Chimpanzee social cognition

Josep Call

In the late 1970s, Premack and Woodruff asked whether chimpanzees had a theory of mind. The answer to this question has remained elusive. Whereas some authors argue that chimpanzees are capable of mental state attribution, others maintain that they simply learn certain cues in ertain situations. Recent studies challenge both views. On the one hand, chimpanzees know much more about seeing than cue-based explanations suggest; on the other hand, this knowledge does not necessarily entail understanding of the mental states of others. The hypothesis I put forward here is that chimpanzees learn cues in social situations but that they are also capable of knowledge abstraction to solve novel problems.

Since the late 1970s, cognitive approaches to the study of animal behavior have attracted increasing research attention. One of the fields in which this 'cognitive revolution' has been particularly stimulating is social behavior (see papers in Refs 1 and 2), and in particular the interaction of social partners. One of the major challenges offered by social partners resides in their reactive nature. Social partners and living prey, unlike fruit on a tree, not only react to an individual's behavior but also behave spontaneously. Thus, one important skill in both cooperative and competitive situations is the ability to predict and anticipate the behavior of conspecifics[3]. Animals that can predict the behavior of their conspecifics quickly and accurately (i.e. are more 'moves ahead' than their conspecifics) – and especially those animals that can predict in novel situations – will have a clear advantage over animals that do not have this skill. Therefore, cognitive mechanisms that make faster, deeper and novel predictions possible would be especially favored in those species with a complex social environment.

Despite its importance, the mechanisms implicated in behavioral prediction are currently poorly understood. In general, two classes of mechanism have been proposed: (1) the cue-based approach, in which individuals learn to respond in certain ways to particular situations, albeit with little understanding of the phenomena and a limited ability to solve novel problems without re-learning each problem[4,5]; and (2) the knowledge-based approach, in which animals not only learn to associate some stimuli with certain responses but also to extract the relationships between stimuli and therefore form general rules that disregard the specific stimuli involved. The gist of this approach is that solving social problems involves the formation of knowledge that allows individuals to predict the behavior of others in novel situations.

In this paper I will argue that the cue-based mechanism is insufficient to explain the variety of social interactions observed in some animals. Instead, I will argue that a knowledge-based mechanism fits the data more closely. I will use two main arguments to support this position. First, I will present some of our recent studies on what chimpanzees know about the visual perception of their conspecifics. Second, I will use an analogy with physical cognition in which there is ample evidence for knowledge-based mechanisms. I will conclude by presenting the basic points of the knowledge-based approach, comparing it with other approaches and discussing some unresolved issues.

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What chimpanzees know about seeing

Tomasello *et al.* found that chimpanzees tended to use visual (but not auditory or tactile) gestures when recipients were looking at them[6,7] (Box 1). This result led us to investigate the understanding of visual perception in others with two additional paradigms: gaze-following and social competition.

First, we found that chimpanzees followed the head direction of both humans and conspecifics to targets located above and behind the subject[8,9], thus replicating previous studies on this topic[10,11]. Recent studies have also shown that monkeys and apes are capable of picking up information about eye direction independently from head direction[12–14]. Additional studies showed that gaze-following could not simply be explained as a low level mechanism of the type 'turn in the direction in which others are oriented and then search until you find something interesting' as postulated by Povinelli and Eddy[11]. In particular, Tomasello *et al.* showed that chimpanzees followed gaze around barriers of different types by moving to new locations where they could see what was behind the barriers – seemingly to see what the experimenter was looking at[15]. More importantly, chimpanzees who saw a human experimenter looking above and behind them ignored a distractor object that was presented to them when they turned and continued to track the human's gaze to the back of the cage. Also, Call *et al.* found that upon following human gaze and not finding any interesting sight (just the ceiling of the cage), chimpanzees looked back at the experimenter, presumably to ascertain if they were looking at the same location[8]. These results are incompatible with a low-level explanation and suggest that chimpanzees understand that their informants are looking at something specific in a particular location.

