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ADVANCED REVIEW

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How animals collaborate: Underlying proximate mechanisms

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Abstract

Collaboration or social interactions in which two or more individuals coordinate their behavior to produce outcomes from which both individuals benefit are common in nature. Individuals from many species hunt together, defend their territory, and form coalitions in intragroup competition. However, we still know very little about the proximate mechanisms underlying these behaviors. Recent theories of human cognitive evolution have emphasized the role collaboration may have played in the selection of socio-cognitive skills. It has been argued that the capacity to form shared goals and joint intentions with others, is what allows humans to collaborate so flexibly and efficiently. Although there is no evidence that nonhuman animals are capable of shared intentionality, there is conceivably a wide range of proximate mechanisms that support forms of, potentially flexible, collaboration in other species. We review the experimental literature with the aim of evaluating what we know about how other species achieve collaboration; with a particular focus on chimpanzees. We structure the review with a new categorization of collaborative behavior that focuses on whether individuals intentionally coordinate actions with others. We conclude that for a wider comparative perspective we need more data from other species but the findings so far suggest that chimpanzees, and possibly other great apes, are capable of understanding the causal role of a partner in collaboration.

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apes, collaboration, comparative psychology, cooperation, social cognition

1 | INTRODUCTION

Cooperative behavior is widespread in the animal kingdom. Individuals from many species engage in behaviors that benefit others or are beneficial to both the actor and the recipient. The focus of this review is on "collaboration," which

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we define in the same way as Melis and Semmann (2010) and Melis and Warneken (2016): Behaviors in which two or more individuals coordinate their actions to produce outcomes from which both individuals benefit (e.g., obtaining a common resource). Examples include group hunting, intergroup conflict, and territory defense. From an ultimate perspective it is easy to understand why behaviors associated with positive payoffs or direct fitness benefits for the actor evolve (although mechanisms to avoid cheating are still necessary). However, from a proximate perspective, collaboration raises interesting questions about how individuals coordinate actions.

Collaboration plays a very special role in humans (*Homo sapiens*), since societies are built around related and unrelated individuals working together (e.g., cooperative hunting, childcare, paying taxes, playing in a sports team; Boyd & Richerson, 2009). In recent years it has been argued that situations of interdependence and the need to work together with others was a significant contributor to human cognitive evolution (e.g., Gavrilets, 2015; McNally, Brown, & Jackson, 2012; Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012). In particular, socio-cognitive skills, such as joint attention, forming shared goals, and communicative skills, would have been particularly useful to facilitate coordination (Tomasello et al., 2012; Tomasello, Carpenter, Call, Behne, & Moll, 2005). Several models provide evidence for coevolution between collaboration and cognition (e.g., Dos Santos & West, 2018; Gavrilets, 2015; McNally et al., 2012). These models support the view that, in situations of interdependence, higher cognition can lead to greater gains through increased collaborative efficiency and success, and so higher cognition can evolve in cooperative societies (although the exact form of this cognition is not specified in these models).

To understand the evolutionary relationship between cognition and cooperation we need comprehensive knowledge of the cognitive mechanisms underlying collaboration in human and nonhuman animals. In this review, we will discuss what we know so far about how animals achieve collaboration.

1.1 | Comparative approach to collaboration

Understanding the importance of collaboration in humans and its evolutionary history comes, in part, from comparisons with other species. Great apes, chimpanzees (*Pan troglodytes*) in particular, provide a conceptual model of the last common ancestor between humans and the African great apes (Pilbeam & Lieberman, 2017). But this comparison goes beyond our phylogenetic proximity, as cooperation is integral to their social lives: chimpanzees spend time grooming each other, form complex coalitions and alliances within their groups, hunt together, share food, males patrol their community boundaries, and engage in coalitionary attacks in intercommunity conflict (Mitani, 2009).

In addition to observations of these behaviors in wild communities, collaboration in chimpanzees has been subject to decades of experimental study, starting with the studies of cooperative problem-solving by Crawford in the 1930's (Crawford, 1937, 1941; Melis & Semmann, 2010). We will focus on this body of experimental literature to discuss the proximate mechanisms supporting collaboration and our review will also reflect the bias toward chimpanzees in this literature.

While great apes undoubtedly provide a rich source of information about the evolutionary origins of human collaboration, a broader comparative perspective is important for understanding the potential selection pressures that contribute to the evolution of collaborative skills (MacLean et al., 2012; Many Primates et al., 2019). For example: there are numerous species, including large social carnivores such as lions (*Panthera leo*) and wolves (*Canis lupis*), that rely more heavily on group hunting than chimpanzees (Schaller & Lowther, 1969; Smith, Swanson, Reed, & Holekamp, 2012). Species like common marmosets (*Callithrix jacchus*), take a more cooperative approach to breeding, more comparable to human child rearing practices than the great apes (Burkart, Hrdy, & Van Schaik, 2009). This has been argued to promote cognitive skills supporting collaborative interactions (Burkart et al., 2009; Miss & Burkart, 2018, but see Thornton & McAuliffe, 2015, Thornton et al., 2016). Understanding the proximate mechanisms of collaboration should be informed by cognitive skills shared by our closest living relatives, but also by species solving analogous problems across the animal kingdom that may have converged on similar solutions.

1.2 | Categorization of collaborative behavior

A useful starting point thinking about how nonhuman animals collaborate is the categorization of cooperative hunting offered by Boesch and Boesch (1989) to describe hunting in chimpanzees. Typically, on encountering potential prey, one or more male chimpanzees will initiate a chase and others can join with larger hunting parties increasing hunting success. At the end of the hunt the captor retains the largest portion of the prey, however, a significant proportion of the rest of the group get meat too (Gilby, Thompson, Ruane, & Wrangham, 2010; Newton-Fisher, 2015; see Surbeck, Fowler, Deimel, & Hohmann, 2009, for hunting in bonobos, *Pan paniscus*). There is extensive discussion about the proximate mechanisms of group hunting in chimpanzees: ranging from whether individuals engage in planned collaboration based on shared goals, to whether group hunting is primarily a by-product of individual actions (Boesch, 2002; Gilby & Connor, 2010; Tomasello et al., 2005).

Boesch and Boesch (1989) describe group hunting behavior in chimpanzees with four increasingly complex behavioral categories: *similarity*, *synchrony*, *coordination*, and *collaboration*. The definitions in Boesch and Boesch (1989) are based on detailed descriptions of hunting behavior but they are also used to infer the related cognitive abilities (Boesch, 2002). Intentions to coordinate are indicated in three of the categories (synchrony, coordination, and collaboration), as, for example, when stating that individuals "try to relate to each other" in time (synchrony) or time and space (coordination; Boesch & Boesch, 1989). Collaboration, the most complex category, is defined as "Hunters performing complementary actions, all directed toward the same prey" (Boesch & Boesch, 1989) and the authors suggest that to achieve this requires individuals to consider both the actions and perspectives of others (Boesch, 2002). This implies that chimpanzees take into account the mental states of others when making decisions about hunting strategies. For comparison, Boesch and Boesch (1989) also use their framework to categorize group hunting behavior in large carnivores (lions; spotted hyenas, *Crocuta crocuta*; wild dogs, *Lycaon pictus*, and wolves). They conclude that collaboration occurs rarely among these species and that they may lack some of the (cognitive) abilities of apes, such as being able to take the visual perspective of others.

