



# Cooperation: Behavioral manifestations and neural mechanisms

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Cooperation is one of the defining features of our species. Our ability to work together in groups was pivotal to our evolutionary history and is crucial for maintaining current societies. Despite its significance, the questions of what drives cooperation, how it emerges, and what determines its success or failure remain largely unresolved. In recent years, a growing body of research across species has begun to address these fundamental questions using diverse behavioral and neural approaches. In this review, we discuss the key features of cooperative behavior and summarize recent advances in understanding its behavioral and neural basis. We highlight the critical roles of partner information and flexible behavioral strategies in facilitating cooperation and provide an integrated overview of neural mechanisms spanning the entire cooperative process, from recognizing and monitoring partners to employing adaptive behavioral strategies, making cooperative decisions, executing joint actions, and evaluating outcomes.

## Addresses

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## The concept of cooperation

Cooperation is the process in which two or more individuals work together to achieve shared goals [1,2]. It was pivotal to our evolutionary history and is crucial for maintaining current societies [3,4]. In behavioral ecology, cooperation primarily encompasses mutualism (mutualistic cooperation) and reciprocity (reciprocal cooperation), which are typically distinct from altruism (altruistic behavior) (Figure 1). These concepts are

distinguished by the timing of benefits (immediate or delayed) and whether there is a net cost to the actor. Mutualistic cooperation occurs when a behavior produces immediate positive effects for both actor and recipient, typically requiring real-time coordination and joint decision-making [2,5–7]. By contrast, reciprocity involves providing benefits to another individual with the expectation of future return, implicating delayed mutual exchange [1,8–10]. Altruism refers to voluntary, often unilateral, actions that benefit others and promote social bonding even in the absence of direct personal gain [11–15] (Box 1). In game theory, cooperation is studied as a strategic interaction in which individuals balance self-interest with collective benefit under conditions of interdependence [16,17] (Box 1).

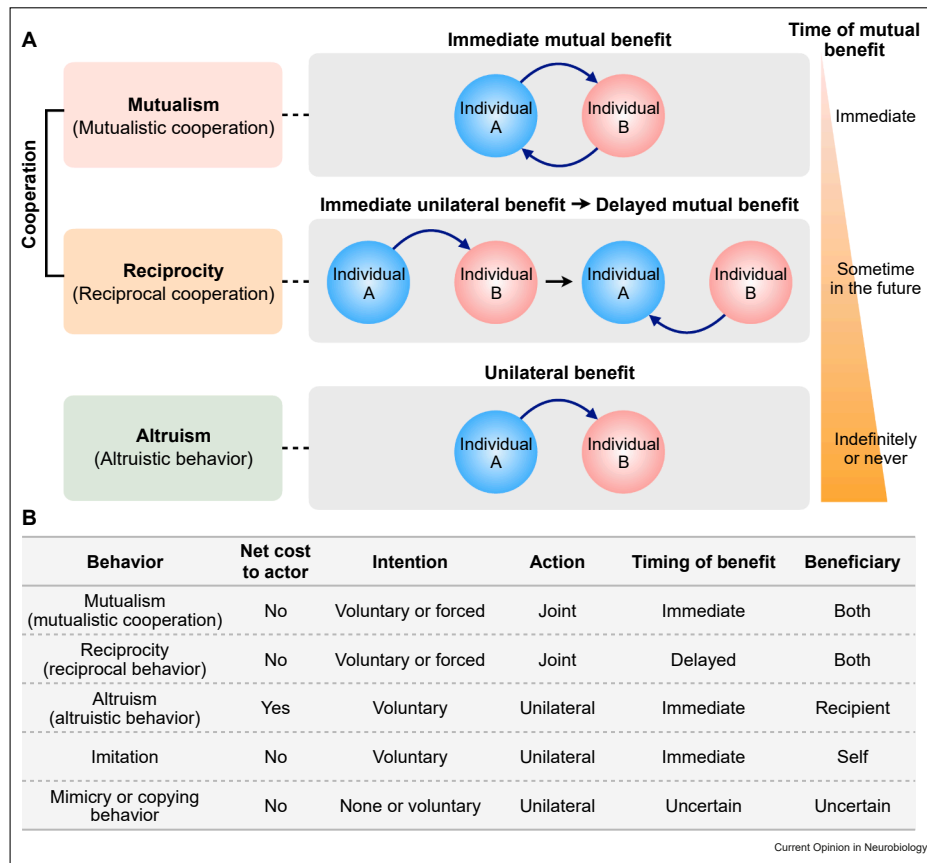
## Mutualistic cooperation—what it is and what it is not

