The psychology of primate cooperation and competition: A call for realigning research agendas

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Abstract

Cooperation and competition are two key components of social life. Current research agendas investigating the psychological underpinnings of competition and cooperation in non-human primates are misaligned. The majority of work on competition has been done in the context of theory of mind and deception, while work on cooperation has mostly focused on collaboration and helping. The current impression that theory of mind is not necessarily implicated in cooperative activities and that helping could not be an integral part of competition might therefore be rather misleading. Furthermore, theory of mind research has mainly focused on cognitive aspects like the type of stimuli controlling responses, the nature of representation and how those representations are acquired, while collaboration and helping have focused primarily on motivational aspects like prosociality, common goals, and a sense of justice and other-regarding concerns. We present the current state of these two bodies of research paying special attention to how they have developed and diverged over the years. We propose potential directions to realign the research agendas to investigate the psychological underpinnings of cooperation and competition in primates and other animals.

Keywords: social cognition, collaboration, mindreading, social preferences, primates

Introduction

Cooperation and competition are two key components of social life. Coalitions and alliances represent the quintessential example illustrating how individuals simultaneously compete against some group members and cooperate with others [1-3]. Since many social species such as primates, hyenas, coatis, dolphins and corvids typically interact with multiple partners over extended periods of time, keeping track of friends and foes (for both oneself and other group members) can become a quite challenging enterprise. In fact, it is precisely this fluid state of affairs that constitutes one of the main reasons why social life is thought to be particularly complex, and why some authors placed a particular emphasis on social as opposed to non-social aspects to explain the evolution of cognition (e.g. [4, 5]).

Further elaboration of this idea led Whiten and Byrne [6] to focus on the tactics deployed by primates to cooperate and compete with others, the so-called Machiavellian Intelligence hypothesis, whereas Dunbar's [7, 8] Social Brain hypothesis focused on keeping track of social relations. Those hypotheses, with cooperation and competition at their core, were instrumental in setting up the stage to investigate in greater detail the psychological processes underlying cooperation and competition in primates and other animals. However, the way researchers have investigated the psychology of cooperation and competition is quite different, so different that one can speak about misaligned research agendas. Whereas work on competition has mainly been studied in the context of theory of mind and deception, work on cooperation has focused on collaboration and helping. Such dissociation can be misleading because it may give the impression that theory of mind is not implicated in cooperative activities and conversely, that helping could not be an integral part of competition.

More importantly, the psychological aspects investigated with regard to competition and cooperation differ substantially. Whereas theory of mind has focused on cognitive aspects, things like the type of stimuli controlling responses [9], the nature of representation [10] and how those representations are acquired [11], collaboration and helping have focused primarily on motivational aspects. More precisely, those studies have focused on whether individuals behave prosocially towards others [12], can work together for common goals [13], and have a sense of justice [14, 15] and concern for the needs of others [16]. In this chapter we will present these two bodies of research emphasizing how they have developed and diverged over the years. Although our review will concentrate on primates (mainly chimpanzees since the most elaborated work has been done on them), we will include work on non-primates whenever possible. In the last part of this chapter we will propose how to realign the research agendas aimed at investigating the psychological underpinnings of cooperation and competition.

Mindreading

The onset of research on theory of mind is easy to pinpoint: Premack and Woodruff's [17] seminal paper and the commentaries that accompanied it. Premack and Woodruff reported a set of provocative findings about a chimpanzee seemingly attributing intentions to a human solving physical problems. Several commentators challenged these findings both on theoretical and empirical grounds thus launching a debate that continues to this day fuelled by new empirical findings and additional alternative interpretations (see [18]). Whereas some argue that there is no evidence of theory of mind, others think that there is evidence of some aspects of theory of mind [19-21]. These disagreements, however, should not obscure the fact that real progress has taken place in this area over the years. Although not all questions have been answered to everyone's satisfaction, it is uncontroversial that some of the interpretations that were tenable a few years ago are no longer viable as explanations for some of the existing data. Let us review some of this evidence.

