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Collaboration in Great Apes

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Abstract

Observations from both naturalistic and experimental contexts reveal substantial collaborative abilities in our closest living primate relatives. Great apes flexibly coordinate behavior, mutually communicate to negotiate the start and end of joint social activities, and demonstrate group-specific patterns of collaboration. The basis of these abilities, however, is debated, with some arguing for fundamental discontinuities in the cognitive and motivational underpinnings of collaboration in humans compared to other primates. Continued research will help to clarify these issues and illuminate key questions, such as the extent to which collaboration can be learned, how norms facilitate collaboration, and how communication and collaboration are linked. These efforts will further clarify the mechanisms that support and stabilize collaboration as well as the factors that may have favored the emergence of expanded collaborative proclivities in the human lineage.

Introduction

Humans last shared a common ancestor with chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) approximately 7–10 million years ago. With these other ape species, humans share many traits, such as large, complex brains; tool making and use; reliance on skills and behaviors that are transmitted socially and often sustained over generations; and remarkably complex social lives, including relationships with group members that span decades. A distinctive characteristic of the human niche is a propensity for cooperative behaviors that vary dramatically in scope relative to those observed in other primates (Fuentes 2018). These behaviors include a multitude of collaborative endeavors, which manifest at all scales and in ever-expanding, imaginative ways. Much of what underpins our collaborative abilities and motivations, however, is debated. Studying our closest living relatives can help illuminate the evolutionary basis of our cooperative capacities, including what is essential for successful collaboration.

Examples of cooperative behavior, in which individuals act for the benefit of others, abound among nonhuman primates (henceforth primates). For

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example, primates share food, groom each other, and defend each other from attack. To be considered collaboration, a cooperative act needs to go further and demonstrate coordination between two or more individuals working together toward a common goal. The extent to which nonhumans of any species intentionally coordinate their behavior toward an agreed-upon goal is contentious. Some argue that both the cognitive ability and the motivation to share collaborative intentions are exclusive to humans.

Observations from both natural and experimental settings, however, are converging on the perspective that our closest living relatives possess robust collaborative abilities. Nonhuman great apes can intentionally, flexibly coordinate behavior, and in some cases these collaborative behaviors meet criteria for shared intentions toward a common goal. Further, there is evidence that apes enter and exit joint activities in similar ways to humans, suggesting that they treat (and may think of) these endeavors as shared ones. Finally, apes may choose to conform to group-specific patterns of behavior, suggesting that shared social norms could influence when and under which conditions apes collaborate. What follows is a discussion of this evidence, focused particularly on chimpanzees, as research to date has centered largely on this species, as well as a discussion of ongoing and future directions in this exciting area of research.

The Evolution of Cooperative Behavior

An aptitude for and profound reliance on cooperation are considered hallmarks of the human species. Cooperation in primates has long captured scientific curiosity, as it may help elucidate the evolutionary basis of these proclivities in our lineage. More broadly, the diversity of cooperative behaviors in primates offers an opportunity to examine what supports and constrains the evolution and expression of cooperation (Kappeler and van Schaik 2006). *Cooperation* involves organisms acting in ways that are beneficial to others, or to both others and the actor. Cooperative behaviors are also sometimes referred to as *prosocial*, which refers more specifically to behaviors performed by one individual for the benefit of another. Costly, cooperative behaviors toward non-kin are further identified as *altruistic*.

On the surface, cooperative behaviors may seem an anathema to a basic premise of evolution by natural selection: that individuals should act in ways that maximize their own welfare and reproductive success (fitness). This apparent puzzle has been reconciled via theoretical advancements in several respects. Two processes that can help explain cooperation include kin selection, wherein an individual's inclusive fitness is improved if help is given to other individuals who share the individual's genes, and reciprocal altruism. Reciprocal altruism suggests that helping another individual pays off because that individual is then more likely to assist the helper in return at a future time

(Axelrod and Hamilton 1981). In addition, behaviors that assist a recipient may also be beneficial to the helper (Cronin 2017). For example, mutual benefits likely result from common cooperative activities in chimpanzees such as territorial boundary patrolling, coalitionary tactics between two individuals against a third, group hunting, and meat sharing (Mitani 2009). Additional processes of cumulative cultural learning, cultural evolution, and gene–culture coevolution are hypothesized to have exerted profound influences on the capacity for and scale of cooperative behavior in humans. For example, selection for norm psychology and the associated importance of reputation and punishment may help maintain cooperative group living (Chudek and Henrich 2011). Understanding the evolution and operation of these dynamics in the social lives of other primates is a promising avenue of ongoing study.

