of the resource by communicative signals,
256 and confirming and disconfirming this understanding, two or more interactants would have
257 increased their efficiency in foraging, hunting or other joint activities. In absence of language,
258 gesturing to different referents in environment may have acted as a translation of another's
259 intent into communicative signals, thus assisting interactants in making the mapping between
260 communicative signals and real world events.

261 The use of hand signals to coordinate joint activities in hunter-gatherer groups can provide
262 insights into how this process may have worked, as the hunter-gatherer lifestyle was the
263 dominant one for the vast majority of human evolution⁴³. When hunting, many different
264 hunter-gatherer groups use an extensive range of hand signals to coordinate joint activity –
265 these include Congo Pygmies⁴⁴, Aboriginal Australians⁴⁵ and two Kalahari Khoe speaking

266 groups⁴⁶. Further, a cross-cultural comparison of hunter-gatherer groups demonstrated that
267 hand signals occur more frequently in societies that have a higher dependence on hunting for
268 subsistence⁴⁷. Thus use of hand signals appears to be important in coordinating joint
269 activities across groups of hunter-gatherers.

270 The context of joint activity may have provided a training arena for the acquisition of
271 linguistically based communication from learnt, ritualised signals in our hominin ancestors⁹.
272 The intentionality in gestural communication suggests that language evolution may have
273 occurred primarily in gestural domain. However, gestures frequently co-occur with
274 vocalisations; whereby gestures intentionally convey meaning to recipients, vocalisations are
275 unintentional from signaller's perspective^{5,18-20}. The scaffolding of vocalisations by
276 intentional gestures may have enabled an attribution of meaning to vocalisations and a
277 gradual move towards intentional communication in the vocal domain^{17,48,49}. Studying the
278 processes of vocal and gestural intentional communication in both humans and non-human
279 primates in the context of coordinating joint activity may thus provide important insights into
280 language evolution²³⁻²⁵.

281 **Methods**

282 **Subjects**

283 The subjects were two chimpanzees (*Pan troglodytes*) - Panzee (female, 18 years old)
284 and Sherman (male, 30 years old). Both chimpanzees had been reared from an early age by
285 human caregivers and given extensive exposure to lexigrams. For details of their rearing and
286 experimental histories, see²⁹. The current task has been used to examine recall memory,
287 performance in simulated foraging problems, and use of the lexigram keyboard, but the
288 communication strategies used have not previously been systematically examined through

289 video analysis. For full details of the task and the enclosures, see^{29,30,33}. The experiments
290 complied with ethical regulations and approved by the committee

291 **Design and Procedure**

292 Each chimpanzee was tested individually in the outdoor enclosure, taking part in 6
293 trials. In each trial, Experimenter 1 hid a food item 3-45 m from the outdoor enclosure under
294 natural cover (e.g. log, soil, leaves, branches) in a trial-unique location in the surrounding
295 woodland, whilst the chimpanzee was watching (Supplementary Table S1), concealing any
296 signs of hiding place (e.g. breaking up of soil). The chimpanzee could not enter the woodland
297 itself. In order to retrieve the food, the chimpanzee had to recruit the assistance of an
298 uninformed person (Experimenter 2) and direct him to the food item. Experimenter 2 was a
299 keeper, familiar to the chimpanzees, and experienced in conducting the experiment.
300 Additionally, three trials for each chimpanzee were conducted with a keeper familiar to the
301 chimpanzees but naive to this experimental task.

302 Experimenter 2 started near the outdoor enclosure and watched for the chimpanzee's
303 initial directional gesture, then walked in that direction, and stopped to take further directions.
304 Experimenter 2 also would face and "query" the chimpanzee periodically by pointing (with a
305 1.5m stick) in various directions of possible travel, by noting which of these directions
306 evoked immediate bobbing/shaking responses by the chimpanzee (rather than continued
307 pointing), and by moving further in that direction, iterating the process. If the food was
308 found, it was offered to the chimpanzee. During the trials, both the chimpanzees and the
309 experimenter's behaviour were videotaped.

310 **Behavioural Coding**

311 **Chimpanzee behaviour**

312 Behavioural responses of the chimpanzee to the experimenter's pointing gestures were coded.
313 A response started immediately after the pointing gesture of the experimenter was made and
314 ended when the experimenter made another pointing gesture, started walking, or searched
315 through the groundcover with the stick. *Indicative gestures* made by the chimpanzees that
316 were coded included any movement which appeared to be aimed at specific distal target or a
317 lexigram keyboard, using both extended index finger and open hand. The morphology of
318 indicative gestures towards the hidden object was described in terms of the arm, forearm and
319 finger positions and classified into: indicate up (arm, forearm and finger directed vertically
320 up) or indicate down (arm, forearm and finger directed horizontally or down). Additionally,
321 the direction of gesturing was recorded using the following categories: object (pointing in the
322 direction of the object), other direction.

323 *Non-indicative gestures* coded included armshake, defined as any shaking or swinging of one
324 or both hands or arms repeatedly; bobbing (subject bobs and weaves with head or whole body
325 in bowing position upwards or forwards) and rocking (subject stands or sits and rocks its
326 body from side to side or from forwards to backwards). Two additional behavioural responses
327 recorded were scratching and vocalisations (for full descriptions of categories coded see
328 Supplementary Table S2).

