Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals

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Abstract

Humans extensively help others altruistically, which plays an important role in maintaining cooperative societies. Although some non-human animals are also capable of helping others altruistically, humans are considered unique in our voluntary helping and our variety of helping behaviors. Many still believe that this is because only humans can understand others' goals due to our unique theory of mind abilities, especially shared intentionality. However, we know little of the cognitive mechanisms underlying helping in non-human animals, especially if and how they understand others' goals. The present study provides the empirical evidence for flexible targeted helping depending on conspecifics' needs in chimpanzees. The subjects of this study selected an appropriate tool from a random set of seven objects to transfer to a conspecific partner confronted with differing tool-use situations, indicating that they understood what their partner needed. This targeted helping, i.e. selecting the appropriate tool to transfer, was observed only when the helpers could visually assess their partner's situation. If visual access was obstructed, the chimpanzees still tried to help their partner upon request, but failed to select and donate the appropriate tool needed by their partner. These results suggest that the limitation in chimpanzees' voluntary helping is not necessarily due to failure in understanding others' goals. Chimpanzees can understand conspecifics' goals

and demonstrate cognitively advanced targeted helping as long as they are able to visually evaluate their conspecifics' predicament. Yet, they will seldom help others without direct request for help.

Keywords: targeted helping, theory of mind, understanding other's goal, chimpanzee, altruism prosociality

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Introduction

Humans extensively help others altruistically, which plays an important role in maintaining cooperative societies. How have humans evolutionarily achieved this cooperative trait? Previously, many theoretical studies have explained why altruism and cooperation evolved from an ultimate perspective. These studies have addressed the "why", but not the "how". Many non-human animals demonstrate cooperative abilities (1-3), and recent empirical studies have also revealed that some non-human primates can help or share food with conspecifics without any direct benefit to themselves (cotton-top tamarin (*Saguinius oedipus*): 4, capuchin (*Cebus appella*): 5-7, marmoset (*Callitrix jacchus*): 8, bonobo (*Pan paniscus*): 9, chimpanzee (*Pan troglodytes*): 10-14). However, our understanding of the cognitive mechanisms involved remains limited and urgently requires further investigation, especially from a comparative perspective.

Regarding the cognitive mechanisms involved in helping, much focus has been given to "targeted helping" (also known as "instrumental helping" (10-11)) defined as help and care based on the cognitive appreciation of the need or situation of others (15).

Targeted helping is considered to be linked to the cognitive capacity for empathy. For now, among non-human animals, only some great ape, cetacean, and elephant species demonstrate this form of helping behavior (15). By definition, the animals are expected to understand the others' needs. However, to date, empirical studies clearly demonstrating this cognitive ability in non-human animals are lacking. If and how the animals understand the others' goals and help others effectively are core questions which have to be examined if we are ever to deepen our understanding of the evolution of cooperation.

Among those animal species known to demonstrate targeted helping, chimpanzees, one of our closest living relatives, help others upon request, but seldom voluntarily in contexts requiring assistance provisioning (12-13). This concurs with observations of food sharing among chimpanzees in the wild (16-17). Interestingly, in our previous experiments (12), observation of a conspecific in trouble did not elicit chimpanzees' helping behavior. A recent study has documented chimpanzees' spontaneous generosity in a prosocial choice test (14). Other studies, however, indicate that chimpanzees fail to give food spontaneously to a conspecific even at no cost to themselves (18-20), between a mother and her infant (21-23), and in reciprocal contexts

(21-22,24-25). Direct request, e.g. an out-stretched arm directed at a potential helper, may be required to prompt targeted helping in chimpanzees (26).

Why do chimpanzees seldom help others without being requested? One plausible explanation from the perspective of cognitive mechanisms is that chimpanzees cannot understand others' goals upon witnessing another's predicament. Many still believe that humans are unique in this respect, because we are the only animal species endowed with unique theory of mind abilities enabling us to understand the goals and to share the intentions of others (27). Warneken and Tamasello (10) empirically demonstrated that chimpanzees, compared to humans, have a limited range of helping behaviors, and suggested that this is because of the inability of chimpanzees to interpret what others need in different situations. Nevertheless, we still know little about the cognitive mechanisms underlying helping behavior in non-human animals, and no study has empirically examined if and how chimpanzees understand others' goals in these types of helping contexts.