Throughout the 1980's and 90's, most non-human primate studies on theory of mind abilities were based on equivalent studies with human children with methodologies in cooperative contexts (e.g. [22-25]). The cooperative/communicative paradigm with humans invariably required long training regimes and produced not much convincing evidence for mindreading skills in non-human primates (see [26, 27] for reviews). Hare et al.'s [28] study marked a turning point in how mindreading experiments were conducted with primates and other species including dogs, goats and ravens [29]. These authors abandoned the information donation paradigm based on gesture comprehension that had dominated the previous decade and placed pairs of chimpanzees in a competitive situation. Subordinate chimpanzees could outsmart dominant individuals in a food competition game only if they could assess what dominant individuals could and could not see. The results differed considerably from those from previous studies. Subordinates preferred to take those food pieces that dominants could not see, and they did so spontaneously without any training. Results of this and subsequent studies suggested that chimpanzees and some other species know what others can and cannot see and hear, and also who has seen what in the past (see [30-33]). Crockford et al. [31] study is particularly important for two reasons. First, it confirmed that chimpanzees keep track of 'who has seen what' in a field experiment. The authors found that chimpanzees were more likely to produce a snake alarm call upon encountering a snake when their potential audience were unaware of the snake's presence. Second, unlike most other studies reporting positive evidence of mindreading in animals, this study used a cooperative (i.e., donating information) rather than a competitive situation.

Nevertheless, these findings were open to alternative interpretations. Povinelli and colleagues (e.g. [9, 19, 34, 35]) argued that chimpanzees did not really attribute mental states to others, they read their behaviour and had learned (or were predisposed) to behave in appropriate ways. However, some of their proposed explanations were ruled out quite quickly with additional data. For instance, Hare et al. [36] showed that chimpanzees responded to the face orientation of competitors, not just body orientation. Also Hare et al. [37] demonstrated that Hare et al.'s [28] original findings were not simply a result of chimpanzees preferring to take pieces in the vicinity of barriers. Other explanations, however, were not so easily ruled out by those data.

Most notably among them was the so-called evil eye hypothesis, i.e., individuals avoid food pieces that have been seen by others. Or put in behavioural reading terms, the observable cue that chimpanzees might have used was based on a geometric appreciation of the line of sight between the competitor and the food. Note that geometric gaze following has been described in primates and corvids [38-40]. Applied to the competitive case, it meant that if the competitor’s line of sight to the food’s current location was not blocked by any visual barrier, then the individual should refrain from approaching/selecting that food. Leaving aside the fact that such a computation already involves a certain kind of perspective-taking (see [10]), a kind of direct perceptual perspective-taking at the very least, and that in some experiments it requires the subject to keep a memory of the event tied to a particular individual (e.g. [37]), it is true that this explanation alone could account for many of the existing findings. However, in the last few years several studies have appeared that make this explanation untenable. We turn to this evidence next.

Schmelz et al. [41] directly addressed the evil eye hypothesis by preventing the subject from seeing the competitor seeing the food and thus completely eliminating any possible cues for the subjects during the study. Schmelz and colleagues [41, 42] adopted Kaminski et al.'s [43] paradigm in which pairs of chimpanzees competed by taking turns in selecting containers where food was hidden, but improved it in two important ways. First, they added non-social controls that were procedurally identical to the experimental conditions with the only difference that no competitor was present in the opposite cage. Second, although the subject knew whenever a competitor was present, they did not see each other at all during testing. Subjects therefore had no chance of reading behavioural cues from the competitor and had to infer the competitor's choice.

In one study [41], there was a hole on one side of the sliding platform that only the subject knew about. While the competitor's view to the platform and the subject was blocked, the subject observed the baiting of one food item placed inside that hole, covered by a plastic board resting flat on the platform, and another identical food item on the other side of the platform with an identical plastic board leaning against it and therefore acquiring a slant. Afterwards, her view of the platform was blocked too. If the subject could then choose first (and also in the non-social controls), she had no reason to prefer one side as there was identical food on both. However, if she could only choose after the competitor, she had to think about which side the competitor had already chosen. The subject had to consider that from the competitor's point of view there were two plastic boards (one flat, one slanted) and that the competitor was unaware about the hole in the platform. The competitor could therefore only infer the presence of food under the slanted board. If the subject understood this, she should avoid that side when she chose after the competitor, which is what she did compared to all other conditions, thus suggesting that chimpanzees knew that others make inferences. Behavioural reading and associative learning cannot easily explain this finding.

