Chimpanzees modify intentional gestures to coordinate a search for hidden food

Anna Ilona Roberts, Sarah-Jane Vick, Sam George Bradley Roberts & Charles R. Menzel

***Nature Communications* 5, Article number: 3088 (2014)**

doi: https://doi.org/10.1038/ncomms4088

Chimpanzees modify intentional gestures to coordinate a search for hidden food

Abstract

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

Introduction

The ability to appreciate that others have comprehension states and that these states can affect their behaviour is hypothesised to underpin the emergence of complex forms of communication in human evolution1-3. In intentional communication, the signaller has a goal and influences the comprehension state of the recipient by flexibly modifying their communication 4-6. Communicative persistence is a key indicator of intentionality in humans and other primates and it precedes the transition to linguistically based communication in human infants7. There is growing evidence for intentionality and communicative persistence in great ape gestural signalling – defined as voluntary movements of arms, legs or bodily postures8. Communicative persistence can be evidenced by a signaller's repetition or elaboration of signals in relation to different comprehension states of the recipient, until their goal is obtained, or failure is clearly indicated[7,9,10]. However, understanding communicative persistence in non-verbal animals is not straight-forward; it is difficult to disentangle whether a signaller influences recipient's comprehension of the meaning of the signal or influences directly their behaviour (i.e. makes them do something without assessing any comprehension about the goal) [5,11]. Studying episodes of coordination, where individuals communicate with one another in turn-taking sequences to achieve a goal that could not be accomplished individually, enable the nature and complexity of communicative persistence to be determined12-14. Communicative persistence in these contexts requires coordination of attention and communication to a task, goal and to one another, providing evidence that signallers perceive others as entities with comprehension states about the goal15. For instance, if persistence reflects a particular internal state, contingent upon changes in the availability of the goal itself, then only repetitions of the original signals would be expected to occur. If, on the other hand, senders are aware of the impact that their signals will have on the recipient, then they should elaborate their signalling flexibly, contingent upon recipient's comprehension about the goal[9,16].

In examining the ability of signallers to influence recipients, studying gestural communication is particularly useful because gestures are directional[17,18], meaningful[19,20] and can draw attention of the recipient to specific spatial locations in the environment[21]. These characteristics of gestural communication allow researchers to determine the signaller's goal in gesturing, in particular in relation to the meaning of elaborations, and to identify their role in effectively influencing the recipient. If communicative persistence is an unintentional expression of frustration at the goal itself, then diffuse, uninformative elaboration would be expected to occur[9]. If on the other hand, signallers perceive recipients as capable of comprehension about the goal, then they should elaborate by the use of informative signals which refer to the role of the recipient in pursuit of the desired goal, i.e. inform the recipient what they want him to do[22]. For instance, when signallers direct their gestures to the recipient, but fail to achieve the desired response, they may direct the recipient's attention to the desired referent in the environment by the use of indicative gestures such as pointing. However, when recipients respond appropriately to the signal, signallers may use non-indicative gestures such as bobbing to affirm the recipient's comprehension about the goal.

Results from observational and experimental studies show some evidence for communicative persistence in wild and captive apes. However these are restricted to less complex experimental tasks or conspecific social interactions which did not require face to face behavioural coordination from a distance through gestural signals, as in the present case, to achieve a goal[19,20,23-27]. For example, when presented with two food items (desirable and undesirable), in close proximity and visible during a fixed delay interval, great apes persisted with gesture production only following the (predetermined) delivery of the undesirable and not the desirable food items[6,28]. However, as the experimenter neither initiated nor responded to the apes' communicative efforts prior to the food delivery, it is unclear whether the apes' gestures following food delivery were in response to the experimenter's behaviour (delivery of the undesirable food) or to the experimenter's apparent lack of comprehension of the apes' gestures[19]. Moreover, recent research demonstrates that when two chimpanzees required help of one another to retrieve a desirable food reward, they relied on a relatively simple leader-follower strategy, rather than using a more elaborated form of communication to coordinate food retrieval[12]. Thus, the issue of whether great apes can flexibly persist in communication to intentionally influence recipients remains unresolved[2].