Defining Collaboration

A subset of cooperative behaviors meets further criteria for *collaboration*. Collaboration comprises two or more individuals working together to achieve benefits, or two or more individuals coordinating their behavior to produce outcomes from which both individuals benefit (Boesch and Boesch 1989; Melis and Warneken 2016). Collaboration can be considered on a spectrum, from functionally collaborative behaviors in which individuals have no underlying intention to coordinate actions, to intentionally collaborative behaviors in which individuals purposefully coordinate their behavior. Shared benefits that result from individual agents acting in parallel in response to the same environmental conditions or the same social cues can be described, respectively, as "by-product" or "socially influenced" collaboration. In these cases, the appearance of coordinated efforts is a mere by-product of individuals adopting the strategy that best advances their individual aims (Duguid and Melis 2020). A key challenge in the study of collaborative behavior is thus to evaluate what participants understand and desire regarding a partner's efforts.

The Underpinnings of Collaboration in Great Apes

According to Tomasello and colleagues (e.g., Moll and Tomasello 2007; Tomasello and Carpenter 2007), true collaboration necessitates *shared intentionality*: the ability to create and share mental states in the service of achieving a goal. Collaborators are posited to possess a "bird's-eye view" enabling them to conceive abstractly how all actors' behaviors fit together. In addition to this cognitive ability, collaborators must also possess the motivation to sustain joint commitment to the shared goal. A quintessential human example of shared intentionality collaboration on a small scale would be individuals adopting

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different roles to complete collective foraging tasks from which rewards are equally distributed (Apicella and Silk 2019; Tomasello et al. 2012).

Observations from naturalistic settings as well as recent methodological and theoretical advancements from varied disciplines suggest a reconsideration of the scope and underpinnings of intentional, flexible collaboration in great apes (Table 2.1). First, in chimpanzees, experimental studies reveal a robust understanding of a partner's causal role, which likely facilitates collaboration even if shared intentionality is not present (Duguid and Melis 2020). Second, multiple ape species create and sustain joint commitment to social activities in ways

Table 2.1 Example evidence in great apes for key cognitive and motivational criteria proposed to underlie collaboration from either experimental (E) or naturalistic (N) contexts. Adapted from information in Duguid and Melis (2020), Heesen et al. (2021), and Samuni et al. (2018a).

Criterion	Indicator	Example of Positive Evidence
Understand that a partner is necessary	Wait for a partner before acting	Chimpanzees inhibit pulling in loose-string task until partner is present (E)
Understand that a partner has a causal role	Recruit a partner	Chimpanzees solicit or manipulate others into joint action; open door for partner when needed; pick best collaborators (E)
	Choose collaborative vs. solo apparatus	Chimpanzees opt to work alone unless involving a collaborator will maximize reward (E)
Represent and support specific actions that a partner needs to perform	Provide information or instrumental help	Chimpanzees communicate location of and provide key to access two tools; partner accesses tools and passes one back to communicator; partners work together for reward (E) Orangutans pass tool to bring partner closer to cooperative vs. solo apparatus (E)
Co-represent one's own and partner's actions as part of an overarching activity	Act in different roles	Chimpanzees flexibly adopt roles of driver, chaser, blocker, or ambusher during group hunts (N)
Track partner contributions	Share proceeds of collaboration	Chimpanzees share meat preferentially with hunt participants over bystanders (N)
Share intent to act together	Mutually communicate	Chimpanzees flexibly gesture to coordinate grooming handclasp (N)
Commit to task completion	Communicate to start and end social interactions	Chimpanzees and bonobos moderate "entries" and "exits" of social interactions according to rank, social bond strength (N)
	Resume interrupted social activities	Bonobos adopt same role and groom same location as before interruption (N)

that are analogous to how humans do so; joint commitment to a shared goal is essential for realizing collaborative goals (Heesen et al. 2021). Third, long-standing field observations suggest that chimpanzees may, in fact, demonstrate shared intentionality. This capacity could rest on sophisticated abilities for perspective taking and role reversal, but new arguments also highlight how shared intentionality in great apes could emerge from social norms (Papadopoulos 2023). Several of these advancements frame the selective pressures of collaboration as arising in response to social as well as ecological challenges. These developments have implications for understanding the processes that support the evolution and expression of collaborative behavior across taxa, including what supports or inhibits successful collaboration.