Although mutualistic cooperation involves the instantaneous benefits shared by two or more participants, it can sometimes be confounded with coincidental coordination, imitation, mimicry, or copying behavior that incidentally yield mutual benefits (Figure 1, Box 1). Even when a behavioral task provides an opportunity for two individuals to obtain rewards through joint action, this does not necessarily mean they are using cooperative rather than alternative strategies for obtaining rewards. Recent studies have provided a clearer operational framework to distinguish genuine cooperation from alternative, non-cooperative behavioral strategies (Figure 2) [5–7]. Specifically, *three key criteria* help establish true cooperation:

- (1) *Coordination must exceed coincidental co-occurrence of actions*: Two or more individuals may show coordinated behavior without cooperating. For example, two people entering the same elevator each morning display coordinated timing but pursue independent goals (arriving to work on time) based on shared routines rather than partner-specific information. Similarly, individuals may show coincidental coordination when their actions independently converge onto a similar timing after a common environmental cue.

To test for genuine cooperation, researchers can use two complementary approaches. First, computationally

Figure 1



**Spectrum of cooperation.** Mutualism (mutualistic cooperation) involves simultaneous actions by both individuals that produce immediate, shared benefits. Reciprocity (reciprocal cooperation) occurs when one individual initially helps the other, and the partner later returns the favor, yielding delayed mutual benefits. Altruism (altruistic behavior) represents a unidirectional act in which one individual incurs a cost to benefit another without an immediate or guaranteed return. Imitation, mimicry, and copying behavior are alternative forms of behavioral coordination that do not involve cooperation.

shuffling behavioral sequences reveals whether temporal co-occurrence exceeds chance levels (Figure 2b); if individuals' actions are still aligned when their action sequences are temporally shuffled, coordination was likely coincidental [5,7]. Second, experimentally preventing partner information exchange (using barriers or separate chambers) tests whether coordination depends on real-time social interaction (cooperative condition without social communication; Figure 2c) [5,7]. If individuals continue to succeed without access to partner cues, they are not cooperating but rather responding independently to shared environmental contingencies.

(2) *Each and all participants' behavior must be mutually contingent, not merely sequential.* Cooperation requires reciprocal engagement where *each* and *all* participants must actively monitor and adapt to each other's actions in real time. This differs from asymmetric "following" behavior, where one participant initiates an action and the second participant

responds based solely on that cue, without the first participant adjusting to the second's behavior. Such sequential interactions may appear cooperative but lack the bidirectional contingency characteristic of true cooperation. Cooperation also differs from imitation or behavioral copying, where one individual observes and reproduces another's specific actions without requiring feedback between partners.

To test for mutual contingency, one can examine whether role reversal disrupts performance. Leader-follower relationships may emerge during cooperation; however, if the interaction primarily relies on a fixed leader-follower structure, where one individual consistently initiates and the other consistently responds, this suggests sequential following rather than reciprocal coordination. In contrast, genuine cooperation should be robust to role switching, where both individuals actively monitor and adapt to their partner rather than merely

**Box 1. Defining and distinguishing behaviors related to cooperation.**

**Reciprocity** is a form of social exchange in which one individual provides a benefit to another with the expectation that the favor will be returned in the future. Unlike mutualistic cooperation, where both partners gain simultaneously, reciprocity involves a temporal delay: the initial actor may incur a cost or gain less benefit at the time of action, while the partner benefits immediately, and the roles reverse later. This mechanism is thought to stabilize cooperation in evolutionary contexts by discouraging free-riding and promoting repeated interactions among partners. In neuroscience and psychology, reciprocity is often studied through iterated game-theory tasks (e.g., the Prisoner's Dilemma or Trust Game), which reveal how memory, reputation, and social norms shape the expectation of future return.