We developed a new experimental paradigm aimed at examining chimpanzees' ability and flexibility in helping effectively a conspecific pending on his/her specific needs. This experiment required participants to select and transfer an appropriate tool to a conspecific partner so that he/she could solve a task to obtain a juice reward. We set up one of two tool-use situations, i.e. a stick-use situation or a straw-use situation, in the potential recipient's booth. Seven objects including a stick and a straw (Figure 1) were supplied on a tray in an adjacent booth occupied by a potential helper. The potential recipient could not directly reach any of the tools available in the adjoining booth, but could demonstrate request by poking his or her arm through a hole in the panel wall separating the two booths. In previous experimental studies (10-13), a potential helper was never confronted with a behavioral choice when given the opportunity to help. These experiments therefore failed to examine whether chimpanzees actually understood what others needed. In our study, the helper had to select a tool from an array of seven objects to effectively help his/her partner accomplish the task he/she was confronted with. We also developed and compared two conditions in which a potential helper could or could not see the partner's tool-use situation. Our study highlights notable cognitive mechanisms underlying helping behavior in chimpanzees.

The setup of the present study is fairly similar to previous experiments conducted by Savage-Rumbaugh and colleagues (28). However, there are clear differences between this latter study and our own. In these previous experiments, the two chimpanzee participants correctly chose and donated tools which their partner requested using symbols. This study significantly promoted our understanding of symbolic communication abilities in chimpanzees; however, it provided limited insight into their helping behavior and its mechanisms. In addition, pre-test training artificially shaped the subjects' symbolic communication and also their giving and sharing interactions. The potential recipient chimpanzees were trained to indicate which tool they needed by selecting a corresponding lexigram, and the potential donors were trained to select and transfer the tool corresponding to the presented lexigram. The performances were established through standard fading, shaping, chaining, and discrimination procedures, as also used in studies with pigeons (29). In order to eliminate these possibilities, we developed significantly different procedures. First, although the chimpanzees were all trained in solving the two tool-use tasks presented to them, the experimenter never performed any other type of training or shaping of behavior of the participants. Second, we allowed our subjects to communicate with each other without symbols or any other form of artificial communication medium. With

these modifications, we investigated how chimpanzees understand what others require based on their natural communicative abilities, and whether or not they can flexibly and spontaneously modify their helping behavior according to the others' needs.

Results & Discussion

The first ***"Can see" condition***

We first tested the chimpanzees in a "can see" condition, where the panel wall was transparent so that a potential helper could see his/her partner's tool-use situation in the adjacent booth. Overall, object offer (at least one object regardless of whether it was a tool or a non-tool object) from potential helpers was observed on average in 90.8% (N = 5, SEM = 3.4) of trials. In the familiarization phase prior to testing (eight 5-min trials for each participant), where the chimpanzees could freely manipulate the seven objects without any tool-use situation, object offer was observed only in 5.0% (N = 5, SEM = 3.1) of trials, suggesting that the chimpanzees were not motivated in transferring objects to their partner for its own sake. Object offer mainly occurred following recipient's request. Upon-request offer accounted for 90.0% (N = 5, SEM = 5.7) of all offers. This

result concurs with previous findings that direct request is important for the onset of targeted helping in chimpanzees (12-13,26).

The chimpanzees, except Pan, first offered potential tools (a stick or a straw) significantly more frequently than the other non-tool objects (Ai: 87.5%, Cleo: 97.4%, Pal: 93.5%, Ayumu: 78.0%; Fisher's exact test: $p < 0.05$ for each of these four participants, with a chance level set at 50% due to the binary choice between tool and non-tool objects; see Table S1 for the individual details). In Pan's case, she most frequently offered a non-tool brush (79.5% of her first object offers). When we eliminated brush offer from the analysis, her offer of the potential tools was also significantly above chance level (88.6%; Fisher's exact test: $p < 0.01$ with a chance level set at 50%). This bias towards offering a stick and a straw suggests that the chimpanzees distinguished the potential tools from the other useless objects. The chimpanzees' prior experience with these tools in previous experiments may explain this bias (12).

159 We then examined the chimpanzees' first offer, limiting our analysis to the
160 potential tools only: which tool, a stick or a straw, they chose to transfer to the partner.
161 Among four of the five chimpanzee participants we tested, there was a significant
162 difference in the first offer between the partner's two tool-use situations (Fisher's exact
163 test: $p < 0.05$ for each of the four participants; see Table 1 for details). Helpers selected
164 to offer more frequently a stick (or a straw) when their partner was confronted with the
165 stick-use (or the straw-use) situation than when he or she was faced with the straw-use
166 (or the stick-use) situation (Figure 2a; Video S1; see Table S1 for individual details).
167 Therefore the chimpanzees demonstrated flexible targeted helping depending on their
168 partner's predicaments. This result suggests that the chimpanzees understood which tool
169 their partner required to solve successfully the tool-use task he/she was confronted with.