One thing was problematic though. Subjects selected the slanted board 50% of the time in the social condition when they selected after the competitor, which may indicate indifference between the two options. In a second study [42] when the competitor chose one food location, the piece of food was not actually removed but remained there. Therefore, whatever the subject chose, she was non-differentially rewarded in every condition, completely ruling out any possibility for associative learning. In this study, the two food locations were boxes with pictures: one picture of ten food pellets, the other one empty. All subjects had shown a strong preference for the food picture in a pre-test when they did not know what was actually inside the box. In the test, subjects observed the baiting while the competitor's view was blocked and saw that there was identical food in both boxes. Again there were three control conditions, one in which the subject could choose before the competitor and the two corresponding non-social conditions with no competitor present. Subjects chose the box with the food picture less than expected by chance only in the condition in which the competitor had chosen before them, thus avoiding the same box they had preferred in the pre-test. This suggests that they inferred that the competitor (that had not seen the baiting) would share their own preference for the box with the food picture and avoided it afterwards under the assumption that it was already chosen. Learning and behavioural reading were ruled out to be potential explanations in this paradigm.

This second study established two things. First, it confirmed the pattern of results from the previous study using different stimuli. Second, it showed that preference rather than an inference could explain the results. Subjects seemed to attribute to others their own preferences and chose the opposite when they chose second. Nevertheless, such a result is interesting because it informs us that individuals may make inferences about others based on their own preferences. Could this also be extrapolated to others’ perceptions and knowledge? Are the inferences that subjects make about others’ mental states also grounded on their own mental states? How individuals come to attribute perception and knowledge has been a topic of much discussion in the literature and some have argued that only by showing an extrapolation from self-experience to others one can be sure that individuals are attributing mental states rather than using observable cues or behavioural rules. If I have experienced a seemingly opaque barrier to be in reality transparent, will I also attribute this mistaken perception to others? This idea is precisely the basis of the so-called "goggles experiment" [19, 44, 45]. A subject is initially exposed to two pairs of dark goggles that only differ in rim colour. Once she wears them though, she also discovers another interesting feature. Whereas one can see through one of the goggles, the others are completely opaque and one cannot see through them. Would this individual who has experienced the properties of these goggles attribute seeing or not seeing to another individual who is wearing one or the other? This elegant test, however, has been notoriously difficult to implement for practical reasons. Chimpanzees do not typically wear goggles and using begging to request from one or another experimenter has not proven a very fruitful method.

Karg et al. [46] have recently implemented a version of the googles experiment by capitalizing on the competitive task developed by Hare et al. [36] a few years earlier and a recent study on human infants that used blindfolds to test this same question [47]. Here, there were two boxes on either side of the experimenter who was facing the subject in front of her cage. Before the test, the experimenter established a competitive situation such that she put food inside these boxes and whenever the subject tried to reach inside one to grab the food and the experimenter could see it, she withdrew and removed it. In the test proper, two lids of these boxes were introduced; one was a see-through flyscreen while the other one was opaque. While both were in an upright position, the subject could experience the properties of the lids when the experimenter moved food behind them. Then the lids were closed over the two boxes in such a way that from the point of view of the subject, both lids now looked identically opaque. However, from the point of view of the experimenter the screen was transparent while the other lid was opaque. Both boxes were baited with identical food and the chimpanzee subject could then reach inside one of them to obtain the food reward. In order to be successful, the subject had to understand the perspective of the experimenter and avoid the side of the transparent screen, even though both lids looked identical from the subject's current point of view. In a control condition, there was a transparent lid instead of the screen that remained transparent from the point of view of the subject at all times. In another non-social control, the chimpanzee could again choose between the screen and the opaque side but the human competitor had left the apparatus before so that there was no reason to avoid the side of the screen. Results showed that the chimpanzee subjects made no difference between the screen condition and the fully transparent condition and chose the opaque side more than expected by chance in these conditions but chose randomly in the non-social control condition. This suggests that chimpanzees understood the perspective of the human competitor and passed the well-known "goggles experiment". Again this skill was shown in a competitive context.