Second, we probed further the ability of chimpanzees to infer what other chimpanzees can and cannot see by using a social competition paradigm[16]. Menzel pioneered the use of competitive situations to investigate social tactics and deception in chimpanzees and found that a subordinate chimpanzee learned to avoid taking hidden food in the presence of a dominant

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Box 1. Chimpanzee gestural communication

Young chimpanzees use around 30 gestures to communicate with groupmates in various contexts[a,b]. For instance, they extend their arm to beg for food, slap the ground to call attention to themselves and put their arm around their mother's back to ask to travel to a different location. These gestures fall within three basic sensory modalities: visual, auditory and tactile (Fig. I). Visual gestures rely solely on visual information; auditory gestures rely mainly on sound production and tactile gestures depend mainly on establishing physical contact with the recipient (e.g. arm on the mother; Fig. I). Tomasello *et al.* found that chimpanzees use gestures from these three sensory modalities differentially, depending on the spatial orientation of the recipient[a,b]. In particular, young chimpanzees use visual gestures preferentially when the recipient is looking at them. In contrast, auditory, and especially tactile, gestures are used regardless of the attentional state of the recipient. One possible conclusion from these data is that chimpanzees know that if their visually based gestures are to work, others must see them.

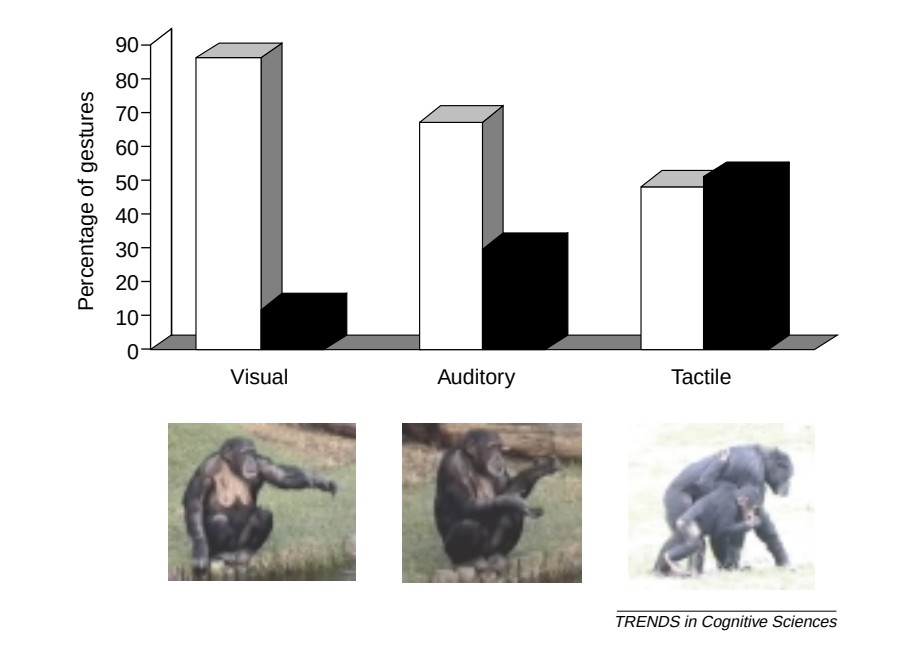

Fig. I. Mean percentage of gestures in each of three sensory modalities used by young chimpanzees ($n = 20$) as a function of the attentional state of the recipient. Open bars, the recipient is looking; black bars, recipient is not looking.