Flexible Coordination with a Partner

Understanding a Partner's Causal Role

Robust evidence indicates that at least some primates can intentionally and flexibly coordinate their behavior, which is a necessary building block for collaboration. This capacity results from the abilities to view others as intentional agents and to recognize the causal role of such agents in social situations. These behaviors, termed "actively coordinated collaboration" by Duguid and Melis (2020), do not necessarily involve shared intentionality but clearly reflect an understanding of a partner's role as well as the motivation to collaborate with them. Experimental evidence comes from studies using paradigms such as the loose-string task (Hirata and Fuwa 2007), in which a rope is looped through an out-of-reach platform, on which rests a reward. The two ends of the rope are then threaded into an enclosure, but the ends are too far apart for one subject to pull simultaneously. An individual must pull simultaneously with a partner to avoid the string becoming unthreaded from the platform and thus useless in drawing in the reward. Chimpanzees understand when a partner is needed for this task and will recruit a partner if necessary. Tool transfer tasks have demonstrated that chimpanzees will go even farther than recruitment, taking steps to facilitate a partner's actions when needed (Duguid and Melis 2020). Tool transfers have been documented between chimpanzees in the wild and comprise a functional form of teaching (Musgrave et al. 2016). Across captive and wild settings, these observations highlight chimpanzees' capacities to appreciate what a partner requires to complete a task.

There is also evidence for these capacities in other apes. In one study, for example, an orangutan (A) could not access a reward, but her partner (B) could if A provided a tool. Once A passed the tool to B, B could either manipulate a social apparatus, which would provide a reward to both A and B, or a nonsocial apparatus, which would reward only B. When A passed the tool closer to the social apparatus, this had the effect of bringing B closer to that location than to the nonsocial apparatus. Despite A's apparent efforts to influence her partner,

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however, B did not necessarily choose the social apparatus, highlighting the critical role of motivation in success at collaborative tasks (Völter et al. 2017).

Cognitive versus Motivational Constraints

Differentiating whether participants are *unwilling* or *unable* to collaborate poses a central challenge (Yamamoto 2020). For example, chimpanzees prefer, at least sometimes, to work alone rather than to collaborate (Bullinger et al. 2011). In contrast to humans, chimpanzees often do not assist others in the absence of a request, even if they understand what another requires (Yamamoto 2020). Thus, while cognitive factors may place limitations on the scope of collaboration, it is equally important to identify motivational constraints.

Such constraints could reflect multiple factors, such as interspecific differences in psychology across taxa or differing developmental experiences. In addition, context is likely of considerable importance. For example, in the Goualougo Triangle, Republic of Congo, chimpanzees have been observed transferring tools to conspecifics without an explicit preceding request. In addition, they transfer termite-gathering tools to each other more frequently than do chimpanzees in Gombe, Tanzania. There are notable differences in the complexity of tool tasks between these two different chimpanzee populations. The differences in transfer behavior are present despite similar requesting behavior in both populations, suggesting a difference in willingness in association with tool tasks of differing complexity (Musgrave et al. 2020). It will be instructive in future research to identify ontogenetic factors that give rise to and maintain this type of intraspecific variation in cooperative social interactions.

Joint Commitment in Great Ape Social Interactions

Studies of *joint commitment* have provided novel insights into how great apes initiate and sustain social interactions. Joint commitments can be thought of as both an achievement and a process involving pursuit of endeavors to which two or more individuals feel reciprocally obligated (Heesen et al. 2021). Mutual communication to resume interacting after an interruption provides clues that partners feel such an obligation. For example, experiments have been conducted involving triadic play sessions between a bonobo, a human, and an object. When humans deliberately and abruptly ended a play session, bonobos spontaneously produced gestures in an attempt to reengage the human partner. The bonobos did not simply attempt to gain possession of the objects involved in the play session but communicated to resume the joint activity, potentially indicating that they viewed the play session as a joint commitment (Pika and Zuberbühler 2008).