Despite all this progress in methodology and evidence for several aspects of mindreading in chimpanzees, positive evidence for the one task generally considered to be the benchmark of a full-fledged theory of mind – the false belief test – is absent. The well-established paradigms of Hare et al. [37] and Kaminski et al. [43] found little, if any, evidence to suggest that chimpanzees were able to know when a conspecific had a false belief. Krachun et al. [48] also yielded negative results in another competitive paradigm. Given the positive results of these exact methodologies with regards to other skills, these negative findings are especially striking. However, it remains possible that chimpanzees and other species (e.g. rhesus macaques) simply have not been confronted with the appropriate context in which they might pass a false belief test yet. It is also possible that this specific skill is unique to humans.

In sum, chimpanzees avoid target objects even without seeing the partner seeing them and they can decide whether a human competitor will see them reaching through one of two apparently opaque barriers based on their own previous personal experience with those barriers. These findings rule out explanations based on the evil eye hypothesis and geometric estimation, unless one wants to postulate that even though chimpanzees do not directly perceive geometry, they can imagine it based on the likely position of the objects and the competitor at a given point in time. At the very least, one has to postulate that chimpanzees are capable of imagining geometric projections between currently unobservable agents and objects. Furthermore, there is evidence showing that they do use personal information to attribute perceptions to others. Although most of the work has focused on chimpanzees, it is possible that other species may show comparable abilities. For instance, scrub jays have been reported to respond to currently unobservable cues and to use experience projection when competing with conspecifics [49]. Does this close the debate on theory of mind in nonhuman animals? Obviously not, it simply shows that some of the crude explanations purely based on the perception and association of certain cues do not support the weight of the existing evidence, which does require explanations based on more abstract constructs.

Collaboration and helping

Similar to the history of mindreading studies, the experimental study of cooperation in primates also had a rough start. Crawford’s [50] study on chimpanzee collaboration, defined as two or more individuals working together to obtain a goal, marks its beginning. Pairs of chimpanzees simultaneously pulled ropes attached to a box containing out-of-reach food. Such a setup represented a natural extension of the classical string pulling problems that became so popular during the last century (see [51] for a review) except that two rather than a single individual were required to bring the reward within reach. Unlike the individual string pulling task, which is solved spontaneously by many species [51], the collaborative version of this problem proved to be quite a challenge for chimpanzees. Crawford [50] had to scaffold chimpanzees in various ways including to get them to work together.

Although by the end of the 1990's numerous field studies had documented cooperation in the form of coalitions, group hunting and territorial defence in multiple species (e.g. [52, 53]), there was still very limited experimental evidence about the psychological underpinnings of cooperative problem solving in animals without human intervention or training (for a review see [27]). In studies by Chalmeau and Gallo [54, 55], chimpanzees learned to obtain food through collaborative activity and take the presence of another individual into account but the understanding of each other's roles and their common goal could not be shown conclusively. Furthermore, only a handful of individuals cooperated and social coercion rather than collaboration seemed responsible for the success of some individuals. But similar to mindreading research, things changed and the last decade has witnessed a flurry of research activity that has reinvigorated this field of research.

A new apparatus design by Hirata and Fuwa [56] constituted a major breakthrough in collaboration studies. Although the apparatus was still based on Crawford’s original design, it completely eliminated the possibility of solving it individually (by pulling harder than the experimenter had anticipated) by replacing weights for a clever system of a sliding rope. Unless both ends of the rope are pulled together, the food remains in place. Using Hirata and Fuwa’s apparatus, Melis et al. [13] tested chimpanzees and found that whenever the subjects could not achieve pulling both ends simultaneously by themselves, they opened a door for another individual to enter so that the problem could be solved cooperatively. Moreover, when given the choice between two potential partners, subjects preferably chose the one they knew to be more effective in cooperatively obtaining the food. Interestingly, Hirata and Fuwa's [56] chimpanzees also cooperated but they were not as effective as those tested by Melis and colleagues [13]. Here, chimpanzees only learned to cooperate through trial and error over time and never solicited collaboration from a conspecific partner. Furthermore, they had trouble waiting for a partner and their cooperation was best when paired with a human not another chimpanzee. Recently, Suchak et al. [57] observed pairs and trios of chimpanzees pulling together a food tray. These chimpanzees were tested in a group setting (without pre-training) and could therefore freely choose their partners. Success rates and efficiency increased over time while futile attempts to solve the problem individually decreased.