**Altruism** refers to voluntary actions intended to benefit another individual, such as helping, sharing, comforting, or providing resources. Unlike mutualistic cooperation, which requires both partners to act together to achieve a joint outcome, prosocial behavior can be unilateral: one agent acts in a way that benefits the other, regardless of whether they themselves gain a direct reward. In evolutionary terms, prosociality is thought to promote group cohesion and social bonding, and it can occur even when the actor incurs a personal cost. In experimental animals, prosocial behavior has been studied using paradigms such as food-sharing tasks, door-opening tasks, and consolation behaviors (e.g., helping trapped conspecifics in rats or allogrooming stressed partners).

**Imitation, mimicry, and copying behavior** refer to replicating another individual's actions, gestures, postures, or behavioral choices. In ethology and neuroscience, these behaviors are distinguished from true cooperation in that they do not necessarily serve a shared goal or require real-time coordination between partners. Copying involves reproducing another individual's behavior, such as choosing the same lever, object, or path, often occurring mechanically through reinforcement or attention to salient social cues, without requiring understanding of the partner's intentions or the causal structure underlying their actions. Imitation represents a more sophisticated form of social learning where the observer intentionally reproduces an action to achieve a similar outcome or learn a specific skill from the demonstrator, implying partial goal understanding. A related phenomenon, mimicry, involves automatic or low-level replication of observable behavior driven by perceptual or motor resonance, such as matching a partner's movement, or facial expression, typically occurring without conscious intent. Unlike cooperation, which relies on predicting and adjusting to partner's actions, these observational learning behaviors serve primarily as adaptive shortcuts that allow individuals to exploit others' successful strategies without engaging in trial-and-error learning.

**Game theory** is a mathematical framework for analyzing situations in which the outcome of one individual's decision depends not only on their own actions but also on the actions of others. It provides tools to study strategic interactions, where agents (or "players") choose among possible actions (or "strategies") with associated payoffs that reflect costs and benefits. In social behavior research, game theory has been widely applied to understand cooperation, competition, reciprocity, and negotiation, using paradigms such as the Prisoner's Dilemma, Dictator Game, Ultimatum Game, and Stag Hunt. These models allow researchers to formalize concepts like trust, fairness, and mutual benefit, and to predict under what conditions cooperation emerges or breaks down. Importantly, game theory bridges biology, psychology, economics, and neuroscience by linking abstract models of decision-making to measurable behavior and neural processes.

following a predetermined or conditioned behavioral sequence [5].

- (3) *Decisions must involve active partner coordination, not merely passive responses to social cues.* Even if both individuals' behaviors are mutually contingent, a participant may still make decisions based on a passive presence or action of the other participant without actively coordinating with them and responding to the other's actions. For instance, if an individual makes a decision based on another participant's presence at a particular location—but does not require mutual adjustment of actions in response to each other's actions—this represents *social cue-dependent decision-making* rather than *cooperative decision-making*. While both individuals may receive benefits, each participant makes an independent decision triggered by social cues rather than mutually adjusting their own behavior in response to other's actions.

To test whether coordination depends on active partner information versus passive social cues, one can introduce a control that mimics passive social presence. For example, replacing the cooperative partner with a recorded playback, a predictable mechanical stimulus, or a visible but non-cooperative conspecific that provides similar social cues (unilaterally cooperative condition; Figure 2c) can reveal whether the individual adjusts behavior based on dynamic partner actions or simply responds to the presence of social stimuli [5–7]. If participants still receive reward when the partner's behavior becomes non-contingent or is replaced by a static cue, the individual is likely relying on passive social cues rather than engaging in genuine cooperative behavior.