170

171 ***The "Cannot see" condition***

172 In order to investigate how the chimpanzees understood which tool their
173 partner required, we next developed the "cannot see" condition. In this condition, the
174 panel wall was opaque so that a potential helper could not readily see his/her partner's
175 tool-use situation unless he/she purposely stood up and peaked through a hole

approximately 1m above the floor. In this condition, the chimpanzees continued to help, offering at least one object (regardless of whether a tool or non-tool) in 95.8% of trials on average (N = 5, SEM = 1.9). There was no significant difference in the frequency of object offer between the previous "can see" condition and this "cannot see" condition (paired t-test (two-tailed): $t = -2.1$, $df = 4$, $p = 0.099$). Upon-request offer (71.7%, N = 5, SEM = 18.3) again predominated over voluntary offer (28.3%, N = 5, SEM = 18.3), although the ratio of voluntary offer significantly increased from the previous "can see" condition in two individuals (Ayumu and Cleo; Fisher's exact test: $p < 0.05$, respectively). This increase in voluntary offer was likely due to a carry-over effect from the previous condition. The helper had possibly learnt that he/she was expected to offer an object to his/her partner in this new experimental condition.

As in the "can see" condition, the chimpanzees, except Pan, first offered potential tools (a stick or a straw) significantly more frequently than the other non-tool objects (Ai: 89.4%, Cleo: 88.9%, Pal: 100%, Ayumu: 93.0%; Fisher's exact test: $p < 0.01$ for each of these four participants with a chance level was set at 50%). Pan again showed a particular preference for offering a brush (55.3% of her first object offer); however, when we eliminated brush offer from the analysis, her offer of the potential

194 tools was also significantly above chance level (100%; Pearson Chi-square test: $p <$
195 0.01 with a chance level set at 50%).

196

197 The most important and suggestive difference between the "can see" and
198 "cannot see" conditions appeared when we examined which tool, a stick or a straw, the
199 chimpanzees offered first, and compared this between the two tool-use situations
200 presented in the partner's booth. Contrary to the "can see" condition, where we found a
201 significant difference in stick/straw choice depending on the partner's predicament,
202 such a difference disappeared in the "cannot see" condition in all participants except
203 one subject (see Table 1 for statistics). Ayumu was the only individual who selected the
204 appropriate tool even in the "cannot see" condition; he stood up and assessed his
205 partner's situation by peaking through the hole before selecting and transferring the
206 appropriate tool (Figure 3). Therefore, for Ayumu, the "cannot see" condition was
207 equivalent to the "can see" condition. However, the chimpanzees who did not visually
208 assess their partner's situation in the "cannot see" condition, failed to select and offer
209 the appropriate tool needed by their partner (Figure 2b; Video S2; see Table S1 for
210 individual details).

The chimpanzee helpers understood their partner's goals only when they could visually appreciate their partner's situation. Potential recipients performed request behavior similarly in form and frequency in the "cannot see" condition and in the "can see" condition (mean percentage of trials in which request was observed: "can see": 85.0% N = 5, SEM = 7.3; "cannot see": 71.3% N = 5, SEM = 18.1; paired t-test (two-tailed): $t = 1.1$, $df = 4$, $p = 0.35$). Therefore, chimpanzee request behavior on its own failed to convey any reliable information on the requester's specific needs, i.e. the appropriate tool needed. This means that, although request behavior might elicit the onset of chimpanzee helping, it is insufficient on its own for effective targeted helping. Ayumu's behavior, i.e. selecting and transferring the appropriate tool after assessing his partner's situation by peaking through the hole, further demonstrates that the chimpanzees depended on visual assessment of their partner's situation to acquire the necessary information to appropriately help their partner.