Interestingly, much of the research attention focused on the determinants of cooperation rather than on its cognitive underpinnings. Thus, Melis et al. [58] rediscovered that tolerance was a major determinant of cooperation (see [59]), especially when working together to access food. This became quite evident when Hare et al. [60] compared chimpanzees and bonobos using Hirata and Fuwa’s apparatus. When food was distributed into two piles and each partner could get a share of the food after pulling from their respective ropes, both species cooperated well. However, when food was clumped into a single pile, which meant that one individual could potentially monopolize it, bonobos continued to cooperate (and simply co-fed next to each other) whereas chimpanzee cooperation broke down as dominant individuals monopolized all the food available and subordinates stopped cooperating.

One thing that quickly became apparent is that even though chimpanzees could cooperate with others in a competent manner, their motivation to do so seemed quite different from that observed in humans. More specifically, studies with human children have shown that they prefer to play together with another individual even if succeeding in the game does not require collaboration with a second person – the joint activity seems to be rewarding to humans in its own right [61]. Bullinger and colleagues [62] directly tested chimpanzees motivation to cooperate with conspecifics by giving them a choice between entering one of two different rooms: one with a "solo option", i.e. where they could pull in food with a rope by themselves; the other with a "collaboration option", i.e. where they could engage in the same collaborative pulling action described earlier and acquire an identical amount of food for themselves as in the solo option. Chimpanzees preferred to work alone but this preference was completely reversed when the collaboration option produced an extra piece of food than the solo option. In contrast, children presented with the same dilemma preferred the social option even if it paid the same as the individual option.

Although no instance of food stealing was observed between chimpanzee pairs, perhaps chimpanzees avoided the social option because there was a possibility, albeit remote, that the food may be taken by the other individual. Another possibility is that children, unlike chimpanzees, prefer to do things together. It has been argued that humans [63] and cooperative breeding primates in general [64] are more prosocial towards conspecifics in terms of sharing goods and information whereas species like chimpanzees are more egocentric. Note that cooperation may work among chimpanzees because it is mutualistic and all individuals get rewarded simultaneously. When the reward is delayed for one of the partners and one has to take turns, cooperation often breaks down in chimpanzees, even for pairs that have been cooperating in previous sessions (e.g. [65]).

However, there are some cases where after two subjects complete a task and only one gets rewarded, the subject that just received the reward continues working until her partner obtains the reward too [66] or where reciprocal exchanges between individuals ensue [67]. More compelling still are those cases involving helping defined as actively facilitating access (or the means to access) some good without obtaining any tangible benefit. Chimpanzees comply with requests, including requests from humans, by handing objects, sharing food and even releasing latches so that others can access rooms with food [68-70]. Control conditions in some of these studies indicate that subjects are aware of the consequences of their actions.

These studies on helping have been interpreted as an indication that subjects are concerned about the welfare of others. In other words, the prosocial acts observed in numerous studies are grounded on empathic concern and demonstrate that individuals possess other-regarding preferences [69, 71]. However, this interpretation has been challenged on methodological and conceptual grounds. First, Tennie et al. [72] have argued that some of the prosocial acts may have originated from a combination of novelty about the experimental situation (including the stimuli used) and stimulus enhancement. In other words, the design of the tasks that only involved a choice for the subjects between helping and doing nothing may have been responsible for the results. More specifically, Tennie and colleagues [72] basically replicated earlier study designs in which chimpanzee subjects could choose to help conspecifics to access food without the prospect of receiving it themselves over doing nothing, but they also introduced a new condition in which chimpanzee subjects could actively block the access to food for conspecifics or do nothing. Results showed no difference between the two conditions, chimpanzees were just as likely to help as they were to block the access to food. Any benefit or harm to conspecific recipients caused by the subjects' behaviour apparently only arose out of initial interest in the apparatus and the only possible action they could perform. In both the beneficial and the harmful condition, this behaviour was extinguished after several trials so that neither a prosocial or spiteful motivation could be detected.