329 **Experimenter behaviour**

330 The trial started when Experimenter 2 arrived outdoors and began to interact with the
331 chimpanzee (as opposed to when they interacted indoors), and the end of the trial was the
332 moment the food item was found and removed from its location. The experimenter's search

333 behaviour (pointing with the stick) was recorded when the experimenter was standing in one
334 place. All potential pointing gestures made by the experimenter whilst walking were
335 excluded because they were not responded to by the chimpanzees and it was not always
336 possible to reliably determine the accuracy of these pointing gestures relative to the food
337 location. Each time the experimenter made a pointing gesture, the following three pieces of
338 information were recorded. First, the distance of the experimenter to the hidden object,
339 determined from a map of the area of woodland, were categorised as close (0 – 4 m between
340 experimenter and the object) and far (above 4m). Second, the direction of the experimenter's
341 pointing gestures was coded as: point towards the object (experimenter pointing in the
342 direction of a hidden object, the location of which is within the experimenter's field of vision)
343 or point elsewhere (experimenter pointing in a direction other than towards the hidden
344 object). Third, the experimenter's accuracy at indicating distance to the object was recorded,
345 as evidenced by the height at which experimenter held the end of pointing stick relative to the
346 object's location. This was scored as correct, too far or too close, by assessing whether
347 hidden object fell inside, outside or on the circle visually drawn by the end of line extended
348 from the end of the stick held by the experimenter.

349 Finally, the visual attention of the experimenter to the chimpanzee was recorded as attention
350 present (experimenter looking at the chimpanzee, as judged from the direction of his head) or
351 absent (any other direction). The presence of the object was coded as object absent (object
352 hidden) or object found (object located and removed from the hiding place by the
353 experimenter); for these analyses, the behavioural responses of the chimpanzees were
354 recorded when the experimenter was either locomoting or standing and pointing in a direction
355 or inspecting the surface of the ground. A trial ended when the experimenter disengaged from
356 the chimpanzee and left the area.

357 **Analyses**

358 For the main analyses of chimpanzee behaviour during trials with the experienced
359 experimenter, each subject was analysed individually. For each subject, data from all six
360 trials were pooled for analyses, with paired comparisons used to analyse behaviour patterns.
361 As trials varied in length, all behaviours were either converted to rates per minute or
362 proportions of all points. Distance per minute of response was calculated by dividing the
363 distance of the experimenter from the target at the beginning of the trial by the total
364 chimpanzee response duration to the experimenter's pointing gestures during that trial. The
365 additional trials with an inexperienced experimenter, to examine if experience of the
366 experimenter affected the success in finding food, were pooled for both chimpanzees,
367 matching trials in terms of the chimpanzee taking part in the trial and the distance to the food
368 hidden. Non-parametric statistics were used with the alpha level set at 0.05 and all tests were
369 two-tailed. One trial for each chimpanzee was coded by a second observer and agreement
370 (Cohen's Kappa) was good to excellent for both experimenter and chimpanzee behaviour
371 ranging from 0.71 to 0.83.

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490

491 **Tables and Figures**

492 Fig. 1 Chimpanzee behavioural responses to experimenter pointing gestures according to a)
493 experimenter visual attention towards chimpanzee; b) object presence.

494 Fig. 2 Influence of experimenter comprehension of object location (as indicated by accuracy
495 of his pointing) on chimpanzee production of indicative and non-indicative gestures

496 Fig. 3 Influence of experimenter comprehension of distance to hidden food (as indicated by
497 the height of his pointing) on Panzee's production of upward and downward pointing

498 Table 1. Results of statistical tests of Sherman's responses to experimenter's pointing
499 gestures

500 **Figure legends**

501 Fig. 1 The voluntary control of each behavioural response of the chimpanzees was examined.
502 Responses of the chimpanzees were categorised as intentional (as opposed to non-intentional)
503 only when the production was significantly higher when visual attention of the experimenter
504 was present versus absent and the object was hidden versus found. The tests results for each
505 behavioural response type were following: Influence of experimenter's visual attention:
506 Panzee: Point ($p = 0.031$), Manual shake ($p = 0.031$), Bob ($p = 0.031$), Rock ($p = 0.063$),
507 Scratch ($p = 0.063$), Vocalisation ($p = 0.5$), Sherman: Point ($p = 0.031$), Manual shake ($p =$
508 0.031), Bob ($p = 0.031$), Rock ($p = 0.063$), Scratch ($p = 0.250$), Vocalisation ($p = 0.250$);
509 Influence of object hidden versus found: Panzee: Point ($p = 0.031$), Manual shake ($p =$
510 0.031), Bob ($p = 0.031$), Rock ($p = 0.438$), Scratch ($p = 0.313$), Vocalisation ($p = 1$);
511 Sherman: Point ($p = 0.031$), Manual shake ($p = 0.031$), Bob ($p = 0.031$), Rock ($p = 0.438$),
512 Scratch ($p = 0.313$), Vocalisation ($p = 1$). Only those behavioural response types classified as
513 intentional were considered in further analyses. All statistical tests were performed using

514 Wilcoxon signed-ranks test, two-tailed, with exact probabilities used, $n = 6$ trials for each
515 individual.

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