Both chimpanzees and especially bonobos exchange communicative signals, such as gestures and mutual gaze, when entering and exiting joint commitments with each other, similar to politeness efforts that humans deploy to manage their public reputation or "face." Humans calibrate their signaling when entering and exiting social encounters according to the relationship between partners: leave-taking between less familiar partners, for example, is imbued with more politeness efforts compared to leave-taking between close friends. Similarly, bonobos exhibited shorter entries and exits with lower-ranking and socially close partners, suggesting that relationship quality has subtle impacts on how individuals enter and exit joint commitments. Bonobos are generally considered more tolerant than chimpanzees, which potentially facilitates greater communication, but more work is needed to clarify the basis for the species differences observed between bonobos and chimpanzees. Both bonobos and chimpanzees showed more elaborate exiting behavior when ending play compared to grooming sessions. As play sessions are faster-paced and can more easily escalate in intensity, greater care may be required to close these interactions successfully (Heesen et al. 2021).

These studies of joint commitment illustrate that great apes tailor signaling to share social experiences. Going forward, it will be illustrative to document interindividual variation in signaling behaviors to further understand the potential fitness benefits of variable skill in navigating these types of encounters, as well as the implications for the functioning of primate social groups as a whole. These interactions also provide an opportunity to probe definitional questions about how social interactions, when characterized by mutual coordination, might constitute collaboration. In such cases, achieving a successful, mutually fulfilling social interaction—rather than, for example, a specific resource—could comprise the immediate goal.

It may also be fruitful to examine communicative signaling in a broader set of interactions that require careful coordination to sustain participation by multiple individuals, including those which might not typically be considered collaboration. For example, chimpanzees in Central Africa make and use tools to gather termites from both subterranean and aboveground termite nests (Sanz et al. 2004). In the subterranean context, chimpanzees use a robust, wooden puncturing tool to access the underground nest before using a flexible herb stem to extract termites. Puncturing into these nests is a physically difficult task, so once created, the tunnels themselves have value. For example, infants and juveniles lack adequate strength to puncture the soil and thus must share or reuse tunnels created by older, stronger individuals (Musgrave et al. 2021). Careful coordination of activity could be needed for multiple individuals to negotiate simultaneous exploitation of fishing tunnels.

Applied across contexts and species, these approaches have rich potential to illuminate how primates and other animals initiate collaborative activities, what is necessary to do so successfully, and how signaling failures could contribute to the breakdown of collaborative activities. Future work could also help to clarify how the perspective of joint commitment, as a process, informs other proposed categorizations of collaborative behavior (Duguid and Melis 2020) and in what ways these processes of joint commitment overlap with shared intentionality, as described by Tomasello and colleagues (e.g., Moll and Tomasello 2007; Tomasello and Carpenter 2007).

Shared Intentionality Collaboration

Similar to the concept of actively coordinated collaboration (Duguid and Melis 2020), shared intentionality collaboration involves multiple agents coordinating their behavior to accomplish a common goal. Shared intentionality is hypothesized to further involve the ability to conceive abstractly of participants' interlocking roles. In addition, partners should be motivated beyond their own immediate gains and view a task as a joint endeavor to which both individuals are committed (Moll and Tomasello 2007). For example, children can take on the different roles in a collaborative task and will continue the task even after they have been rewarded; they also share proceeds according to whether they worked together or alone (summarized in Duguid and Melis 2020). Whereas experimental studies have typically not detected these proclivities in captive apes, there is potential evidence for indicators of shared intentionality in observations of wild chimpanzees.

Potential Shared Intentions among Wild Chimpanzees

One possible candidate behavior is group crossing of village roads by wild chimpanzees at Bossou, Guinea. Adult males have been observed to coordinate a crossing in several ways. Two males may simultaneously adopt different roles: one waits in the middle of the road during the crossing, scanning the road and waiting for others to cross quickly, while another male typically takes the position of the last individual at the rear of the group (summarized in Yamamoto 2020). Another candidate example is group hunting by chimpanzees in Taï Forest, Côte d'Ivoire. These chimpanzees regularly hunt monkeys, with hunts happening almost every day during the rainy season months. During a hunt, key criteria for collaboration have been observed: individuals occupy different roles and sharing is based on partner effort. The specific roles for chimpanzees in group hunts, described by Boesch (2002), include driver, chaser, blocker, and ambusher. The driver follows and thus moves the prey in a particular direction, typically without trying to capture the monkey himself, while blockers position themselves in trees to prevent prey from escaping. A chaser attempts to catch up with a fleeing monkey. Finally, an ambusher positions himself where he will not be easily detected, in the monkey's perceived escape route. As the monkey flees toward him, the monkey must either turn back, toward the chaser(s), or attempt to retreat down into the lower canopy, where the chimpanzees have better success capturing it. During the hunt, individuals may shift to different roles depending on the actions of other chimpanzees and the monkey's attempted escape routes.