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

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

Results

Communicative exchanges

The chimpanzees used intentional gestures to coordinate search efforts with the experimenter (see also accompanying Supplementary Movie 1 of the task), for the food, hidden at various distances and locations (Supplementary Table S1), gesturing only when the experimenter was visually oriented towards them (Fig. 1a). These gestures were informative, goal-directed and either indicative (e.g. manual pointing) or non-indicative (manual shake and bobbing of the head or body)[1] in terms of their ability to draw the recipient's attention to specific spatial locations(Supplementary Table S2)[6]. The experimenter and chimpanzee spontaneously influenced and shaped the directionality of each other's behavior by taking multiple turns in responding to indications of the location of food. On Panzee's trials, the mean (SD) number of turns prior to finding the hidden food per target location was 36.3 (30.57) as compared to 43.5 (30.62) for Sherman. The majority of these turns involved intentional communication by the chimpanzees, the mean (SD) proportion for Panzee and Sherman were 0.76 (0.15) and 0.81 (0.06) respectively (Supplementary Table S1), which was significantly higher than the proportion of turns lacking intentional communication for both Panzee (Wilcoxon signed ranks test; $n = 6$, t = 0, $p = 0.031$) and Sherman ($n = 6$, t = 0, $p = 0.031$). By alternating their communication in this manner, the chimpanzees and the experimenter were able to obtain the hidden food. Although the mean (SD) proportion of turns responded to with incorrect experimenter pointing directions was high for both Panzee: 0.74 (0.18) and Sherman: 0.78 (0.17), most trials were successful (11 out of 12) and the food item was found quickly, within a large area of woodland. The mean (SD) duration of trials was 2.30 (1.8) minutes for Panzee and 3.02 (1.5) minutes for Sherman.

Strategies of chimpanzees to lead experimenter to the food

By modifying their communication in response to changes in the experimenter's behaviour, relative to the location of the hidden food, the chimpanzees were able to successfully retrieve 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 reunion[18].

to the experimenter's spatial proximity to the target location. Both Panzee (Wilcoxon signed ranks test; $n = 6$, t = 0, $p = 0.031$) and Sherman ($n = 6$, t = 0, $p = 0.031$) displayed a higher rate of non-indicative gestures when the experimenter was near to the target location (within 0-4m), as compared to far from the target location (over 4m). Gesturing ceased as soon as items were found by the experimenter (Fig. 1b), indicating that gesture production did not simply reflect high arousal in anticipation of food delivery[31]. Instead, the chimpanzees produced non-indicative gestures to provide positive feedback to the experimenter as he approached the target location, and ceased once this goal had been met.

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

In contrast, Sherman only responded to the overall proximity of the experimenter to the target location with manual shaking and bobbing (Table 1) and Panzee's method increased the efficacy of the experimenter's search on this task[30]. There were no significant differences between the chimpanzees in the experimenter or in the chimpanzee distance to the target at the start of the trials, or trial duration (Supplementary Table S1) but the distance covered by the experimenter during their search, corrected for chimpanzee communicative effort (duration of responses), was significantly greater for Panzee's than Sherman's trials (Mann – Whitney test, $n = 12$, $t = 26$, $p = 0.041$). This shows that Panzee's skills at communication were more efficient at directing the experimenter to the food and the success of the task was influenced by the ability of chimpanzees to communicate its location[30]. Additionally, when comparing performance by experimenters who were familiar and unfamiliar with the chimpanzees' behaviour on this particular task, the success rate of the inexperienced experimenter was also high (5/6 trials were successful) and the trial duration did not differ between experimenters across trials matched for distance to hidden food (Mann – Whitney test, $n = 12$, $t = 37$, $p = 0.818$; Supplementary Table S3). This indicates that success was not solely determined by the experimenter's experience on this particular task, but was instead the result of intentional communication between the chimpanzees and experimenters.

Discussion

The communicative flexibility reported in this paradigm[29,30,32,33] goes far beyond that reported in previous studies, where apes were faced with an unresponsive experimenter[6,28] or where conspecific social interactions did not require face to face behavioural coordination though intentional gestural signals to achieve the desired goal[19,20,23-27]. Here, chimpanzees dynamically and flexibly modified their intentional gestures in relation to the naïve experimenter's search efforts towards the hidden food, to successfully guide the experimenter to the food item. Such communicative persistence, particularly in turn-taking episodes of communication where individuals respond communicatively to one another, is a key marker of intentional communication in humans and primates[7,11]. This study therefore provides some of the clearest evidence to date for such communicative persistence, and thus intentional communication, in chimpanzees.