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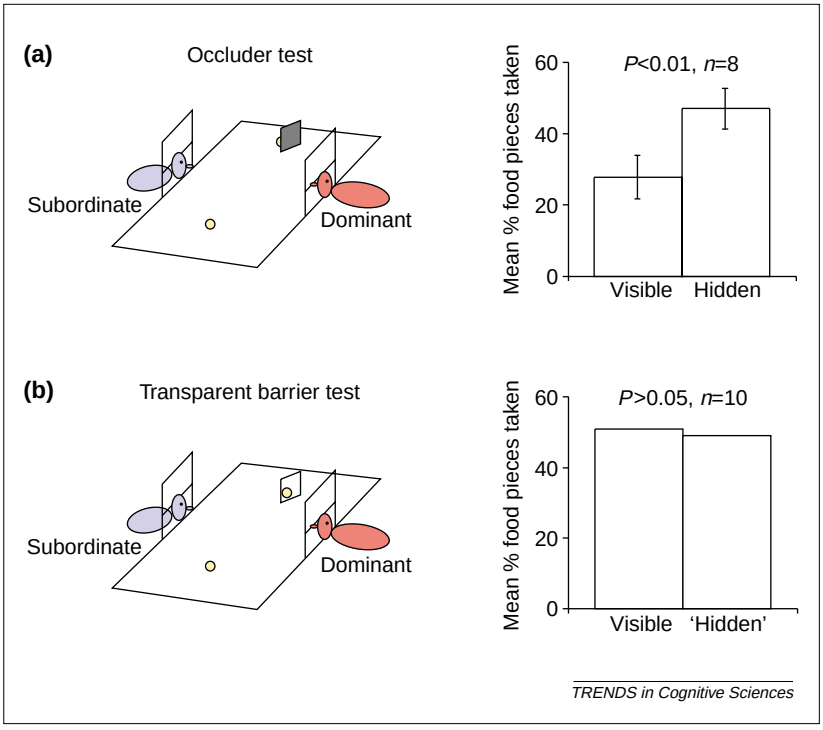

Fig. 1. Mean percentage of pieces of food retrieved by subordinate chimpanzees as a function of whether food pieces could be seen by the dominant chimpanzee. In the occluder test (a) one of the pieces of food is hidden from the dominant chimpanzee, and this increases the likelihood of its being retrieved in preference to the visible piece. When both pieces of food can be seen by the dominant animal (b), there is no difference in retrieval percentage.

animal[17,18]. In our studies, we investigated how subordinate–dominant pairs of chimpanzees competed over two pieces of food placed in a cage.

We placed a subordinate and a dominant individual in two rooms on opposite sides of a third room. In the occluder test, we placed two food pieces and an opaque barrier in this third room so that the subordinate was able to see both food pieces whereas the dominant was able to see only one (and the opaque barrier). We let both individuals enter the room and observed who took which pieces of food. We gave subordinates a small head start so that they would make a choice before they saw where the dominant animal was going. Subordinates took significantly more pieces that were hidden from the dominant animal than visible pieces. In the transparent barrier test, we replaced the opaque barrier with a transparent barrier and found that subordinates' preference for hidden pieces disappeared, presumably because they knew that the transparent barrier did not block the dominant's visual access to the food (Fig. 1).

In the uninformed test, we used two opaque barriers and a piece of food placed behind one of the barriers on the subordinate's side. The subordinate witnessed the baiting and saw that we kept the dominant's door closed. Then we released the subordinate and observed whether she approached and/or took the food. We compared this condition with a control condition (not