However, Bailey, Myatt, and Wilson (2013) and others such as Smith et al. (2012), have argued that collaboration, that is, individuals performing complementary roles, is quite common among carnivores. Their argument is not that these species have the same cognitive abilities of apes but and that the behavior can be achieved with simple rules and some degree of associative learning (Bailey et al., 2013).

This difference in interpretation highlights a challenge of inferring behavior through observational studies, which is that different psychological mechanisms can lead to superficially similar behaviors. Thus, discerning whether individuals are *trying* to coordinate with each other or whether their collective behavior is the result of parallel but independent actions becomes difficult to distinguish from observations. Experimental studies provide opportunities to overcome this challenge (Noë, 2006; Tomasello et al., 2005). By making comparisons in controlled settings, we can isolate specific abilities of interest and test to which extent animals employ active strategies of coordination with the partner. Experimental studies also allow for controlled comparisons between groups and species (see Many Primates et al., 2019; MacLean et al., 2014, for examples of large-scale comparisons between species).

In addition to the difficulty of inferring proximate mechanisms from observations alone, there is not a clear consensus among researchers regarding which proximate mechanisms (motivational and cognitive) qualify for joint action to be considered "truly collaborative" or a "team task." The dichotomy often made when discussing collaborative problem-solving behaviors is between (a) rudimentary forms of collaboration based on lower levels of explanations (e.g., operant conditioning, associative learning, and social facilitation) and (b) complex collaboration, based on shared intentionality, as in adult humans. However, there is a wide gap between these levels in which animals could be incorporating different kinds of knowledge about their social and physical world (e.g., means-ends understanding, causal inferences, and theory of mind skills) into their cooperative problem-solving behavior.

We structure the current review with a new categorization of collaborative behavior. We suggest four categories of collaborative activities that differ from each other with regard to (a) the degree that individuals' decisions to act is influenced by other social partners (e.g., stimulus enhancement, social facilitation), (b) the degree of intentional coordination between partners, and (c) shared commitment to collaborate (see Table 1 for a summary). Our first two categories: *by-product collaboration* and *socially influenced collaboration* do not involve intentional coordination. Rather, collaboration is a by-product of individual decisions influenced by external stimuli (both social and nonsocial). Our third category *actively coordinated collaboration* is the one we are particularly interested in because this addresses the gap between socio-cognitively simple and complex collaboration. Our fourth category is *collaboration based on shared intentionality*, which involves the full set of cognitive and motivational mechanisms typical of adult humans engaging in true team tasks. With this categorization we do not have a priori expectations about what collaboration looks like, for example, we do not assume different roles are an indication of the most cognitively complex forms of collaboration.

For each of our categories we evaluate the experimental evidence, concentrating particularly on the third category: actively coordinate collaboration.

TABLE 1 Summary of categories of collaboration

Category	Proximate mechanisms	Dependent measures
By-product collaboration	• Independent decision-making • Actions influenced by external events/stimuli, not by conspecifics	• Solving the loose-string task with no adjustment for partner presence or behavior (e.g., by pulling the rope as quickly as possible)
Socially influenced collaboration	• Socially influenced timing of actions ○ For example, social facilitation, stimulus enhancement, operant conditioning • No intentional strategies to facilitate coordination with partner(s)	• Being more likely to interact with a collaborative task when others are present • Visual access facilitating success • Learning to wait for the partner in the delayed loose-string task (using rope tension and partner presence as cues) but inflexible strategy.
Actively coordinated collaboration	• Intentional temporal and spatial coordination • Means-end problem-solving • Knowledge of the causal role of partner ○ At its simplest level: Partner presence-understanding or knowledge about partner's actions ○ In more complex forms: Representation of partner's and own's actions as part of overarching goal • Can involve different levels of knowledge about partner's goal-directed behavior such as mental state understanding	• Waiting for a partner in the delayed loose-string task is a flexible strategy that translates to other measures below. • Distinguishing when the partner cannot perform her/his role • Choosing collaborative (over individual) task only when a partner is available • Novel solutions/interventions to make possible and support the joint action: ○ Recruiting partner ○ Helping collaborators to fulfill their role ○ Passing the necessary tools to partners ○ Directing partners to the location of hidden tools
Collaboration based on shared intentionality	• Intentional temporal and spatial coordination • Representation of partner's and own's actions as part of overarching goal. • Mutual awareness of shared goals (shared knowledge about each other's intentions and goals) • Commitment to shared goals • Merit-based sharing of proceeds of collaboration	• Completing the shared goal: Supporting the partner to reach her goal even when own goal has been achieved • Taking leave from ongoing collaboration • Sharing proceeds of collaboration according to participation • Communication to initiate and coordinate the intention to collaborate

2 | FOUR CATEGORIES OF COLLABORATION: REVIEWING THE EVIDENCE

In this section we describe the four levels of collaboration: by-product collaboration, socially influenced collaboration, actively coordinated collaboration, and collaboration based on shared intentionality and evaluate the evidence for each of them in nonhuman animals (see Table 1 for a summary).

2.1 | By-product collaboration

Individual actions that can result in a mutual benefit because individuals happen to act closely in proximity and/or time. In this category, increased success is a by-product of (simultaneous) similar actions toward the same goal. Individuals respond to their own goal, which can be the same as that of other individuals, but there are not any mechanisms in place to facilitate coordination. The fact that individuals direct similar (and sometimes simultaneous) actions toward the same goal is the result of being in a group and being exposed to the same environmental stimuli. According to our definition, this category would not actually qualify as "collaboration"—it is only cooperation in terms of cost–benefit outcome and thus more akin to Noë's "instrumental cooperation" (Noë, 2006). For example, sailfish (*Istiophorus platypterus*) hunt in groups and attack shoals of sardines (*Sardinella aurita*). The attacks are not coordinated but multiple individuals attacking the sardine shoals injure the fish and increases hunting success for the individual sailfish. There is no evidence for roles or spatial coordination of any type (Herbert-Read et al., 2016). These types of situations, in which individuals gain from acting in parallel to others, could be contexts in which the forms of collaboration described in our other three categories evolve, if individuals benefit further by coordinating with others.

2.2 | Socially influenced collaboration

Individual's decisions to pursue a specific goal or perform a specific behavior are influenced by the presence or behavior of others. For example, in the context of hunting, it could be that seeing/hearing others hunt increases an individual's likelihood of hunting. This would result in individuals acting simultaneously and directing similar actions toward the same target, but without trying to relate to each other spatially ("synchrony" following Bailey et al., 2013; Boesch & Boesch, 1989). The difference between this category and the previous one is that individuals are responding to social information. There could be different psychological mechanisms involved, including social facilitation, stimulus enhancement, simple associative mechanisms, and even socio-cognitive skills allowing individuals to make inferences about others' goals, perception, or knowledge.