The second "Can see" condition

In order to confirm that the difference in appropriate tool selection between the two conditions (significant difference in the "can see" condition and non-significant in the following "cannot see" condition for three of the participants) was not due to the experimental order of the two conditions, we repeated the "can see" condition for these three participants. We observed object offer in 97.9% (N = 3, SEM = 0.93) of the trials, and upon-request offer accounted for 79.4% (N = 3, SEM = 3.2) of all offers. The three chimpanzees first offered potential tools (a stick or a straw) significantly more frequently than the other non-tool objects (Ai: 81.3%, Cleo: 95.7%, Pal: 100%; Fisher's exact test: $p < 0.01$ for each of these three participants with a chance level set at 50%). As in the first "can see" condition but not in the "cannot see" condition, we again confirmed a significant difference in the chimpanzees' choice, a stick or a straw, in their first offer between the partner's tool-use situations (Fisher's exact test: $p < 0.01$ for each of the three participants; see Table 1 for details). The three participants significantly more frequently selected and transferred a stick (or a straw) when their partner was confronted with the stick-use (or the straw-use) situation than when the partner was faced with the straw-use (or the stick-use) situation (Figure 2c; see Table S1 for individual details). This confirms that the chimpanzees demonstrated flexible targeted

helping with an understanding of which tool their partner needed when they could visually assess their partner's situation.

General Discussion

This study provides the empirical evidence for chimpanzees' flexible targeted helping based on an understanding of others' goals. When helpers could visually assess their partner's predicament, they appropriately selected out of seven objects an appropriate tool to transfer to their partner so he/she could obtain a reward. This kind of targeted helping is cognitively advanced; it is clearly neither a programmed behavior nor an automatic stimulus response. Even without shared intentionality and sophisticated communicative skills such as language or pointing, chimpanzees can understand others' goals when situations are visibly obvious and understandable.

The present study also offers novel insights into the cognitive mechanisms underlying helping behavior in chimpanzees. Firstly, chimpanzees are motivated to help others upon request even when they cannot properly assess the others' predicament. Our results show that even if visually prevented from understanding their partner's needs,

the chimpanzees persisted in helping their partner upon request, although their tool choice often failed to correspond to their partners' requirements (Video S2). Although Pan failed to choose an appropriate tool on first offer even in the "can see" condition, she persisted in offering objects to her partner upon request. It is clear that all chimpanzees, including Pan, were motivated to respond to their partner's request. Secondly, even when chimpanzees understand the needs of others, they seldom help others unless directly requested. Our results also suggest that chimpanzees are able to understand what others need by simply witnessing the situation. Therefore, the limitation in chimpanzees' voluntary helping (10-13,18-25) cannot solely be explained by a failure in understanding others' goals. Chimpanzees may not provide assistance to others unless requested in spite of being able to understand others' goals. Combining these two points, we suggest that both understanding of others' goals and detection of directed request are essential prerequisite in eliciting targeted helping in chimpanzees.

A crucial question for future research is to investigate similarities and differences in targeted helping and its mechanisms among humans, chimpanzees and other non-human animals. In humans, sometimes only observing others in trouble seems to suffice in prompting the onset of helping even without directed request (e.g.

279 spontaneous donation to disaster victims); however, the prevalence of this form of
280 helping in humans remains debated. A recent study on human toddlers' prosocial
281 behavior (30) revealed that 18-month-old infants helped an unfamiliar adult in trouble,
282 but required considerable communication from the adult about his/her needs.
283 Meanwhile, 30-month-old infants helped an adult more spontaneously, possibly due to
284 their acquired empathic abilities. The authors suggested that toddlers' helping develops
285 with their abilities to understand others' subjective internal states. The chimpanzees'
286 helping behavior in the present study was fairly similar to that of the 18-month-old
287 toddlers. However, our results showed that chimpanzees helped others upon request
288 even without proper knowledge of the others' needs, and also seldom helped others
289 unless being requested even when they understood the others' goals. In this respect,
290 humans and chimpanzees might differ in the onset mechanisms involved in prompting
291 helping behavior.

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293 It is still too early to make any firm conclusions on similarities and differences
294 in helping behavior and its mechanisms between humans and chimpanzees because of
295 the lack of proper and rigorous comparative studies. In previous studies with human
296 infants (10, 30), the experimenters (recipients of infants' helping) expressed their needs

not only by gesture but also using language. This might prevent direct comparison between humans and non-human animals. The previous studies also did not clearly distinguish expression of desire and demonstration of request directed toward the potential helpers, which confounds any evaluation of how the toddlers understood the others' goals. The present study proposes a rigorous potentially comparative methodology and novel perspectives for studying mechanisms of targeted helping. Further comparative studies with humans, chimpanzees, and other non-human animals, especially bonobos, who also demonstrate considerable helping and cooperative behavior (9, 31), will no doubt shed further light on the evolution of targeted helping.