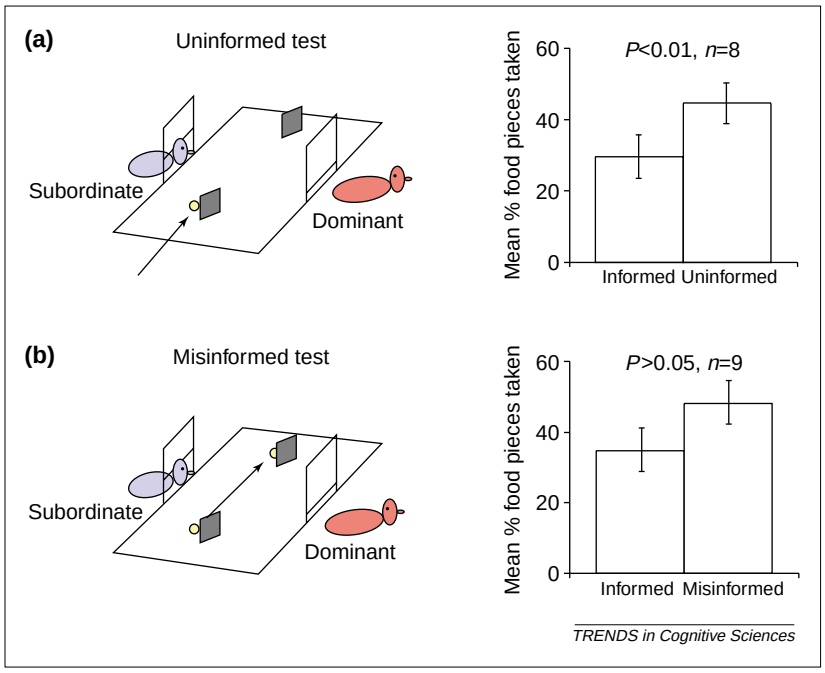

Fig. 2. Mean percentage of pieces of food retrieved by subordinate chimpanzees as a function of whether the dominant chimpanzee had witnessed the baiting process. When the dominant had not witnessed the baiting process, either by being uninformed (a) or being misinformed (b), the subordinate was more likely to retrieve the food item.

depicted) in which the dominant was allowed to witness the baiting procedure.

In the misinformed test we placed a piece of food behind an opaque barrier on the subordinate's side while both subjects watched. Once the food was behind the barrier, we closed the dominant's door and moved the food piece to behind the second opaque barrier, still on the subordinate's side. We released the subordinate and observed whether she approached and/or took the food. We compared this condition with a control condition (not depicted) in which the dominant witnessed the food being moved behind the second barrier.

In both the uninformed and misinformed conditions, subordinates took more food than in their respective control conditions, seemingly because they knew that dominants were either not informed or misinformed about the food location. Moreover, subordinates in the uninformed condition entered the room more often than in the control condition (Fig. 2).

In the dominant switch test, we adapted the uninformed test setup to include the subordinate and two dominant animals. In the switch condition, we placed a piece of food behind an opaque barrier on the subordinate's side, allowing one of the dominants and the subordinate animal to witness the baiting. We then closed both doors and exchanged the dominant who had witnessed the baiting for a naïve dominant. We compared this condition with a control condition in which the dominant was not exchanged. We released the subordinate first, after they had seen who the dominant was. Subordinates took significantly more food in the 'switch' condition than in the control condition, presumably because they knew that the new dominant had not witnessed the baiting (Fig. 3).

These experiments showed that subordinates preferentially approached and took those pieces of food that were hidden (behind a barrier) from the dominant. Control tests ruled out the possibility that subordinates were using either behavioral cues from the dominant (e.g. its mere presence or intention movements) or contextual cues (e.g. perhaps the piece in front of the barrier looked as if it was closer). Also, when we replaced the opaque barrier with a transparent barrier that did not prevent the dominant's visual access to the food behind the barrier, we found that the subordinates' preference for the 'hidden' piece of food disappeared, seemingly because they recognized that the transparent barrier was not serving to block the dominant's visual access to the food. This situation is particularly important because it represented a novel situation for these chimpanzees, who had not encountered transparent barriers before when competing with conspecifics.

The experiments also investigated whether chimpanzees were able to take into account past information, such as whether the dominant had seen the baiting[19]. We found that subordinates preferentially retrieved and approached food that dominants had not seen hidden or moved, which suggests that they were sensitive to what dominants had or had not seen during baiting. In an additional experiment, where the dominant who had witnessed the baiting was switched for another dominant who had not witnessed the baiting (compared with a situation in which the dominant was not switched), our results indicated that subordinates retrieved more food when the dominant had been switched than when she was not switched, thus demonstrating subordinates' ability to keep track of precisely who had witnessed what. This result ruled out the possibility that subordinates were using just the sequence of door opening and closing to decide which food to take and suggests that chimpanzees have the ability to represent what their competitors can or cannot see.

To summarize, our studies on chimpanzee gestural communication, gaze-following and food competition reveal that, in some situations, chimpanzees know much more about seeing than recent analyses[5,11,20] have suggested and supports previous claims of chimpanzee (and ape) sophistication in this domain[21–23]. The ability of chimpanzees to respond appropriately in these various domains after: (1) removing behavioral and contextual cues; (2) adding distractors; and – more importantly – (3) presenting novel problems, suggest that they are doing more than learning to associate certain behavioral or contextual cues with certain responses. Instead, they suggest that chimpanzees can extract knowledge from their experiences and use this knowledge to solve social problems.