Second, in the vast majority of studies requests must be made for the prosocial act to occur. Often when such requests receive no response, requests are repeated and amplified, something that is not surprising given that such is one of the features of intentional gestural communication [73]. It is therefore conceivable that prosocial acts are aimed at eliminating the requests rather than relieving the need of others. This idea has been around for a while in the literature in what has become known as the “sharing under pressure hypothesis”. Wrangham [74] suggested that much chimpanzee food sharing in the wild was done under intense pressure from beggars, who left as soon as they obtained a piece of meat. The idea that prosocial acts are a consequence of harassment [75, 76] can also be applied to many of the experimental settings used, i.e. when the recipient was actively reaching for the food and rattling on a chain, a low-cost way for the subjects to suppress this noise was to just release the food/token. An "opt-out" control condition in which the subjects could choose between helping and e.g. leaving the test situation could address this possibility. Children, in contrast, often provide help even when no such requests are directed at them [68, 77][JC1], thus eliminating the sharing/helping under pressure idea.

One way to eliminate the sharing under pressure for those species that begged intensely is to experimentally prevent the beggar from interfering with the donor but give the opportunity to the donor to provide food. This is what has been done in numerous studies. In a now widely used test paradigm, Silk and colleagues gave chimpanzees the choice between a 1/1 and 1/0 option, i.e. they could either choose one piece of food for themselves while simultaneously providing one piece of food for a conspecific, or they could just choose one piece for themselves and nothing for the conspecific [12]. In this and most other studies, chimpanzees were shown to choose randomly between these options and therefore they were seemingly only interested in their own benefit (see [77, 78] for reviews). Horner et al. [79] have criticised the studies because the apparatus needed to implement the choices is deemed to be too complex for chimpanzees even though control conditions in several of these studies showed that chimpanzees were fully aware of the consequences of their actions on their partners' location (e.g. [80, 81]). Instead, Horner et al. [79] advocated using a token exchange paradigm with different tokens are associated with certain outcomes to avoid this problem. However, it is not clear that tokens solve the problem because it is unclear whether chimpanzees understand how they function - Horner et al. [79] provided no evidence that chimpanzees understood the consequences of selecting certain tokens with regard to the food distribution to their partners. Recently, Amici et al. [82] tested chimpanzees and other primates with both the token exchange and the platform paradigms using protocols as similar as possible to those used in previous studies. They found no conclusive evidence of other-regarding preferences in either paradigm for any species. Interestingly, they also found that chimpanzees did not understand the value of the tokens when they were tested individually. In contrast, Claidiere et al. [83] found that chimpanzees and capuchin monkeys displayed other-regarding preferences in a version of the platform paradigm in some of their experimental conditions, but also yielded some inconsistent results that might call the subjects' full understanding of the apparatus and condition into question.

In sum, collaboration and helping are well documented in experimental contexts in primates and other animals. This means that it is now possible to investigate the psychological underpinnings of cooperative acts such as coalitions and food sharing observed in wild and laboratory populations. Although there is no shortage of prosocial acts, defined as doing something that benefits another individual (e.g. two individuals working together to obtain a mutual benefit, or even an individual providing a service to another one without apparent retribution), the motivational substrate underlying those acts is still a matter of intense debate. Some authors argue that primates display other-regarding preferences while other authors explain the evidence available in terms of self-regarding preferences. A major task for the next generation of studies will be to precisely pinpoint the motivational substrate of the various prosocial acts described in the literature.

Conclusions and future directions

Focusing on both cooperative and competitive contexts has been important in helping comparative psychology move forward in two main ways. First, it has helped researchers to design better experiments and in doing so they have allowed researchers to uncover the cognitive abilities and motivational substrates underlying them. As a consequence, comparative psychology is now much richer both methodologically and conceptually than just a few years ago. We now know that chimpanzees and other species are sensitive to what others can and cannot see and, at least chimpanzees, can estimate this not just by direct perception but also by attributing their own perceptions and preferences to others. However, it is currently unclear whether chimpanzees also engage in level 2 perspective-taking. Cooperation has also been experimentally documented in various settings and species. Social tolerance has been confirmed as a major determinant of cooperation and work on chimpanzees seems to suggest that they prefer to work alone, but will cooperate with others for higher payoffs, and helping occurs but is mainly mediated by requests. It is currently unclear if prosocial acts in nonhuman primates are based on empathic concern or represents a form of harassment reduction or a response to novelty. Future studies will be required to address these and other outstanding issues in mindreading and cooperation research.