Materials and Methods

Participants were socially housed chimpanzees at the Primate Research Institute, Kyoto University (KUPRI). All participants had previously taken part in a variety of perceptual and cognitive studies, including experiments which examined their helping behavior in a similar setting as the present study (12). We tested five chimpanzees paired with kin (two mothers Ai and Pan were paired with their offspring Ayumu and Pal respectively, and three juveniles Ayumu, Pal and Cleo were paired with

their mother Ai, Pan and Chloe respectively), since these kin pairs demonstrated frequent tool-giving interactions in previous experiments (12). All participants were experts at the two tool-use tasks presented in the current study. The present study was approved by the Animal Care Committee of the Primate Research Institute of Kyoto University, and the chimpanzees were tested and cared for in accordance with "the Guide for the Care and Use of Laboratory Primates, 2nd edition" produced by the ethics committee of the Primate Research Institute of Kyoto University (2002).

The paired chimpanzee participants were tested in two adjacent experimental booths (136 cm × 142 cm and 155 cm × 142 cm, 200 cm high). A hole (12.5 cm × 35 cm) in the panel-wall divider separating the two participants was located approximately 1m above the floor. Each participant acted as either a potential helper or a potential recipient. We set up one of either two tool-use situations (the stick-use situation or the straw-use situation) in the recipient's booth (for details see 12), and supplied in the helper's booth seven objects (a stick, a straw, a hose, a chain, a rope, a brush, and a belt) randomly presented on a tray (26cm × 36cm) (Figure 1). Only one of the seven objects (a stick or a straw) could serve as an effective tool to successfully obtain the juice reward under either tool-use situation. In order to ensure that the chimpanzees were

equally familiar with these seven objects, we carried out a familiarization phase of eight 5-min trials (one trial a day) prior to testing, where the participants could freely manipulate these objects in the experimental booth without any tool-use situation.

We developed two conditions: the "can see" condition (as the test) in which the panel wall between the two booths was transparent, and the "cannot see" condition (as the control) in which the panel wall was opaque. In the latter condition, helpers could not readily see which tool-use situation their partner was faced with, unless he/she purposely stood up and peaked through the hole. In either condition, chimpanzees could transfer objects or poke their arm through the hole. We first conducted 48 trials (random order of 24 trials of the stick-use and 24 trials of the straw-use situations) of the "can see" condition. Thereafter, we carried out 48 trials of the "cannot see" condition, and again 48 trials of the "can see" condition if participants' performance differed between the first "can see" and "cannot see" conditions. A trial started when we supplied the helper's booth with the tray loaded with the seven objects, and ended either when the recipient succeeded in obtaining the juice reward upon being offered the appropriate tool, or when 5 minutes had passed without appropriate tool transfer. We conducted two or four trials per day.

We recorded the participants' behaviors and interactions with three video cameras (Panasonic NV-GS150), and analyzed what object the helper offered the recipient (see also 12). We counted a helper's "offer" when a participant held out a tool towards a recipient, whether the recipient actually received it or not. Only the helper's first offer was retained for analysis. We categorized object offer into two types: ''upon-request offer'' and ''voluntary offer''. In upon-request offer, the giver offered a tool to the recipient upon the recipient's request. In voluntary offer, the giver actively offered a tool to the recipient without the recipient's explicit request. When a tool was taken away by the recipient without owner's offer (tolerated-theft transfer), this transfer was categorized as "no offer". We counted a recipient's "request" when the recipient poked an arm through the hole. We used paired t-test (two-tailed) to compare the chimpanzees' averaged performance between the two experimental conditions, and Fisher's exact test (two-tailed) to individually compare the rates of a helper's performance between two categorical variables.