Physical and social problem solving

The second argument I will put forward in favor of a knowledge-based approach in social cognition is based on an analogy with physical cognition. Unlike the field of comparative social cognition, the field of comparative physical cognition has produced many studies showing that animals not only learn certain

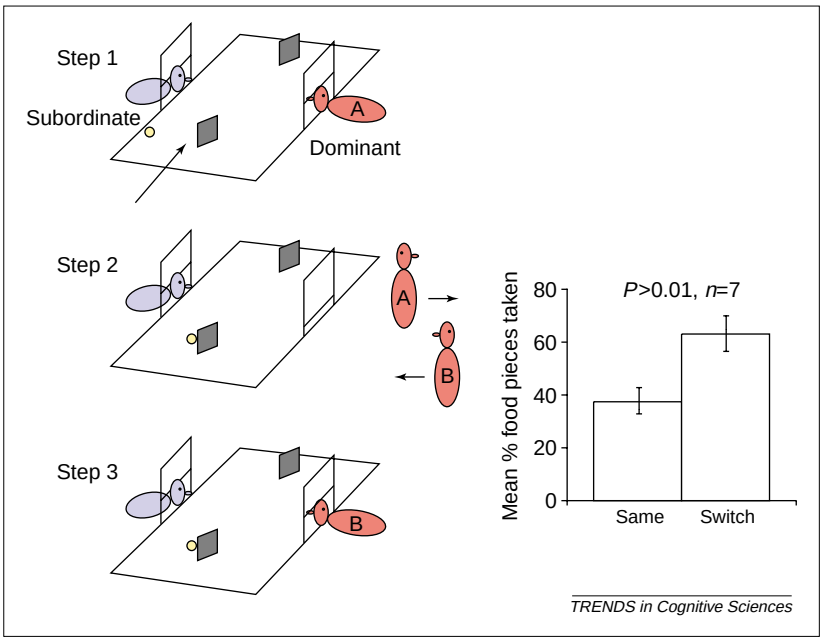

Fig. 3. Mean percentage of pieces of food retrieved by subordinate chimpanzees as a function of whether the dominant chimpanzee who witnessed the baiting process was the same one who competed over the food with the subordinate (an adaptation of the 'uninformed' test of Fig. 2). When the dominant animal was switched (Steps 2 and 3) the subordinate was more likely to retrieve the food. This suggests that the subordinate is able to represent what its competitors can or cannot see.

stimulus–response connections but that they can extract some rules, categories and knowledge that go beyond the information available. For instance, dolphins, sea lions, corvids, parrots and primates are capable of various types of relational categories such as oddity or sameness–difference problems[24–27]. Squirrel monkeys and chimpanzees can discriminate between pairs of stimuli that represent the same (or a different) relationship to a sample stimulus[28–30]. Sea lions, pigeons and primates show some evidence of stimulus equivalence[31–33]. Chimpanzees, sea lions and monkeys can solve transitivity and ordinality problems[34–37]. Many species can categorize stimuli based on perceptual features[24,26,38,39] and chimpanzees can categorize based on functional rather than perceptual features[40]. Finally, chimpanzees, squirrel monkeys and pigeons can mentally combine symbols representing quantities to either designate the total sum or net the largest amount[41–43].

All these experiments represent, in one form or another, examples in which performance cannot be explained simply by invoking associations between familiar stimuli because they involved the presentation of novel pairs of stimuli or situations not encountered before. Instead, they strongly suggest that subjects operate on general rules that disregard the specific stimuli involved, that they extract the relationship between stimuli or that they operate mentally on arbitrary symbols. Rumbaugh *et al.* have eloquently invoked the notion of 'emergents' to account for the varied and good performance of subjects in these novel situations for which they were not specifically trained[44]. These authors argue that emergents are a property of complex nervous systems and that, unlike traditional learning mechanisms such as operant and classical conditioning, they represent solutions that appear without specific training.