Intraspecific Variation in Collaborative Behavior

An alternative interpretation of these group hunts is that rather than being collaborative, they are simply a by-product of all individuals attempting to capture prey. In other chimpanzee populations, evidence for collaborative hunting has not been detected. It is also possible that the cognitive and motivational underpinnings of hunting vary by population. One possible reason for this difference is that the dense, closed canopy forest at Taï permits arboreal monkeys many escape routes, and so coordinated efforts could be required for chimpanzees to be successful in capturing prey. Several findings at Taï support the interpretation of group hunting as a collaborative activity. Group hunts are indeed more successful than individual hunts, and individuals who initiate a hunt have been observed vocalizing to solicit the participation of others (Boesch and Boesch 1989). In addition, there is a positive relationship between hunting participation and meat sharing (Samuni et al. 2018a), indicating a link between hunter efforts and distribution of rewards. Finally, urinary oxytocin among Taï chimpanzees is elevated following a hunt, and it is similarly elevated following the sharing of both meat and non-meat foods. This pattern suggests that the observed, elevated oxytocinergic activity in the context of group hunting is not an artifact of general stress but is specifically associated with the prosocial interactions that occur in this context (Samuni et al. 2018b). Given that individuals preferentially share all food types with close social associates, these dynamics illustrate how the oxytocinergic system likely helps mediate a feedback loop, such that collaborative acts and enduring social bonds are mutually reinforcing (Samuni et al. 2018b).

Complementary evidence for intraspecific variation in chimpanzee cooperative tendencies comes from observations of several groups of sanctuary-living chimpanzees. In a resource-donation experiment, levels of prosocial helping varied according to group (van Leeuwen et al. 2021). In all three groups studied, helping behavior increased over time. These observations highlight the importance of considering intraspecific variation when drawing conclusions about any given species' potential for collaborative behavior. In addition, it is important to consider that experiments over short time periods may not provide a full picture of prosocial potential. Continued, explicit focus on variation and plasticity are needed to explore the extent to which cooperation can be learned (Vale and Brosnan 2020) and what role group-specific norms might play in maintaining this variation.

Social Norms and Shared Intentions

How Social Norms Support Collaboration

Social norms are a vital correlate of collaboration. Norms facilitate inference and enforcement regarding how to behave in a complex cultural niche,

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including when and how to cooperate with others. Norms can also increase the effectiveness of social transmission of information (Chudek and Henrich 2011). Shared intentions are hypothesized to facilitate, and ontogenetically precede, normative behavior (Tomasello and Carpenter 2007). Conversely, according to the *normative model* (Papadopoulos 2023), shared social norms (Andrews 2020) can serve as the necessary ingredient to support shared intentions. By helping individuals understand and predict others' behavior across different contexts, social norms make it easier to align and coordinate their own behavior with others. Andrews (2020) suggests that norms can be identified when animals choose to conform to a pattern of behavior and outlines four prerequisites for this "naïve normativity":

1. The ability to identify agents
2. The capacity to sense in-group versus outgroup differences
3. An aptitude for social learning of group behaviors
4. The ability to respond to appropriateness

There is ample evidence that apes recognize each other, differentiate in-group versus out-group members, and socially learn group-specific behaviors such as tool use. Most of the debate centers around the fourth criterion: To what extent do apes respond to appropriateness? This question is fundamental for recognizing norms, understanding how norms guide collaboration, and illuminating broader questions about the role of normative behavior in the sociality of great apes and other species, including humans.

Responding to Appropriateness: Punishment and Rebuke

How chimpanzees respond to appropriateness is typically evaluated by looking for clear evidence of *punishment* or *rebuke* of norm violators. In wild chimpanzees, a possible example comes from punishment directed at those who are aggressive to infants, as this behavior can elicit strong punitive responses from third-party group members. There is mixed evidence for third-party punishment by chimpanzees in experiments; negative results have historically bolstered claims that this phenomenon, and thus true normative cognition, is unique to humans. There are several issues, however, with this interpretation. First, individuals in the wild have many opportunities to interact with each other over extended periods of time and to select with whom they want to cooperate. Long-standing groups are thus more optimal for investigating social norms and punishment, as norms result from *social*, not biological, *processes* (Andrews 2020). Fittingly, punishment appears more likely to occur in the context of experimental setups that allow for naturalistic interactions over extended time periods. Over a ten-month period, Suchak et al. (2016) found that chimpanzees punished freeloaders in a test where multiple individuals needed to collaboratively pull an apparatus for a reward. One of the most effective strategies appeared to be the avoidance of freeloaders, as workers frequently