However, even if individuals have the capacity to represent others' goals or perspectives, by "socially influenced collaboration" we mean that there is no intentional coordination beyond individuals navigating elements of their environment as best as possible. Thus, individuals may respond to what others are doing or where they are situated without trying to coordinate actions in relation to the common goal. Individuals in this category lack awareness that their partner's actions can influence their own individual success.

Wolves show complementary roles during group hunting (e.g., chaser and ambusher encircling the prey) and this would be categorized as collaboration by Bailey et al. (2013). However, Muro, Escobedo, Spector, and Coppinger (2011) use computational simulations to show that collaboration with several different roles can result from independent efforts to approach the prey adhering to two simple rules, (a) get to the closest safe distance from the prey and (b) move away from other wolves to get the best possible view of the prey. This shows that it is not necessary to attribute planning skills and awareness about the causal role of others in the hunt when we observe multiple individuals chasing the same prey and would thus be categorized as socially influenced collaboration. This interpretation can be extended to a wide range of group hunting and other cooperative activities. Several researchers have implicitly argued for a similar interpretation for chimpanzee group hunting (e.g., Gilby & Connor, 2010; Tomasello et al., 2005).

Several studies have looked at partner monitoring during collaborative tasks as a way to infer whether subjects are trying to coordinate actions with one another and have some understanding about the role of the partner. There is evidence that, for example, capuchin monkeys (*Cebus apella*) look at each other during collaborative attempts and that they are more successful cooperating when there is visual contact between partners (e.g., Hattori, Kuroshima, & Fujita, 2005; Mendres & de Waal, 2000; but see Chalmeau, Visalberghi, & Gallo, 1997; Visalberghi, Quarantotti, & Tranchida, 2000). However, individuals could be monitoring partners for other reasons not related to coordination, such as monitoring the partner's position relative to their own or checking the partner's reactions while the actor is manipulating a baited apparatus. Higher rates of interaction with the cooperative task (e.g., pulling on a bar) when partners are present have also been interpreted as evidence for intentional coordination (Cronin, Kurian, & Snowdon, 2005; Mendres & de Waal, 2000) but this effect could also be due to stimulus enhancement or social facilitation (Shettleworth, 2010). Without more direct measures that show an attempt to coordinate with each other these examples fall into our category of socially influenced collaboration.

Common to our first two categories of *by-product collaboration* and *socially influenced collaboration* is that complex coordinated behaviors can emerge from simple rules of independent decision-making not aimed at coordination ("emergent coordination" following Knoblich, Butterfill, & Sebanz, 2011). Individuals act in similar ways but without any plan or knowledge about each agent's role in achieving the common outcome. The similar actions toward the same goal and simultaneity of the actions is the result of agents encountering the same environmental stimuli at the same time (by-product collaboration), or in the case of "socially influenced collaboration" being influenced by and attracted to what others in the group are doing. In the next two categories we discuss the evidence for intentional collaboration, where individuals try to coordinate their actions with others.

2.3 | Actively coordinated collaboration

Individuals try to relate to each other in time and space and have some knowledge about how the presence of a partner and the actions of a partner contribute to their own success. Partners monitor and respond to each other's actions with regard to the common goal. Thus, they employ different strategies to facilitate temporal and spatial coordination with the partner. For example, they can inhibit acting until others are present (waiting for others) and employ more active strategies to initiate and support the joint activity such as recruiting partners or helping partners, either instrumentally or by informing them. Intentional collaboration also comprises "social tool use," a term which has been used to describe interactions in which individuals manipulate others, either physically or psychologically, to achieve their own goals, using the self-initiated actions of another by, for example, handing them a tool they can use to access a reward for both (Bard, 1990; Voelter, Rossano, & Call, 2017). In the case of actively coordinated collaboration, the goals of both individuals are aligned so one could say that there is a bidirectional social tool use in pursuit of the same goal. Therefore, one could argue that actors represent the outcome they want to achieve, the task they need to perform and, at the very least, something about the other agent in achieving this outcome, resembling what others describe as "planned coordination" (Knoblich et al., 2011).

In the following, we review the main lines of evidence and experimental approaches used to investigate whether nonhuman animals show this level of intentional coordination. We start by briefly evaluating the evidence from the most common test of collaboration, the loose-string task. First, we discuss what waiting for a partner can tell us about collaboration. Then, we move on to review the evidence showing that animals know when they need a partner, which has been operationalized with the recruiting paradigm and with choosing collaboration versus solo apparatuses. Finally, we review studies looking at whether individuals represent something about the collaborative task and the partner's actions. This has been approached in three different ways by looking at (a) whether they support the partner toward successfully fulfilling their role in the collaboration, (b) whether representations of their partner's actions impact learning of the roles in the collaborative task (role reversal) or interfere with their own actions (co-representation), and (c) their recognition of whether or not it is possible for a partner to perform their role.

2.4 | Evidence for actively coordinated collaboration

2.4.1 | Waiting for the partner before acting

Being able to wait for a partner has been argued to demonstrate a "basic understanding of the role of a partner" in collaboration (e.g., Plotnik, Lair, Suphachoksahakun, & de Waal, 2011), thus satisfying the minimal requirements for actively coordinated collaboration. This is often measured with the loose-string task: a single rope is looped through an out-of-reach platform. To bring the platform (and any rewards on that platform) within reach both ends of the rope need to be pulled simultaneously to avoid unthreading the rope from the loops on the tray. If the two ends of the rope are too far apart for one individual to reach them, they have to inhibit pulling from their end of the rope until a partner is holding the other end of the rope (Hirata & Fuwa, 2007). In the delay version of this task access to the rope is delayed for one individual so that their partner needs to wait for increasing intervals across trials (Melis, Hare, & Tomasello, 2006). The measure of interest is whether or not the subject inhibits pulling until the partner is ready to pull. So far, there is evidence that chimpanzees, elephants (*Elephas maximus*), kea (*Nestor notabilis*), dolphins (*Tursiops truncatus*), and wolves learn to wait for the partner (Heaney, Gray, & Taylor, 2017; Marshall-Pescini, Schwarz, Kostelnik, Virányi, & Range, 2017; Melis et al., 2006; Plotnik et al., 2011; C. Yamamoto, Kashiwagi, Otsuka, Sakai, & Tomonaga, 2019). In contrast, rooks (*Corvus frugilegus*), African gray parrots (*Psittacus erithacus*) and otters (Asian small-clawed otters, *Aonyx cinereus*, and giant otters, *Pteronura brasiliensis*) have failed this task (Peron, Rat-Fischer, Lalot, Nagle, & Bovet, 2011; Schmelz, Duguid, Bohn, & Völter, 2017; Seed, Clayton, & Emery, 2008) and there are mixed results for domestic dogs (*Canis familiaris*; Marshall-Pescini et al., 2017; Ostojić & Clayton, 2014) and ravens (*Corvus corax*; Asakawa-Haas, Schiestl, Bugnyar, & Massen, 2016; Massen, Ritter, & Bugnyar, 2015).