If emergents, or 'knowledge' as I prefer to call it, are found in physical cognition, it is very likely that they can also be found in social cognition. The main reason for their not being as well known in the social as in the physical domain is because comparative social cognition is still in its infancy. Nevertheless, as discussed above, in areas such as visual perception in chimpanzees, and in vocal communication, we are beginning to accumulate enough evidence to indicate that cues are insufficient to account for the observed phenomena. More research will surely uncover these skills in the social domain.

A knowledge-based social cognition

The ability of chimpanzees to solve problems about visual perception in others, and the vast literature on physical cognition in animals, support the notion that chimpanzees (and possibly other animals) might use knowledge to solve social problems, rather than merely learning to respond to specific cues. Whiten has used the concept of the 'intervening variable', an idea that is closely related to the concept of knowledge presented here, to discuss the issue of 'mind reading' in animals[45,46]. Whiten argues that rather than postulate a one-to-one correspondence between sets of stimuli and responses, another possibility is that a set of stimuli produces a common intervening state, and that this in turn regulates the various responses. For instance, chimpanzees would not merely learn to respond in certain ways to certain types of barrier but would also develop an intervening variable about their conspecific's perceptual (or mental) experience. This would be a more economical model – with fewer links between potential stimuli and responses than a model postulating a one-to-one correspondence between stimuli–responses sets.

Whiten's idea fits well with the current proposal because both models postulate an intermediate state between stimulus and response. However, they differ on the nature of this intermediate state. Whiten favors a kind of meta-representational account[47], that is, chimpanzees could attribute knowledge to their partners. However, we think that another knowledge-based explanation is possible. We have called it 'an explanation of the third kind' (Refs 26 and 48) or representational account[49], to differentiate it from various types of cue-based explanation on the one hand and various types of meta-representational explanation on the other[50] (Box 2). Like the meta-representational account, but unlike the cue-based explanation, this third way maintains that social problem solving is based on using knowledge. However, the two knowledge-based mechanisms differ in the nature of this knowledge. Although the representational account accepts that individuals could have a notion of seeing in others, it does not postulate any insight into the subjective experience of seeing in others. By contrast, this insight into the subjective experience of others is a key component of the meta-representational account. One way to describe this third way is to present it as the social counterpart of insight into physical problems. Some animals have insight into some social problems, which enables them to develop intelligent problem-solving strategies, especially in novel situations. But