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withdrew or stopped pulling until the freeloader moved away from the apparatus. There were also occasions when third parties directly intervened in favor of the victim of freeloading, against the freeloader. Similar to findings of van Leeuwen et al. (2021), chimpanzees began to increasingly favor cooperative behavior as the study progressed, suggesting that extended time periods may be necessary for individuals to converge on a preferred strategy, including a cooperative one, and thus to exhibit rebuke (Suchak et al. 2016). Rebuke may also be more likely to be observed in experimental setups such as that of Suchak et al. (2016), where participants could freely move and interact.

While the observation of rebuke could be a sufficient indicator of norms, it is not a requisite, as the absence of rebuke does not necessarily mean that individuals do not hold expectations about what is appropriate (Papadopoulos 2023). It may, for example, simply be too costly to express rebuke, and violation of expectation could be expressed via more subtle indicators. In addition, outward response to violation of expectation may itself be normative and variable between populations. Thus, while it remains a priority to examine how primates assess the appropriateness of others' actions with respect to social expectations, it will be fruitful to disentangle a role for norms in guiding collaborative conduct from the outward expression of punitive rebuke. Studies should look for patterns of behavior in collaborative contexts and evidence that individuals are choosing to adhere to those patterns, as well as what happens when individuals do not adhere. Detailed observations of communicative signaling in these contexts (Heesen et al. 2021) will help to clarify whether individuals are acting out of expectations about others' behavior or simply based on personal preference (Andrews 2020).

Communication and Partner Choice Facilitate Collaboration

A key insight that emerges from observations of collaborative behaviors in primates across varied contexts is the importance of communication (Duguid et al. 2020). Communication facilitates the "togetherness" of both the commitment to act and the act itself: individuals *together* commit to acting *together* (Papadopoulos 2023). Great apes are capable of both components. Apes can intentionally, flexibly communicate, which is necessary to express a genuine choice to adhere to a behavior pattern and commit to a goal. Willingness to make these commitments is evidenced on the basis that apes can be seen to *opt in* to different activities. For example, chimpanzees have a fission-fusion social system in which they divide into subgroups of variable size and composition, choosing with whom they will coordinate travel. Chimpanzees also readily communicate to coordinate commitments (as described above; see also Table 2.1). Communication has even been documented to coordinate a joint *cultural* practice—the grooming handclasp—in which partners simultaneously raise their arms overhead and clasp their partner's extended arm, wrist, or hand during a grooming bout (Goldsborough et al. 2023).

In both natural and experimental settings, further examination is needed as to which types of signals are used depending on participant identities and contexts (Heesen et al. 2021). In experimental setups, limiting communicative options in any modality (e.g., vocal, gestural) can impact participants' abilities to coordinate action effectively. Thus, future work should continue to allow participants to interact and communicate freely, insofar as is possible (e.g., Suchak et al. 2016), or should explicitly evaluate how communication impacts success at coordinating activities (Duguid et al. 2020). This could help to illuminate outstanding questions such as the nature and reasons for differences between chimpanzees and bonobos in cooperative behavior (Yamamoto 2020). Are bonobos and chimpanzees equally proficient at expressing their interests, but bonobos simply more motivated to respond to requests (Duguid et al. 2020)? Further efforts in this domain will also help to clarify debates regarding when cooperative, helping behaviors that increase in response to communicative acts (e.g., requesting gestures by a partner) are "genuine" versus when they result from a helper's motivation to avoid harassment.

Partner choice is also clearly an important variable in moderating the success of collaboration, and thus situations that allow for partner choice will best reveal collaborative skills. For example, chimpanzees are more likely to cooperate when they can preferentially work with those who are unlikely to monopolize resources, those with whom they have successfully collaborated in the past, and potentially those of close dominance rank or kin (Enigk et al. 2020; Vale and Brosnan 2020). One implication of these findings is that because there can be stark differences across individuals' willingness to collaborate, observations based on a limited number of dyads cannot necessarily be broadly generalized. It is also important to consider the potential for temporal variation in which factors are most important when selecting a partner. These could vary developmentally or according to the unique mix of ecological and social challenges an individual is confronting. Further, collaborative interactions may both rest upon and generate trusting relationships that continue to develop over time.