However, there are two major considerations we need to take into account. First, success could be the result of operant conditioning and subjects learning contingencies such as "pull when partner is present and/or there is tension on the rope" (Seed & Jensen, 2011; Vesper, Butterfill, Knoblich, & Sebanz, 2010; Voelter et al., 2017). Second, there is significant variation in methodology that will influence potential success and make comparisons across species difficult. For example, the length of rope that is extended into the testing room determines how long individuals can pull before the other end of the rope becomes inaccessible for a partner (Hirata & Fuwa, 2007; Schmelz et al., 2017). This is not a relevant factor for long delay times (>10–15 s) but it could determine success at shorter delay times or provide more opportunities to learn contingencies about partner presence and rope tension. Finally, comparisons are made difficult by variations in the delay periods and the number of trials the different species have participated in. Variants of the delay task have partly addressed these issues. For example, in a recent study, pairs of dolphins needed to swim to the far end of their pool to press two buttons simultaneously (within 1 s of each other; Jaakkola, Guarino, Donegan, &

King, 2018). This task removes the possibility of using tension as a cue for pulling and provides evidence toward interpreting waiting for a partner as active coordination.

From the species that have been successful in the delayed loose-string task, including chimpanzees, elephants, wolves, dolphins, and kea (Hirata & Fuwa, 2007; Jaakkola et al., 2018; Marshall-Pescini et al., 2017; Melis et al., 2006; Plotnik et al., 2011; C. Yamamoto et al., 2019), it is clear that this is something that requires some learning. Therefore, it is hard with this measure alone to draw conclusions about subject's understanding of the partner's role and to use it as convincing evidence for intentional coordination. If success in delay tasks does indeed demonstrate that subjects have grasped the causal role of the partner in their success, we would expect them to be able to find novel ways to support their partner acting and performing her role in the task. One obvious first manipulation is to give the subject the choice to recruit a partner (or not) when the problem requires collaboration or choosing appropriately between collaborative and individual tasks depending on the availability of a partner.

2.4.2 | Do animals know when they need a partner?

Recruiting a partner

In the 90's Chalmeau and colleagues conducted some of the first experimental studies of chimpanzee cooperative problem-solving skills and early observations of recruitment behavior (Chalmeau, 1994; Chalmeau & Gallo, 1996). The task required two chimpanzees to pull simultaneously on two handles to release a reward. The task was presented to a group of chimpanzees, but a dominant male (Alfred) monopolized the apparatus and learned to wait for a young female (Amandine) to approach the apparatus and pull one handle before he pulled the second handle. Increasingly, Alfred developed the strategy of catching her and bringing her close to the apparatus, suggesting that Alfred had learned something about the instrumental role of Amandine and was able to intervene and develop an active strategy to facilitate the joint action (see also Schweinfurth, DeTroy, Van Leeuwen, Call, & Haun, 2018; Völter, Rossano, & Call, 2015, for more evidence of social tool use through physical manipulation of others in orangutans and chimpanzees). More subtle forms of recruitment through gesturing were also observed by Crawford (1937), who described how a partner might solicit action from a partner via begging gestures, touches to the shoulder or head, and sometimes a gentle push toward the task (see also Bullinger, Wyman, Melis, & Tomasello, 2011; Crawford, 1937; Duguid, Wyman, Bullinger, Herfurth-Majstorovic, & Tomasello, 2014).

A study by Melis et al. (2006) adapted the loose-string task to specifically test active recruitment behavior in chimpanzees. All subjects had participated previously in the delay task described above, in which they learned to wait for up to 30 s for the partner to approach the apparatus and start pulling. However, they were now required to transfer the knowledge acquired in the delay task to a new problem that involved them unblocking a door to recruit the partner. Subjects had been given experience with the mechanism of the door opening, but never with a partner locked in the room, nor in association with the collaboration platform. The results showed that subjects recruited the partner more often in the collaboration condition than in a solo condition in which they could successfully pull in the tray alone. Therefore, these results suggest that the knowledge acquired in the delay task allowed the actors to employ a novel strategy to initiate successful collaboration using intentional means-end problem-solving behavior, or a sequence of steps to reach the final goal. In this case, the goal is to reach the tray (end) but chimpanzees were able of performing an additional action (opening the door) to reach the subgoal of creating the necessary precondition (partner is in the room) so that they can reach the tray. Furthermore, in a follow-up the same subjects quickly learned to distinguish between effective and poor collaborators, choosing to recruit the best or most effective partner.

A recent study by Range, Kassis, Taborsky, Boada, and Marshall-Pescini (2019) adapted the recruitment paradigm for wolves and dogs to recruit a human partner. In trials in which the wolves or dogs could not pull the rope alone, they were expected to activate the door-opening mechanism to let in a cooperative human partner by standing on a star-shaped marker in the test enclosure. Both species opened the door for a partner more often in the collaborative than the solo condition, especially when the costs of recruitment were lowered (by reducing the distance to the star). However, the authors do state that, since the dogs and wolves were trained to open the door for a human, the results could be interpreted as them employing a set of rules from their experience in previous tasks and training, rather than an understanding of the partner's role in the task.

Some of the most intriguing observations of recruitment behavior in the wild come from inter-species mutualisms such as coral trout (*Plectropomus leopardus*) recruiting moray eels (*Gymnothorax javanicus*) to hunt together (Bshary, Hohner, Ait-el-Djoudi, & Fricke, 2006) or honeyguide birds (*Indicator indicator*) recruiting humans to smoke and chop open bees' nests, (Spottiswoode, Begg, & Begg, 2016). These collaborations rely on the complementary abilities or strategies of both species. In the example of coral trout and moray eels: the trout are fast chasing prey above the reef, whereas the moray eel can access prey hidden in crevices. The coral trout recruit partners by approaching them and performing a shimmying movement, and moray eels show variation in their likelihood to join a trout to hunt (Bshary et al., 2006; Vail, Manica, & Bshary, 2013). Vail et al. (2013) used almost identical experimental methods as Melis et al. (2006) to investigate whether trout distinguish *when* to recruit a moray eel and *with whom* to collaborate. They found that, similarly to the chimpanzees, coral trout recruit a collaborator (a model eel) when they cannot catch the prey and they also learn to recruit a reliable collaborator (one of two different model eels; Vail et al., 2013). It is still unclear which cognitive mechanisms underlie this recruiting behavior in both species. However, as the authors argue, the fish are being presented with a highly ecological problem (Vail et al., 2013), and their recruiting behavior is part of their natural repertoire or a species-specific behavior, whereas the chimpanzees had to discover "the recruiting behavior" as part of an intermediate solution to a rather artificial problem. An important criterion that may help us tap into causal understanding about the role of the partner is the flexibility with which subjects can solve new problems, employing different and new means to facilitate and support the partner's role.