Despite this undeniable progress, or perhaps due to it, we are faced with misaligned research agendas with regard to the psychological substrate of competition and cooperation. Although originally conceived as complementary aspects, cooperation and competition became misaligned because they did not receive the same research attention. Even the Machiavellian intelligence hypothesis which initially considered both aspects [6], became later on more associated with competition than cooperation, partly because the emphasis placed on tactical deception [84] and partly due to the success of some competitive paradigms compared to their cooperative/communicative counterparts (see Mindreading section). Whereas cognition has been mainly investigated in competitive contexts, motivation has been the prime target of studies on cooperation and helping. It is therefore time to attempt to realign these agendas and to do so, we propose two directions. First, aspects of mindreading have to be investigated in the context of cooperation. This does not mean to repeat the same mistakes as in the past, but present cooperative tasks in which taking the perspective of others is crucial to solve them. Can the same mindreading abilities that are deployed in competition also be used to solve a cooperation task? For instance, would individuals pulling strings simultaneously take into account what their partners can and cannot see when they are trying to coordinate obtaining rewards for both partners? If they could, one should revise some ideas about the evolution of mindreading that have placed competition at its core [85]. If they could not, then perhaps perspective taking for cooperative purposes represents a fundamentally different problem, and this may lend support to the theories that have suggested that shared intentionality is crucial [61], not just the motivational aspects, but also the representational ones.

Second, and equally important, is bringing into sharper focus the motivational aspects of competition. Would individuals be more likely to cooperate when such cooperation would entail competing against third parties? If Bullinger et al.'s [62] social vs. solo option study had entailed not just cooperating with a partner but also simultaneously competing against another individual, would this have shifted chimpanzees’ preference for choosing the social over the solo option? In such a case, and given that they also pick the social game when the payoff is higher than the solo game, one could even actually quantify how much individuals would be willing to pay to cooperate to compete. Would the likelihood of joining a partner depend not just on the identity of the partner but also the identity of the opponent? Placing the emphasis on each of these aspects paired with further effort along the path already travelled is likely to bring further progress and a much more balanced body of knowledge regarding the psychological mechanisms underlying cooperation and competition. The core idea here is that mindreading may not just be about competition and social motivation may not just be about cooperation in humans and other animals.

We are aware that our review is biased at least in two ways. First, most of the work that we cited was done with chimpanzees. Although there are now numerous studies that have focused on other species [29,78], it is still the case that the most sophisticated studies, which rule out some of the most resilient alternative explanations (e.g., evil-eye hypothesis) have yet to be done with those species. Future studies are needed to broaden the taxonomic scope beyond basic abilities so that inferences about cognitive evolution stand on a much firmer ground [e.g., 49]. Second, most of the work that we cited was done in the laboratory, not in the field. With the possible exception of playback experiments (e.g. [86]), there are virtually no field experiments on mindreading or cooperation in nonhuman primates comparable to those conducted in the laboratory (see [31, 87] for exceptions). This state of affairs is perhaps likely to change in the coming years since field experiments on social problems (e.g. social learning) have begun to appear in the primate literature with some regularity (e.g. [88-90]). Such a change may denote a change in attitude of some fieldworkers toward field experiments (others like T. Matsuzawa have always combined field and laboratory work, e.g. [90]), which may be partly mediated by the recognition that work in the laboratory and in the field must complement each other.

We are also aware that the existing biases potentially compromise the scope our conclusions. Those same biases, however, also reveal the direction that we must take to overcome them. Briefly stated, jointly focusing on the cognitive and motivational aspects of cooperation and competition paired with adopting a broader taxonomic scope applied to field and laboratory settings represent the ideal combination to further advance our knowledge about the psychological underpinnings of social life in primates and other animals.

Competing interests

We have no competing interests.

Authors' contributions

All authors drafted the manuscript and gave final approval for publication.

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