Box 2. Three families of mechanisms in social problem solving

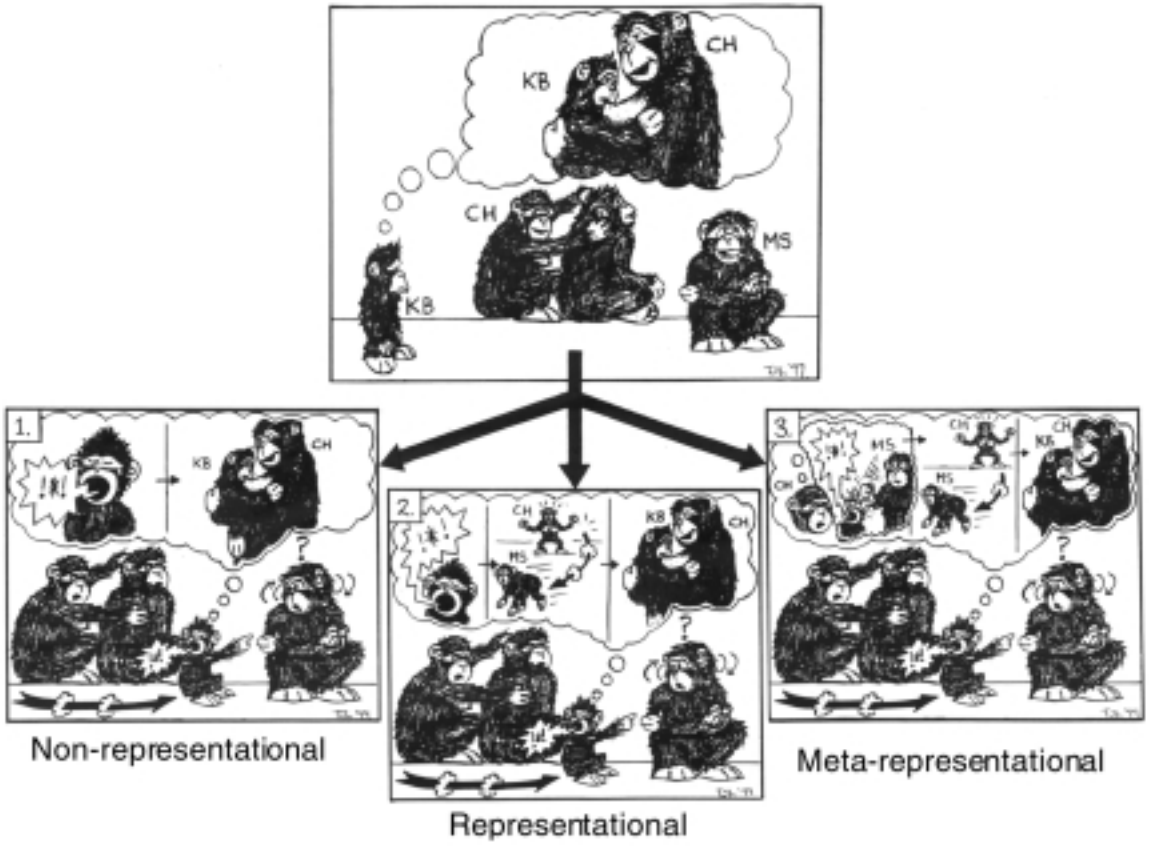

Fig. I. The upper vignette depicts a juvenile chimpanzee (KB) with a problem. He wants to nurse but his mother (CH) refuses him repeatedly, preferring instead to groom an adult male. KB's solution, depicted in the bottom vignettes, consists of using gestures and vocalizations to convey a non-existent attack by an adolescent chimpanzee (MS)[f]. These bottom vignettes depict the three families of mechanism that have been postulated to explain social problem solving of this sort in chimpanzees.

The mechanisms proposed to explain the basis of social complexity can be grouped into three families, depending on the type of representation bestowed on individuals. The main feature of each family is outlined here, together with an example illustrating each (Fig. I) (see Refs a–e for additional information on particular mechanisms). Nishida observed a juvenile chimpanzee (KB) who wanted to nurse but whose mother (CH) refused him repeatedly, preferring instead to groom an adult male[f]. KB used gestures and vocalizations to convey a non-existent attack by an adolescent chimpanzee (MS) in order to get access to his mother's nipple. At least three families of mechanisms can be postulated to explain this behavior:

(1) Non-representational: this mechanism is based on forming an association between screaming and getting access to the nipple in similar situations without access to the causal links between events. For instance, the juvenile screams because in similar situations this behavior has produced the desired outcome.

(2) Representational: this mechanism entails recalling past experiences and combining them in novel situations so that creative problem-solving, rather than just a history of reinforcement, is responsible for the solution to the problem. For instance, the juvenile knows that he has to make his mother approach and comfort him to gain access to the nipple. He also knows that: (1) if an adolescent threatens him and he screams, his mother will protect and comfort him; and (2) once his mother is comforting him, he will have access to the nipple.

(3) Meta-representational: this mechanism is based not only on representing the solutions to problems but also on representing the mental states (such as desires, knowledge and beliefs) of others. For instance, the juvenile knows that: (1) if he screams and there is an adolescent male nearby his mother will *believe* that the adolescent male attacked him; (2) if his mother believes that he is being attacked she will come to rescue and comfort him, which will give him access to the nipple.

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this does not necessarily mean that they also have the ability to imagine the visual experience of others or to understand that the beliefs others hold about things might differ from their own and from reality.

In conclusion, our working hypothesis is that some social interactions in some animals such as chimpanzees are regulated by knowledge about their social environment. This claim is based on some initial evidence on chimpanzee understanding of visual perception in others and a vast body of literature in physical cognition. It is important to emphasize that this knowledge-based approach is not totally opposed to the cue-based approach; it simply incorporates the latter. Animals in social situations (e.g. non-social situations) learn about cues but, in addition, they are capable of abstracting knowledge from those situations. Future studies will have to investigate how widespread social knowledge is across species and determine the nature and acquisition of this knowledge.

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