Recognizing when a partner is necessary by choosing collaboration versus solo apparatuses

Another interesting approach to measure whether or not subjects recognize the need for a partner in a collaborative task is giving them a choice between apparatuses that require collaboration (and hence a partner) and apparatuses that they can use alone. Seed et al. (2008) investigated cooperative problem-solving behavior in rooks using the loose-string task. In an initial experiment they used the delay test but found that none of the subjects waited for a partner. In a second experiment subjects were given a choice between two different platforms: one they could pull alone (solo platform) or one that required collaboration and contained double the amount of food (collaboration platform). They were tested either alone or with a partner. Therefore, they should have chosen the solo platform when alone and the collaboration platform when paired with a partner. However, only two out of six birds seemed to learn to choose the solo platform when they were alone. The authors concluded that is unlikely that rooks had grasped the role of the partner in the cooperation task.

Similar choice tasks have also been used to test several other species (Drea & Carter, 2009; Heaney et al., 2017; Marshall-Pescini et al., 2017; Melis, Hare, & Tomasello, 2009; Peron et al., 2011). Peron et al. (2011) found mixed results for all three African gray parrots they tested. For example, one subject out of three delayed pulling until the other subject arrived, but that same subject did not discriminate in the "choice of platforms"—task. Given the small sample size ($N = 3$) and the mixed results, it is difficult to draw any firm conclusions from this study. Heaney et al. (2017) also presented keas with two different apparatuses, one apparatus requiring them to pull together and one they could pull alone. In this case, there was no active choice between apparatuses as in the previously mentioned studies (Peron et al., 2011; Seed et al., 2008) instead, keas were assessed on their ability to behave appropriately (wait vs. not wait) with both types of apparatus presented in a randomized order across trials. To do this, they simply needed to behave as in the earlier training phases, which makes it difficult to interpret the flexibility of the kea's behavior.

In a slightly different variation of the task, hyenas (Drea & Carter, 2009) and wolves (Marshall-Pescini et al., 2017) coordinated actions between two identical collaboration apparatuses. Going to the same apparatus emphasized the spatial coordination, in addition to temporal coordination of pulling the ropes. Both species were very successful from the start (>70% trials success) without any prior delay task experience. However, for the hyenas, the ropes were not set-up in the same way as in the loose-string task, and pulling the rope without a partner did not result in the other end becoming inaccessible. Repeated pulling attempts could be made and thus individuals did not need to wait for a partner before acting. Whether success in the two-apparatus version also transfers to other paradigms would be an indicator of their understanding of the role of the partner.

Chimpanzees have also participated in tasks in which they have to make a choice regarding which apparatus to pull from in order to coordinate with the partner. Melis et al. (2009) presented pairs of chimpanzees with two loose-string platforms over which partners had conflicting preferences. Subjects waited sometimes up to 3 min for each other, until they converged on the same platform. In another study (Bullinger, Melis, & Tomasello, 2011), focal subjects had to choose between a solo platform and a collaboration (plus partner) platform in order to obtain the same amount of food. In pretests they had been able to discriminate between a solo platform and a collaboration platform depending on the availability of the partner, being rewarded equally often for choosing both types of platform. It was in the test trials that they showed a significant preference for the solo platform, but after increasing the amount of food in the collaboration option, their preference switched to collaboration (and partner) platform.

Recruiting a partner and choosing between collaborative and individual tasks are two further measures that indicate whether individuals in a species understand when they need a partner, in addition to the delay task. If success is driven mainly by an understanding of (or lack of) the role of a partner then we should expect consistency across these variations of the task. Where a species has been tested in at least two, we do see some general consistency: chimpanzees and wolves show success across tasks and rooks were unsuccessful across tasks.

In the next section we move from considering whether individuals know they need a partner, to looking more closely at what they understand about the specific actions that make up a partner's role.

2.4.3 | What do animals represent about the collaborative task and the actions of a partner?

Supporting the partner: Instrumental helping and communication

If individuals have an appreciation of the task or actions the partner needs to perform, we could expect them to help their partner perform these actions, either through instrumental help or by providing information. One way to measure instrumental support is with tool-transfer tasks: when one individual is in possession of a tool and a partner needs that tool to complete her role in the task, do they transfer the tool toward achieving the common goal?

Melis and Tomasello (2013) asked this question by presenting pairs of chimpanzees with a collaboration task in which individuals performed different roles. For each role they needed a different tool and the tools were not interchangeable. The focal subject was given both tools (the tool she needed for her role and the one her partner needed for their role) and they had to discern that the partner lacked the tool to perform her role. Subjects had no prior experience transferring tools to each other, but they did have experience using *both* tools to access food by themselves. Ten out of twelve subjects spontaneously transferred the tool to the partner. There was individual variation regarding how quick subjects “discovered” the transfer solution, and not all but some subjects' first transfer was in response to the partner's request. However, after the first transfer, they all transferred the tools in all trials, handing the tools directly to the partner. An analysis of which tool they transferred also showed that they transferred the correct tool, that is, the tool the partner needed. We cannot rule out the possibility that subjects transferred the tool they did not need themselves. However, when subject's role was the first action in the sequence of two, they often completed their own role before transferring the other tool to the partner, thus, at the time of transfer, both tools were no longer needed by the subject. Follow-up studies with more than two tools could help us distinguish to which extent they are representing the partner's actions as opposed to just knowing that the partner needs to do *something with any tool* (but see S. Yamamoto, Humle, & Tanaka, 2009, 2012, for evidence for selective tool transfer in an altruistic helping paradigm). The transfer of *any* tool gives further support to the hypothesis that they can employ flexibly novel strategies to facilitate coacting with a partner.

In an extension of the tool transfer paradigm, chimpanzees were presented with a new problem that required them to communicate about the location of the tools they both needed to collaborate (Melis & Tomasello, 2019). The two tools were hidden in one of two opaque boxes. One individual in the pair could see the hiding location of the tools (the communicator), whereas the second individual was in a position from which she could open the boxes (the recipient). Communicators learned to position themselves close to the hiding location, at the same time that they offered the key necessary to open the boxes to the recipient. Recipients opened the indicated box, extracted the two tools, gave one back to the communicator and then the pairs collaborated (performing two different roles), and obtained the grapes from the collaboration box. That is, pairs of chimpanzees were able to develop a coordinated strategy that involved: (a) communicators indicating the location of the tools, (b) recipients finding the tools, (c) recipients passing one tool back to the communicator, and (d) the pair collaborating, each using a different tool, to obtain the grapes.

This is not the only study in which great apes have tried to influence and facilitate a partner's actions. Bullinger, Melis, and Tomasello (2014) found that chimpanzees used attention-getting gestures and positioned themselves in front of the hiding location of a tool, so that the recipient could use the tool to deliver food for both. However, recipients did not follow the communicator's signals, communicators stopped communicating, and pairs did not succeed. Voelter et al. (2017) also describe an experiment with orangutans (*Pongo abelii*) in which subjects needed to transfer a tool to a partner, which then the partner could use to manipulate a social-mutualistic option (delivering food for both of them) or a nonsocial option (delivering food only for her/him). Subjects transferred the tool close to the mutualistic option potentially trying to influence the partner into choosing the social-mutualistic option, though partners sometimes followed the communicator's signals but sometimes did not, making their choices according to which would be more profitable for themselves.