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

Moreover, the chimpanzee reactions to the experimenter's behaviour towards the food further clarifies whether chimpanzees communicated with regard for the experimenter. If chimpanzees simply learned the appropriate individual behaviours to get the food without perceiving the role of the experimenter in finding food, they should simply continue repeating the same movement sequences and communicative strategy, rather than modifying their behaviour in relation to experimenter's behaviour towards the food[22]. However, chimpanzees used communicative means which referred to the role of the experimenter, i.e. Panzee and Sherman used manual shaking and bobbing to signal that the experimenter was close to the food. Panzee also pointed higher to indicate experimenter's pointing was too close or pointed lower to indicate that experimenter's pointing was too far. This ability to make distinctions such as 'near' and 'far', is similar to some human pointing gestures[34], and reveals a sophistication comparable to the usage of some deictic words in human language. These strategies can be seen as evidence that chimpanzees understood their own and the experimenters' actions as interdependent of one another to find hidden food.

Additionally, it could be claimed that the communicative strategies employed by the chimpanzees were shaped by the experimenter in repeated sessions of this task, or on similar tasks, ritualising the interactions[35]. In captivity, chimpanzees can point to food locations outside their reach[36-38], and some language-trained apes are more likely to use their index finger than whole hand to point, indicating that gesture use and morphology are influenced by experience[37]. However, communicative persistence more broadly is also evident in wild chimpanzee gestural communication, indicating that the capacity is not unique to enculturated individuals[18-20]. Nonetheless, in this experiment the pointing by Panzee was more elaborate, producing tactics that resemble those evident in human communication[34]. By raising her arm higher when the experimenter incorrectly pointed lower, and lowering her arm when experimenter incorrectly pointed higher, Panzee associated her own behaviour with experimenter's change in pointing height. As Panzee modified her pointing in relation to changes of height of experimenter's pointing relative to location of the food, and not the experimenter's pointing height itself, the specific communicative tactics used indicate considerable flexibility in intentional communication in chimpanzees[39].

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

The different strategies used by Panzee and Sherman reveal the importance of intentional communication in effectively coordinating behaviour[9]. Both Panzee and Sherman responded to the overall proximity of the experimenter to the target location, but also Panzee responded to the experimenter's understanding of her gestures by confirming accurate searches and correcting the experimenter's inaccurate searches. When the experimenter pointed to different referents in the environment, Panzee agreed or disagreed with experimenter's interpretation and was able to achieve the goal of finding food much faster than Sherman, showing that intentional communication can increase the efficiency of attaining goals.

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

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

The context of joint activity may have provided a training arena for the acquisition of linguistically based communication from learnt, ritualised signals in our hominin ancestors[9]. The intentionality in gestural communication suggests that language evolution may have occurred primarily in gestural domain. However, gestures frequently co-occur with vocalisations; whereby gestures intentionally convey meaning to recipients, vocalisations are unintentional from signaller's perspective[5,18-20]. The scaffolding of vocalisations by intentional gestures may have enabled an attribution of meaning to vocalisations and a gradual move towards intentional communication in the vocal domain[17,48,49]. Studying the processes of vocal and gestural intentional communication in both humans and non-human primates in the context of coordinating joint activity may thus provide important insights into language evolution[23-25].

Methods

Subjects

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

Design and Procedure

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

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

Behavioural Coding

Chimpanzee behaviour

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

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

Experimenter behaviour

The trial started when Experimenter 2 arrived outdoors and began to interact with the chimpanzee (as opposed to when they interacted indoors), and the end of the trial was the moment the food item was found and removed from its location. The experimenter's search behaviour (pointing with the stick) was recorded when the experimenter was standing in one place. All potential pointing gestures made by the experimenter whilst walking were excluded because they were not responded to by the chimpanzees and it was not always possible to reliably determine the accuracy of these pointing gestures relative to the food location. Each time the experimenter made a pointing gesture, the following three pieces of information were recorded. First, the distance of the experimenter to the hidden object, determined from a map of the area of woodland, were categorised as close (0 – 4 m between experimenter and the object) and far (above 4m). Second, the direction of the experimenter's pointing gestures was coded as: point towards the object (experimenter pointing in the direction of a hidden object, the location of which is within the experimenter's field of vision) or point elsewhere (experimenter pointing in a direction other than towards the hidden object). Third, the experimenter's accuracy at indicating distance to the object was recorded, as evidenced by the height at which experimenter held the end of pointing stick relative to the object's location. This was scored as correct, too far or too close, by assessing whether hidden object fell inside, outside or on the circle visually drawn by the end of line extended from the end of the stick held by the experimenter.

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

Analyses

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

References

[1] Tomasello, M. & Carpenter, M., Shared intentionality. *Developmental Science* 10 (1), 121-125 (2007).

[2] Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H., Understanding and sharing intentions: the origins of cultural cognition. *Behavioural and Brain Sciences* 28, 675-735 (2005).

[3] Sterelny, K., Language, gesture, skill: the co-evolutionary foundations of language. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367 (1599), 2141-2151 (2012).