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445

Figure Legends

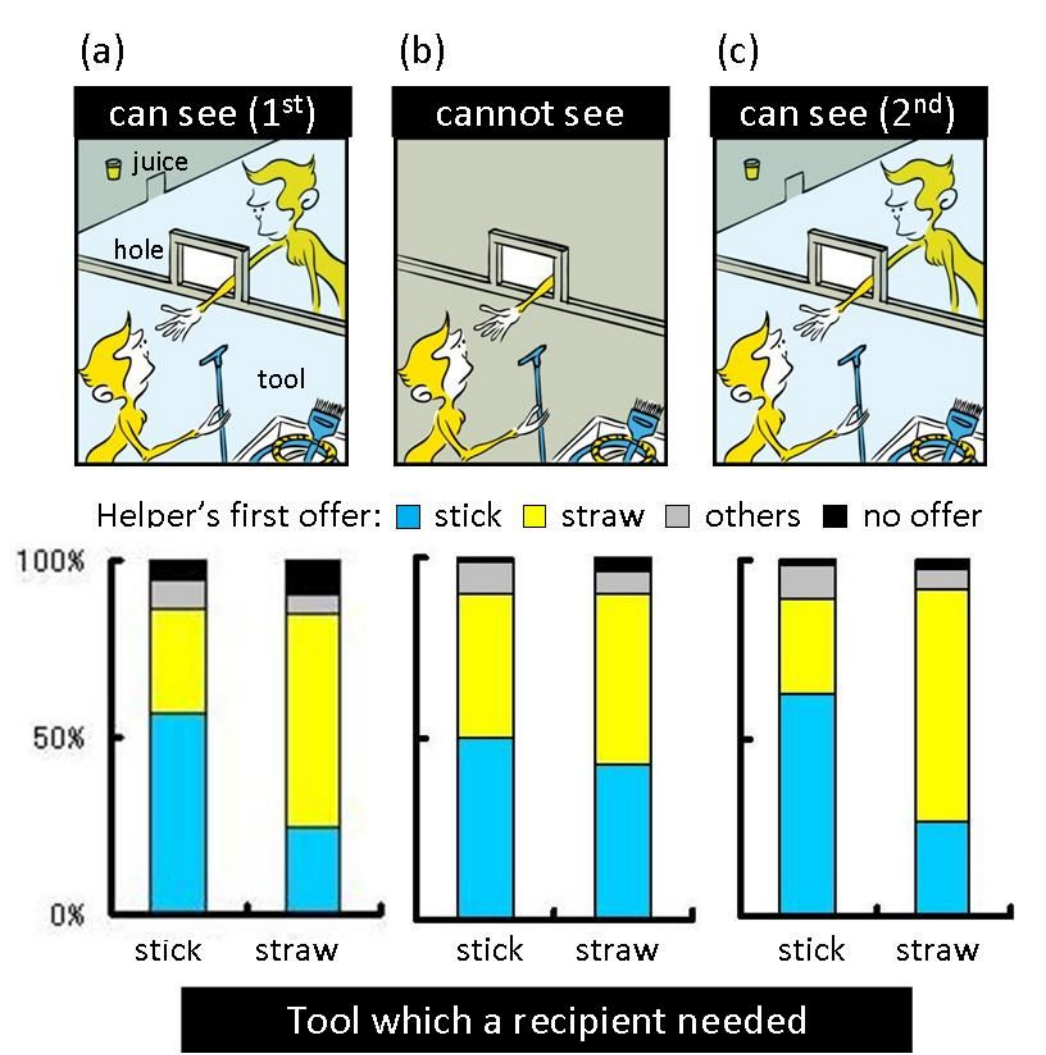
Figure 1. Tool set consisting of seven objects which was supplied to a potential helper. Only one of them (a stick or a straw) was needed for a conspecific to solve either a stick-use or straw-use task in the adjoining booth.

Figure 2. Helpers' first tool selection and offer to their conspecific partner. Each condition ("Can See" or "Cannot See") presented participants in the recipient booth with one of either two tool-use situations (“stick” or “straw”). These graphs were based on the data from three participants (Ai, Cleo and Pal) who completed all the conditions based on an A-B-A design. For the statistical analysis, see Table 1.

Figure 3. Ayumu stood up and assessed his mother’s situation by peaking through the hole in the opaque panel wall separating the two booths. He was the only one to assess so actively his partner’s situation, and to select and transfer the appropriate tool to his partner in the “cannot see” condition.

Table 1. P values of Fisher's exact test (two-tailed) comparing each participant's first offer ratio of stick and straw tools between the two tool-use situations presented in the recipient's booth. Values highlighted in grey indicate a significant difference ($P < 0.05$).

	Can see (1st)	Cannot see	Can see (2nd)
Ai	**0.015**	**0.54**	**0.008**
Cleo	**0.031**	**0.61**	**< 0.001**
Pal	**0.008**	**0.084**	**0.002**
Ayumu	**0.004**	**< 0.001**	—
Pan	**0.48**	**0.44**	—


(a)
(b)
(c)
can see (1st)
cannot see
can see (2nd)
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Helper's first offer: stick straw others no offer
100%
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stick
straw
stick
straw
Tool which a recipient needed


Ayumu