These last experiments provide evidence that two of the great apes (chimpanzee and orangutans) can flexibly influence (or manipulate) others, by supporting them in their goal directed actions, when they also have a stake in it. We use the word "manipulation" for the orangutans' study because partners did not have fully aligned goals, so that individuals transferring the tools tried to influence the partner in a way that was profitable for them. In collaborative tasks such as those by Melis and Tomasello (2013, 2019) both individuals are equally motivated to reach the common goal since their goals are completely aligned, they have to work together in close temporal and spatial proximity, and both individuals are familiar with both actions in the task, so that it seems safe to conclude that they are intentionally employing active strategies, in this last example via communication, to coordinate actions with each other.

There are very few studies of this kind in other species, except for an interesting study with pairs of rhesus macaques (*Macaca mulatta*) by Mason and Hollis (1962). Much like the task by Melis and Tomasello (2019), an informant could see where something was hidden (in this case food) and a partner, the operator, could control the apparatus to deliver the food to both monkeys. The informant could indicate to their partner where the food was by positioning themselves in front of it. However, after 480 trials operators did not show any indication of using this information, even though informants were positioned in front of the correct cart in about 60% of trials (chance would be 25%). After role reversal and many more trials the monkeys did reach a high level of success. The extensive learning period suggests that the operators learned to use the cue of the informant's position, but we cannot infer whether the informant was trying to manipulate or influence the operator or whether they were simply more attracted to and likely to approach the baited option.

Role reversal and co-representation

Role reversal has also been used as evidence for an individual's capacity to pay attention to another's actions and represent both actions as part of an overarching collaborative activity (i.e., seeing the joint action from a bird's eye view). The argument is that if individuals collaborating represent both roles, they should learn about their partner's role while participating and performing their own one. Typically, each subject is introduced to one role and after some experience collaborating, their roles are reversed to measure their proficiency with the complementary role (e.g., Carpenter, Tomasello, & Striano, 2005; Fletcher, Warneken, & Tomasello, 2012; Povinelli, Nelson, & Boysen, 1992). The results from these studies tend to suggest that chimpanzees do not pay that much attention to each other's actions whereas children from around 3.6 years of age do (Fletcher et al., 2012). However, as Fletcher et al. (2012) note, this is not surprising given what we know about social learning in chimpanzees; in contrast to children, they generally *emulate* rather than *imitate* (i.e., they pay attention to the results of others' actions rather than to the specific actions, see, e.g., Tennie, Call, & Tomasello, 2009). Thus, it is possible that they paid attention and represented the fact that a second agent needs to manipulate position "x" of the apparatus, but that more specific knowledge about necessary actions is something they acquired through individual learning. To test this, we would need measures of task proficiency that could differentiate between different contents of the representations.

If individuals represent the actions of their partner as well as their own (co-representation) they may show self-other interference effects when participating in joint action, which can result in reduced performance in some tasks (Milward & Carpenter, 2018). This effect has been shown in human adults and children from 4 years old (Milward, Kita, & Apperly, 2014) and, more recently, in common marmosets (Miss & Burkart, 2018). Pairs of marmosets were presented with a version of the joint Simon task using auditory cues to signal which side of an apparatus (left vs. right) marmosets should pull from. In the original individual Simon task the cues are presented congruently to the action (e.g., the cue to pull left comes from the left speaker) or incongruently (e.g., cue to pull left comes from the right) and responses are delayed during these incongruent trials. This interference does not appear when individuals are asked to complete only one part of the task (e.g., only response to left pull cues) unless they also have a partner who is instructed to complete the other half of the task (the joint Simon task; Vesper et al., 2010). Marmosets also demonstrated interference effects: when auditory cues were played from a location incongruent with the action, marmosets were more likely to choose the wrong tray (or their first reach was toward the wrong tray). These interference effects were present, both when doing the whole task alone and when the task was shared with their partner (i.e., each marmoset had access to one side of the tray) but not in corresponding control conditions. The authors suggest that co-representation is unlikely to be based on theory of mind abilities in this species, although marmosets may have some understanding of others as intentional agents and this may be enough for the interference effect (Miss & Burkart, 2018). To date, this is the only experimental evidence of co-representation in nonhuman primates. In addition, marmosets have not been tested in the recruitment or delay tasks used with other species so it is difficult to interpret how these results may relate to their ability to initiate and engage in collaboration.

Distinguishing when the partner can perform his/her role

Plotnik et al. (2011) found that elephants were successful at waiting for their partners in the delay loose-string task. However, the authors reasoned that one possibility is that the elephants had learned to associate only *the presence* of the partner with success. Therefore, they introduced an interesting variation consisting of coiling the partner's end of the rope, so that it was out of reach, making collaboration impossible. As expected, if they understood that their partner was not able to perform her role, subjects did not pull in this condition. An alternative explanation, also used to explain performance in the standard delay task, is that subjects could have learned the contingency between feeling tension on the rope and their own pulling action to get a reward (Plotnik et al., 2011). A piece of evidence against this interpretation is that some subjects left the apparatus before their partners did, whereas if they had just learned to wait for tension in the rope they should have waited as long as their partners were around (see Heaney et al., 2017, for negative results on a similar test).

In this section on actively coordinated collaboration we looked closely at the evidence for flexibility in finding novel solutions to facilitate or support coordination with the partner. There are still very few studies addressing this topic, although it is promising to see that there are several different approaches being taken.

Summarizing the experimental evidence for our category of actively coordinated collaboration, we see that species from a number of taxa can learn to wait for a partner to enable collaboration (chimpanzees, elephants, kea, wolves, domestic dogs, and ravens; Hirata & Fuwa, 2007; Jaakkola et al., 2018; Marshall-Pescini et al., 2017; Melis et al., 2006; Plotnik et al., 2011), although it is difficult with this measure alone to make conclusions about the proximate mechanisms supporting this skill. We also present findings that apes (mainly chimpanzees) recognize *when* a partner is needed to solve the task (they recruit her and choose the appropriate apparatus depending on the partner's availability). In addition, they also facilitate the actions of their partners in the form of instrumental help and by or indicating the location of hidden tools. Whether their intention is to *inform* or *request action* is unclear at this stage, in either case they are communicating *where* they want the partner to act. In other species, there is a limited number of studies that have looked for evidence of actively coordinated collaboration beyond waiting for a partner. Elephants distinguish when the partner's rope is inaccessible, marmosets show evidence that they represent their partner's actions and wolves and hyenas coordinate spatially as well as temporally. Thus, we have evidence from these different approaches that several species can learn something about the role a partner has in collaboration. This is particularly the case for our closest living relatives. Beyond chimpanzees, the evidence is fragmentary. With the exception of the simultaneous and delay versions of the loose-string task, very few paradigms have been tested across multiple species so we do not have a clear representation of how collaborative skills are spread across the animal kingdom.