It is critical to note that clarity on the roles of communication and partner choice in experimental settings will only be achieved if experiments guarantee participant understanding of a task. There have been discrepant results regarding how social relationships influence whether animals are successful. Do animals, for example, cooperate better when they are closer or further apart in rank? Tests of participant understanding are thus essential for disentangling the effects of these potentially relevant variables (Massen et al. 2020).

Future Directions

Collaboration is of vital importance to human culture. Ontogenetic research suggests that from early in life, humans possess skills and motivations to work

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with others to achieve shared goals. The basis for differences in collaborative skills between humans and nonhumans is multifactorial. The human life history pattern—in which large-brained, slowly developing infants necessitate extensive care and provisioning—has favored the coevolution of cooperative caretaking, in which alloparents collaborate to help raise children (Hrdy 2009). Collaboration for efficient foraging would have conferred additional benefits, selecting for the skills and motivation to coordinate behavior (Apicella and Silk 2019). Cultural evolution and gene–culture evolution have likely further enhanced our capacities for and norms around collaborative behavior (Chudek and Henrich 2011) and perhaps also the cognitive correlates of our social skills (Heyes 2018). In addition, cross-cultural differences in human prosocial behavior highlight the importance of historical processes and cultural narratives, intersecting in dynamic ways to produce significant variation. The question of why we collaborate, generally and in any particular instance, necessitates a consideration of these nuances.

Understanding the basis for the scope and diversity of collaborative behaviors in humans can be aided by a comparative evolutionary perspective derived from studying our closest living relatives. As an example, chimpanzees intentionally and flexibly coordinate their behavior in a range of natural and experimental settings, relying on a rich understanding of how working with a partner can lead to shared benefits. In addition, multiple ape species tailor signaling for entering and exiting joint commitments according to partner characteristics, suggesting that they are sensitive to the social obligations that emerge via these joint interactions. In some cases, their collaborative behaviors show signature criteria used to identify the presence of shared intentions in pursuit of joint goals.

The human ability to use language to mediate entry into and coordination of joint goals over lengthy time scales is undoubtedly an important component of human collaboration and species differences in collaborative ability. King (2004) argues that among nonhuman great apes, both actions and meanings are constructed and embodied, through co-regulated, multimodal (gestural, vocal, touch) communication. When experiments are undertaken, researchers should be sensitive to the critical importance of freedom to communicate and to choose partners, so as to ensure that motivational differences can be disentangled from cognitive variables. In both naturalistic and experimental contexts, detailed assessments of how primates enter, maintain, and exit these joint activities, as well as how this varies (ontogenetically, inter- and intra-specifically) across contexts, will greatly expand our understanding of how communication facilitates collaboration for nonhuman primates. These studies may also help to illuminate the myriad cognitive correlates of collaboration. For example, the success of collaboration could be improved by enhanced abilities to consider what others know or believe, as well as by the ability to evaluate and plan for multiple potential future situations. How these abilities compare across human and nonhuman primates is an important area of ongoing research.

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It is also increasingly apparent that apes may develop group-specific patterns of cooperative behavior, suggesting that norms could play a role in influencing the expression of collaboration. Norms may be critical in providing a common substrate through which social animals align their behavior and within which shared intentionality can manifest (Andrews 2020; Papadopoulos 2023; Whiten et al. 2005). Given the human propensity to embody norms in nearly all aspects of cultural behavior, this topic should be a priority in future comparative research. The study of long-standing groups will be most fruitful in furthering this line of research, as this is where norms will have had the greatest opportunity to develop.

Finally, while a significant portion of research to date on this topic has been conducted with chimpanzees, research across diverse primate taxa will further clarify the phylogenetic and socioecological underpinnings of collaboration. Continued examination of collaborative interactions in natural contexts will also be highly instructive. Play behavior, for example, could be instructive for examining interspecific and ontogenetic dimensions of collaboration. Quantifying variation in collaboration at developmental, interindividual, and between-group levels is a further important emphasis for continued future research, as this will help to elucidate the role of developmental plasticity and the extent of flexibility within species. Each of these steps will provide continued insights into fundamental questions about the evolution and mechanisms of collaboration across the Primate order, including humanity's immense potential for working together.

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