## Cooperative behavior across species

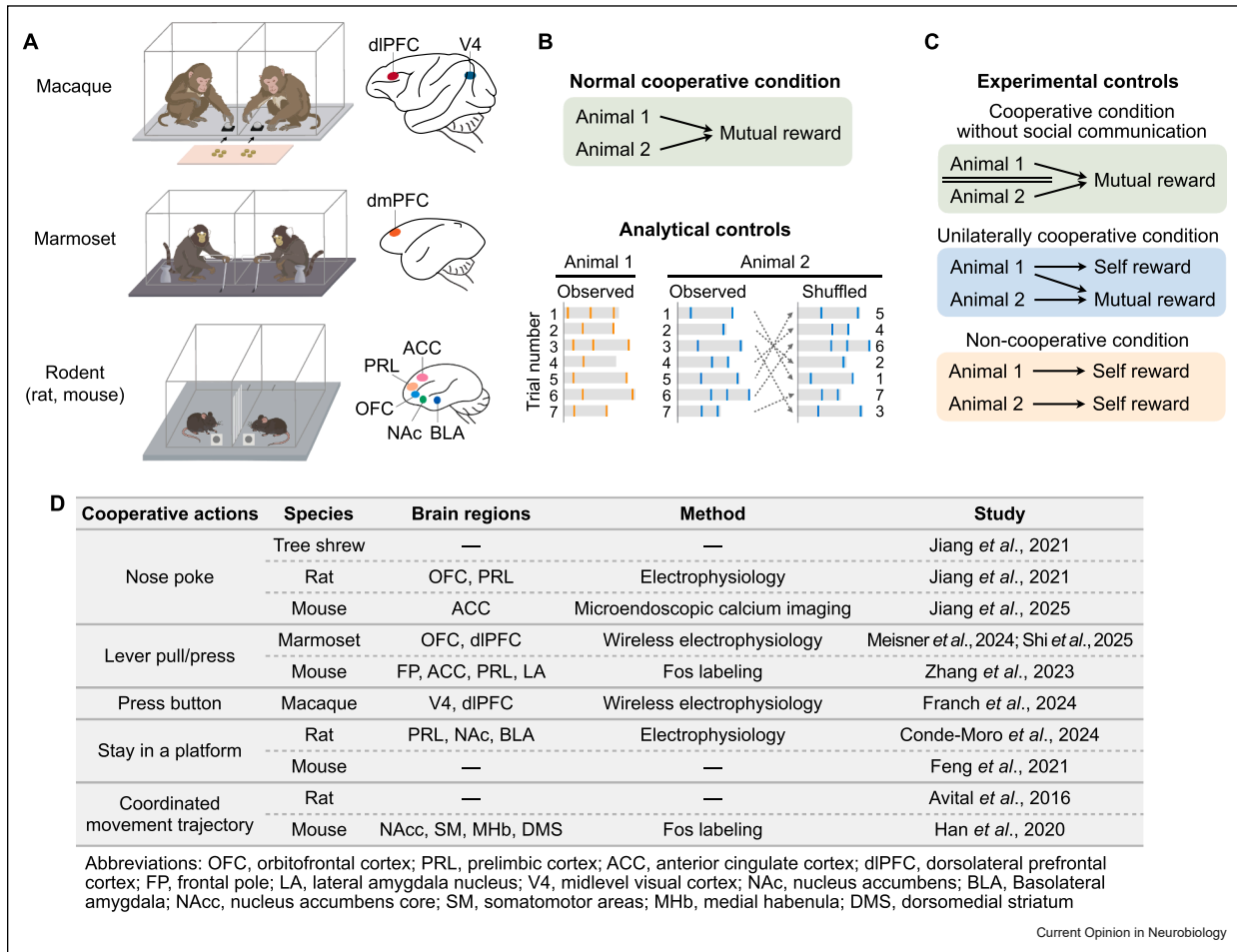
### Cooperation in wild animals and humans

Cooperation is ubiquitous across biological systems, evident among viruses, bacteria, plants, animals, and humans. In the wild, cooperative interactions may occur both within and between species. Notable examples include cooperative hunting [18,19] and collective defense [20]. Compared with non-human species, human cooperation is not only more cognitively sophisticated but also occurs on a vastly larger scale [3,4], encompassing cultural, technological, and scientific enterprises such as the construction of museums, the Olympic Games, and the Human Genome Project. Indeed, cooperation forms the cornerstone of modern human society.

### Cooperation in animal models

There has been a long history of studying cooperation using human-designed tasks that allow quantitative analysis of its specific components. A simple yet well-established paradigm is the classic rope-pulling task, in

Figure 2



**Summary of behavioral paradigms and neural studies of mutualistic cooperation.**

(a) Representative images showing cooperative behavior paradigms in macaques, marmosets, and rodents (mice and rats) with brain regions implicated in cooperative behavior.

(b) Schematic illustrating the normal cooperative condition and analytical controls. In the normal cooperative condition, both animals must coordinate their actions to receive a mutual reward. Analytical controls involve comparing observed cooperative decision sequences with shuffled data, where the trial order of one animal’s behavioral sequence is randomly permuted to estimate chance-level action coordination.