In the next section we discuss a form of collaboration that emphasizes both the cognitive representations of partner's actions as well as the shared motivation to achieve a goal together.

2.5 | Collaboration based on shared intentionality

Our final category comprises of joint action supported by cognitive skills and motivations to share goals and intentions with others (Tomasello & Carpenter, 2007). Collaboration based on shared intentionality is characterized first by sociocognitive skills that allow individuals to form shared representations about the shared goal and shared intentions to reach that goal. Second, by a joint commitment to pursue and achieve the shared goal together. Each individual cognitively represents the shared goal and the different actions necessary to achieve the goal in an agent-neutral way, so that they can reverse roles if necessary and support each other in the process. This means that each individual simultaneously represents their own goal and intention to reach that goal, and the partner's goal and intention to reach the shared goal, and there is mutual/shared awareness of this. This is sometimes also referred to as "we-intentionality" or moving from the third person perspective to a second person perspective, and it involves the cognitive representation of the goal being accomplished by "us" (Gomez, 1996; Siposova & Carpenter, 2019; Tomasello, 2014).

Collaboration based on shared intentionality is a hallmark of human cooperation. It is the shared goal that differentiates the final category of collaboration from actively coordinated collaboration and it relies not only on the capacity to share mental states but also on the motivation to share them (Tomasello & Carpenter, 2007). However, this is not to say that all human collaboration is characterized by shared intentionality. To begin with, these skills need time to develop over infancy and early childhood, and there is still some discussion about when in ontogeny children acquire the capacity for shared intentionality (Brownell, 2011; Butterfill, 2011; Milward et al., 2014; Milward, Kita, & Apperly, 2017). It can be challenging to identify shared intentionality empirically, but there are several signatures of collaborative behavior based on shared intentionality that we can look for and have been demonstrated by young children (from 3 years onward). We briefly describe evidence from three of these hallmarks: commitment to a shared goal, sharing the proceeds of collaboration, and communication supporting collaboration.

2.5.1 | Commitment

Forming a shared goal creates a sense of commitment that the goal be fulfilled for both individuals, shared knowledge that “we are doing X together”. A study by Hamann, Warneken, and Tomasello (2012) created a situation in which pairs of children were working on a task with mutual rewards: they had to move a horizontal tray up a set of mini stairs together. In one version of the task one child already got her reward before the tray was all the way up the stairs, thus her goal (the reward) was complete. However, for her partner to achieve her goal, she would have to continue to work together to move the tray up the final part of the stairs. Children aged 3.5 years, but not 2.5 year olds, were more likely to continue until their partner achieved her goal when they had been moving one tray together than in a control comparison where each child was moving their own tray, suggesting that they had formed a joint goal during the collaboration, and they are willing to pay a cost to fulfill their commitment to a joint goal. In another line of studies, 3-year-old children, but not younger children, take leave if they do end a joint activity, and protest when a collaborative partner does so without taking leave (e.g., Gräfenhain, Behne, Carpenter, & Tomasello, 2009; Kachel, Svetlova, & Tomasello, 2018; Kachel & Tomasello, 2019). In contrast, chimpanzees presented with a task analogous to the stairs used by Hamann and colleagues did not differentiate between contexts of prior collaboration or independent work (Greenberg, Hamann, Warneken, & Tomasello, 2010).

2.5.2 | Sharing

Another characteristic of joint goals is sharing the proceeds of collaboration. Individuals keep track of their partner's contribution to the joint task and share differently than in situations without collaboration. Hamann and colleagues were able to show that 3 year olds are more likely to share rewards equally when they and their partner worked together to produce them, than when they worked independently toward their own goals (Hamann, Warneken, Greenberg, & Tomasello, 2011; see also Melis, Altrichter, & Tomasello, 2013). At this age, children also consider merit and will share the rewards according to the effort a partner put into the collaboration (Hamann, Bender, & Tomasello, 2014; Kanngiesser & Warneken, 2012). Interestingly, some evidence from field observations of chimpanzee group hunting suggests that individuals taking part in a hunt get access to more of the captured meat (Boesch, 1994; Samuni, Preis, Deschner, Crockford, & Wittig, 2018). However, data from other field sites and experimental studies do not find that individuals share more with collaborators and that other factors, such as begging and proximity to the reward, determine how big a share of the reward individuals get (Gilby, 2006; Hamann et al., 2011; John, Duguid, Tomasello, & Melis, 2019; Melis et al., 2011).

2.5.3 | Communication

Collaboration via shared intentionality is also characterized by new forms of communication that support the initiation and maintenance of collaboration. When collaboration is based on mutual or shared knowledge “we both know that we are both intending to do X and that we are attending to each other's intention to do X", eye contact, or a “communicative look,” can be enough to facilitate collaboration by establishing a joint goal and a commitment to cooperate (Siposova, Tomasello, & Carpenter, 2018; Wyman, Rakoczy, & Tomasello, 2013). In both of these studies, children (4- and 5-year-old) choose between an individual task that provides a low value (but still desirable) reward or a collaborative task that results in a higher value reward. The collaborative task only succeeds if their partner also decides to collaborate, but the children do not know which choice their partner makes before they make their own choice. However, if their partner gives them a so-called “communicative look” (mutual eye contact characterized by wide eyes and raised eyebrows) before they make their choice children are much more likely to choose to collaborate. In effect, this look communicates that both individuals *know together* (each individual knows that the partner knows that she knows) best and intended option. Using an equivalent task structure, Duguid et al. (2014) found that 4-year-old children adjust levels of communication (verbal and gestural) before decisions to collaborate to maintain high levels of coordination when the cost of coordination failure increases. In the same task, chimpanzees did not communicate before they made decisions to collaborate but, instead, responded to the increased cost of coordination failure by being less likely to collaborate (Bullinger, Wyman, et al., 2011; Duguid et al., 2014). Without the ability to share their intentions to collaborate, the findings suggest that chimpanzees are more likely to take a risk-free individual option.

The findings to date are consistent with collaboration via shared intentionality being unique to humans. However, determining the exact nature of the differences between nonhuman ape collaboration and human collaboration is still a work in progress.

3 | CONCLUSION

We suggest four categories of collaborative activities and some of their possible underlying proximate mechanisms. Our first two categories, by-product and socially influenced cooperation, do not qualify as true "collaboration" from a psychological perspective, as there is no intentional coordination. The joint action is the consequence of external stimuli or events that influence individual action, or the result of proximate mechanisms, such as social facilitation, or stimulus enhancement, which can lead to (superficially) complex forms of coordinated action. For example, in the basic loose-string task (without a delayed partner), simply by pulling the rope simultaneously purely by chance in an attempt to get to the reward, or by pulling more often when others are present, subjects could succeed. Until more evidence accumulates, we think that many animal species would fall somewhere within the socially influenced collaboration category.