[4] Tomasello, M. & Call, J., Ape gestures and the origins of language in *The gestural communication of apes and monkeys*, edited by J. Call & M. Tomasello (Lawrence Erlbaum Associates, Mahwah, New Jersey, 2007).

[5] Seyfarth, R. & Cheney, D., Signalers and receivers in animal communication. *Annu Rev Pschol* 54, 145-173 (2003).

[6] Leavens, D.A., Russell, J.L., & Hopkins, W.D., Intentionality as measured in the persistence and elaboration of communication by chimpanzees (Pan troglodytes). *Child Development* 76 (1), 291-306 (2005).

[7] Bates, E., Benigni, L., Bretherton, I., Camaioni, L., & Volterra, V., *The emergence of symbols*. (Academic Press, New York, 1979).

[8] Hewes, G.W., Primate communication and the gestural origin of language. *Current Anthropology* 14, 5-24 (1973).

[9] Golinkoff, R.M., I beg your pardon - the preverbal negotiation of failed messages. *Journal of Child Language* 13 (3), 455-476 (1986).

[10] Bruner, J., Intention in the structure of action and interaction in *Advances in infancy research*, edited by L. Lipsett (Ablex, Norwood, New Jersey, 1981).

[11] Tomasello, M., Having intentions, understanding intentions and understanding communicative intentions in *Developing theories of intention.*, edited by P. Zelazo, D. Olson, & J. Astington (Cambridge University Press, Cambridge, 1999).

[12] Bullinger, A.F., Wyman, E., Melis, A.P., & Tomasello, M., Coordination of chimpanzees (Pan troglodytes) in a Stag hunt game. *International Journal of Primatology* 32 (6), 1296-1310 (2011).

[13] Tomasello, M., Carpenter, M., & Liszkowski, U., A new look at infant pointing. *Child Development* 78 (3), 705-722 (2007).

[14] Gomez, J.C., 12 The emergence of intentional communication as a problem-solving strategy in the gorilla. *'Language'and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives*, 333 (1994).

[15] Ratner, N. & Bruner, J., Games, social exchange and the acquisition of language. *Journal of Child Language* 5 (3), 391-401 (1978).

[16] Golinkoff, R.M., When is communication a meeting of minds. *Journal of Child Language* 20 (1), 199-207 (1993).

[17] Roberts, A.I., Vick, S.-J., Roberts, S.G.B., Buchanan-Smith, H.M., & Zuberbühler, K., A structure-based repertoire of manual gestures in wild chimpanzees: Statistical analyses of a graded communication system. *Evolution and Human Behavior* 33 (5), 578-589 (2012).

[18] Roberts, A.I., Roberts, S.G.B., & Vick, S.-J., The repertoire and intentionality of gestural communication in wild chimpanzees. *Animal Cognition* (2013).

[19] Roberts, A.I., Vick, S.-J., & Buchanan-Smith, H., Communicative intentions in wild chimpanzees: Persistence and elaboration in gestural signalling. *Animal Cognition* 16 (2), 187-196 (2013).

[20] Roberts, A.I., Vick, S.-J., & Buchanan-Smith, H., Usage and comprehension of manual gestures in wild chimpanzees. *Animal Behaviour* 84 (2), 459-470 (2012).

[21] Leavens, D.A., Racine, T.P., & Hopkins, W.D., The ontogeny and phylogeny of non-verbal deixis in *The prehistory of language*, edited by R. Botha & C. Knight (Oxford University Press, New York, 2009), pp. 142-165.

[22] Warneken, F., Chen, F., & Tomasello, M., Cooperative activities in young children and chimpanzees. *Child Development* 77 (3), 640-663 (2006).

[23] Menzel, E.W.J., Communication about the environment in a group of young chimpanzees. *Folia Primatologica* 15, 220-232 (1971).

[24] Menzel, E.W.J., Leadership and communication in young chimpanzees in *Precultural Primate Behavior*, edited by E. W. Jr. Menzel (Karger, Basel, 1973), pp. 192–225.

[25] Menzel, E.W.J., *A group of young chimpanzees in a one acre field: leadership and communication*. (Academic Press, New York, 1974).

[26] Menzel, E.W. & Halperin, S., Purposive behavior as a basis for objective communication between chimpanzees. *Science* 189, 652- 654 (1975).

[27] Savage-Rumbaugh, E.S., Rumbaugh, D.M., & Boysen, S., Linguistically mediated tool use and exchange by chimpanzees (Pan troglodytes). *Behavioral and brain sciences* 1 (04), 539-554 (1978).