Our review is strongly biased toward chimpanzees, not only because it happens to be the area of expertise for the authors, but simply because this species has been a focus of research on the cognition of cooperation for the theoretical reasons outlined in the introduction, and there is now a vast range of tasks and different dependent measures trying to tap into the proximate mechanisms of collaboration. This means they are the only species that we can generate a good working hypothesis as to how they collaborate.

We do think that there is enough accumulating evidence to argue that chimpanzees fulfill the requirements for actively coordinated or intentional collaboration, as we have outlined here. In the loose-string task, chimpanzees not only wait for the partner, but they also recruit her/him or choose the solo trays when there is no partner. Beyond this task, chimpanzees also provide instrumental help for partners to fulfill their role by transferring tools, and they influence their partner's actions by indicating the location of hidden tools. So, these studies together suggest that they know *when* they need a partner, something about *what* the partner needs to do and are also able to communicate to the partner *where* to act. We also have evidence from studies looking at their socio-cognitive skills that they treat others as intentional, goal-directed agents. That is, they respond differently when someone is unwilling versus unable to do something (e.g., Call, Hare, Carpenter, & Tomasello, 2004); or to results caused by human intentional action versus those caused by a machine (Engelmann, Clift, Herrmann, & Tomasello, 2017); and they also distinguish who is behind the theft of their food, punishing a conspecific feeding on their stolen food *only* if it was her who stole it (Jensen, Call, & Tomasello, 2007). In other words, chimpanzees seem to recognize the causal role intentional agents have played in creating specific outcomes. Combining this evidence with the results from the collaborative tasks reviewed above, where they actively initiate and support the joint action by waiting, recruiting, and helping the partner gives support to the hypothesis that they understand the causal role of a partner in collaboration.

In addition, they also show sensitivity to what others perceive such as what they can or cannot see or what they have seen, in a number of different contexts (Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001; Kaminski, Call, & Tomasello, 2008; Liebal, Call, Tomasello, & Pika, 2004); skills they integrate into their intentional use of gestural communication (Tomasello & Call, 2019). There is also evidence to suggest that apes predict an agent's actions according to their false beliefs (Krupenye, Kano, Hirata, Call, & Tomasello, 2016, 2017). A recent study even suggests apes could be using this type of knowledge about what others can or cannot see, to facilitate coordination in a collaborative task. Grueneisen, Duguid, Saur, and Tomasello (2017) found that chimpanzees and bonobos were more likely to make the results of their own actions visible to a partner in a collaborative context, providing partners with information they needed for their decisions to coordinate successfully. Future studies could explore the extent to which chimpanzees use theory of mind skills for collaboration. If they do use information about what others can see, hear, or have seen or heard, to make decisions about how best to collaborate, this would challenge previous claims that chimpanzee socio-cognitive skills are mainly employed competitive contexts (Lyons & Santos, 2006; Schmelz & Call, 2016).

As important as demonstrating what chimpanzees can achieve, will be identifying the specific limitations of their collaborative abilities. For instance, tasks involving selective tool transfer indicate that chimpanzees represent something about the task a partner needs to perform, but this does not seem to benefit them in a role reversal task. As another example, what are the limits to the types of information individuals can integrate to facilitate collaboration? There is some indication that chimpanzees can take into account what a partner can see for collaboration (e.g., Grueneisen et al., 2017), but can they also take into account the preferences of others when they coordinate? Finally, we still have a great deal to learn about how chimpanzees use communication in a collaborative context: which facets of the signal or the context facilitated recipient's understanding of the communicators (humans and conspecifics) in Melis and Tomasello (2019), in a way they have not in previous tasks? How flexible are their communicative skills if, for example, approach to a certain target is not a clear signal anymore?

Our category for actively coordinated collaboration is permissive in terms of the psychological mechanisms possibly involved. At its simplest it involves distinguishing the causal role a partner's presence (and possibly actions) plays in achieving one's goal. This means knowledge about the mediating and instrumental role that the partner plays in solving the task. In the more complex forms, it would involve monitoring the goals, intentions, and perceptions, of other individuals in relation to one's own, as well as the capacity to influence their mental states toward those goals. Much can be achieved within this category when individuals understand the actions necessary to achieve a goal and combine this with an understanding of others as goal-directed agents. With this third person perspective, individuals can not only adjust their own behavior to accommodate the goal-directed actions of collaborators but also influence or support their actions toward the common goal. If we extend the category to the limits it could also include what Siposova and Carpenter (2019) term *common* goals: individuals can infer from the situation, or from recursive reasoning that their intentions and goals are aligned. There is no evidence that chimpanzees, or any other species, have common goals in this sense. For this we would need evidence that they are sensitive to others representing one's own intentions and goals, and as far as we know, this has not been addressed empirically.

Markers of our final category, collaboration based on shared intentionality, are not demonstrated until the age of about 3 years in human children. Commitment to completing the shared goal, sharing the spoils of collaboration fairly, and new forms of communication allows humans to collaborate with a level of complexity and flexibility we do not see in other species. Importantly, this comes from a combination of the motivation, as well as cognitive ability, to share psychological states (Tomasello & Carpenter, 2007). In understanding the spectrum of intentional collaboration (our two categories: actively coordinated collaboration and collaboration via shared intentionality) we need to consider how differences in both aspects impact the collaborative behavior we observe. For example, whereas 3-year-old children show a preference for collaboration over working independently when they can achieve the exact same rewards (Rekers et al., 2011), chimpanzees prefer to work alone (Bullinger, Melis, & Tomasello, 2011). However, we have yet to explore how this difference in motivation interacts with the cognitive representations of the role of the partner.

A number of other species have shown being able to wait for a partner before acting (Heaney et al., 2017; Marshall-Pescini et al., 2017; Plotnik et al., 2011). However, as there are alternative ways to interpret success in this task, we would need additional transfer tasks to investigate what these species understand about the role of the partner. So far, beyond the delayed loose-string task other potential examples of actively coordinated collaboration include: orangutans transferring tools to manipulate partners (Voelter et al., 2017), elephants that do not expect partners to pull an out-of-reach rope (Plotnik et al., 2011) and wolves that are capable of coordinating between alternatives (Marshall-Pescini et al., 2017). For chimpanzees, (and to a lesser extent the other great apes), the evidence for actively coordinated collaboration is supported by different collaboration measures and an extensive body of research about how chimpanzees represent the actions and mental states of conspecifics so we have converging evidence to enrich the interpretations of their collaborative behavior. This is less so for many other species and it is a particular challenge if we consider that some of the most striking feats of collaborative hunting are done by species that will never be able to take part in traditional behavioral experiments (such as bubble-net fishing by humpback whales, *Megaptera novaeangliae*; D'Vincent, Nilson, & Hanna, 1985), so to tackle the comparative question will also require an expanding repertoire of experimental methods and measurement techniques.

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The authors have declared no conflicts of interest for this article.

AUTHOR CONTRIBUTIONS

Shona Duguid: Conceptualization. **Alicia Melis:** Funding acquisition, conceptualization.

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