[28] Cartmill, E. & Byrne, R., Orangutans modify their gestural signaling according to their audience's comprehension *Current Biology* 17 (15), 1345-1348 (2007).

[29] Menzel, C.R., Unprompted recall and reporting of hidden objects by a chimpanzee (Pan troglodytes) after extended delays. *Journal of Comparative Psychology* 113 (4), 426-434 (1999).

[30] Sayers, K. & Menzel, C.R., Memory and foraging theory: chimpanzee utilization of optimality heuristics in the rank-order recovery of hidden foods. *Animal Behaviour* 84, 795-803 (2012).

[31] Melis, A.P. *et al.*, Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society B: Biological Sciences* 278 (1710), 1405-1413 (2011).

[32] Menzel, C.R. & Menzel Jr, E., Enquiries Concerning Chimpanzee Understanding in *The Primate Minds: Built to connect with other minds*, edited by F. De Waal & F. Ferrari (Harvard University Press., Cambridge, MA, 2012), pp. 265-287.

[33] Menzel, C., Progress in the study of chimpanzee recall and episodic memory in *The missing link in cognition: Origins of self-reflective consciousness*, edited by H. Terrace & J. Metcalfe (Oxford University Press, New York, 2005), pp. 188-224.

[34] Kendon, A., *Sign languages of Aboriginal Australia: Cultural, Semiotic and Communicative Perspectives.* . (Cambridge University Press, Cambridge, 1988).

[35] Ross, H.S. & Lollis, S.P., Communication within infant social games. *Developmental psychology* 23 (2), 241-248 (1987).

[36] Hopkins, W.D. & Leavens, D.A., Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology* 34, 813-822 (1998).

[37] Leavens, D.A. & Hopkins, W.D., The whole-hand point: The structure and function of pointing from a comparative perspective. *Journal of Comparative Psychology* 113 (4), 417-425 (1999).

[38] Leavens, D.A., Hopkins, W.D., & Bard, K.A., Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 110 (4), 346-353 (1996).

[39] Gillespie-Lynch, K., Feng, Y., Greenfield, P.M., Savage-Rumbaugh, S., & Lyn, H., A cross-species study of gesture and its role in symbolic development: Implications for the gestural theory of language evolution. *Frontiers in Psychology* 4, 160.

[40] Bickerton, D., *Adam's tongue: how humans made language, how language made humans*. (Hill and Wang, 2009).

[41] Kurland, J.A. & Beckerman, S.J., Optimal foraging and hominid evolution: Labor and reciprocity. *American Anthropologist* 87 (1), 73-93 (1985).

[42] BrÃ¤uer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M., Making inferences about the location of hidden food: social dog, causal ape. *Journal of Comparative Psychology* 120 (1), 38 (2006).

[43] Hewlett, B.S., Fouts, H.N., Boyette, A.H., & Hewlett, B.L., Social learning among Congo Basin hunterâ€“gatherers. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366 (1567), 1168-1178 (2011).

[44] Lewis, J., 13 As well as words: Congo Pygmy hunting, mimicry, and play. *The cradle of language* 12, 236 (2009).

[45] Mountford, C.P., Gesture language of the Ngada tribe of the Warburton Ranges, Western Australia. *Oceania* 9 (2), 152-155 (1938).

[46] Fehn, A.-M., Phonology of hunting signs in two Kalahari Khoe-speaking groups (Tsâ€™ ixa and|| Ani).

[47] Divale, W.T. & Zipin, C., Hunting and the development of sign language: A cross-cultural test. *Journal of Anthropological Research*, 185-201 (1977).

[48] Brakke, K.E. & Savage-Rumbaugh, E.S., The development of language-skills in bonobo and chimpanzee. 1. Comprehension. *Language & Communication* 15, 121-148 (1995).

[49] Tomasello, M., *Origins of human communication*. (MIT Press, Cambridge, Massachusets, 2008).

Tables and Figures

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

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

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

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

Figure legends

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

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

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

Acknowledgements The project was supported by Leakey Foundation, the Wenner-Gren Foundation, and HD-056352, HD-38051, and HD-060563 from the National Institutes of Health (NIH). The contents of this article do not necessarily represent the official views of NIH. We would also like to thank John Kelly, Sarah Hunsberger and Betty Chan for their assistance with testing and filming and two anonymous referees for their comments on the manuscript.

Author contributions A.I.R. designed the study, coding scheme, coded the footage, analysed the data and wrote up the paper

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to A.I.R. (anna.roberts@chester.ac.uk).