(c) Experimental controls used to distinguish true cooperation from alternative explanations. The cooperative condition without social communication uses an opaque divider to prevent visual access between animals. The unilaterally cooperative condition allows one animal to receive reward independently while the other requires coordination. The non-cooperative condition provides individual rewards regardless of partner behavior.

(d) Summary table of prior studies examining cooperative behavior across species.

Panels in b and c are adapted from Jiang *et al.* 2025 *Science*.

which two individuals must pull a rope simultaneously to obtain a reward. This paradigm has been used in a wide range of species, including chimpanzees [21], macaques [22], elephants [23,24], dolphins [25], and birds [26,27], all of which can complete the task. These studies in social animals provide valuable opportunities to quantify behavioral patterns during cooperation, but they remain limited in their ability to probe the underlying neural mechanisms of mutualistic cooperation. Recent advances using timing-based coordination have begun to fill this gap [5,6,28,29], offering tractable systems for mechanistic investigation.

This coordination-based task has been examined across multiple species, ranging from non-human primates to rodents, including macaques [28], marmosets [7,29], tree shrews [6], rats [6,10,30–34], and mice [5,35–37]. These paradigms typically require two individuals to coordinate their actions within a defined time window, such as simultaneously nose-poking, pressing buttons, pulling levers, performing coordinated movements, or jointly remaining on a platform, to obtain mutual benefits. To facilitate learning, a curriculum training strategy is often implemented, in which task difficulty is gradually increased, for example, by progressively

shortening the time window for coordinated actions [5–7].

In a mutualistic cooperation study in mice, two subjects were trained to coordinate their actions to obtain shared rewards by simultaneously nose-poking within a narrow time window [5]. In this study, multiple control conditions were implemented to demonstrate that mutualistic rewards arise from active coordination rather than coincidental or cue-dependent behaviors [5]. First, computational shuffling of behavioral sequences revealed that successful coordination exceeded chance levels, indicating animals were not simply adopting timing-based strategies independent of partner information (Figure 2b). Second, blocking visual communication with an opaque divider caused cooperative performance to drop substantially, confirming that partner information is essential (Figure 2c). Third, conditions where animals received individual rewards regardless of coordination—either both animals independently (non-cooperation) or only one requiring coordination (unilateral cooperation)—failed to elicit cooperative behavior above chance, ruling out behavioral mimicry or following of social cues (Figure 2c). A study of mutualistic cooperation that required synchronous level pressing in freely moving marmosets has also found that *social* vision is critical: cooperation was significantly impaired both by an opaque divider between animals and when marmosets coordinated with a fully visible automated lever not controlled by the partner [7]. Together, these controls establish that genuine mutualistic cooperation requires active coordination involving partner information perception, mutual benefits, and bidirectional behavioral adjustments—distinguishing it from timing-based coincidence, social cue-dependent decision-making, or behavioral copying.

Animal models with social deficits, such as those carrying *Shank3* mutations associated with autism spectrum disorder [36], exhibit disrupted coordination during cooperative tasks, including obtaining fewer rewards, exhibiting reduced cooperative efficiency, and displaying increased latency to initiate trials. These behavioral alterations provide a mechanistic link between impairments in cooperative behavior and underlying neurodevelopmental dysfunction.

## Behavioral components of cooperation

### Partner information in cooperation

Successful cooperation requires flexible coordination between participants. Participants need to dynamically adjust their behavior according to partner's status and anticipate forthcoming actions [5]. In rodents, the importance of partner-related information has been systematically examined by disrupting or removing access to such cues [5,7,31]. Physically approaching the other participant allows an individual to monitor

partner's state more closely [5,6]. When visual contact between partners is blocked, cooperative performance decreases sharply or is disrupted almost completely. To acquire partner-related information, visually oriented primates such as macaques and marmosets rely heavily on social gaze [7,28]. For example, freely moving marmoset dyads adjust the level of reliance on a social gaze-dependent cooperative strategy depending on the partner identity [7].

### Behavioral strategies facilitating cooperation

To achieve efficient cooperation, animals develop diverse behavioral strategies that enable them to monitor their partner's behavior and coordinate their actions. In addition to approach and social attention, waiting represents a more advanced coordination mechanism, in which animals actively wait for their partner when the partner is absent or distant. For example, chimpanzees, elephants, Barbary macaques and peach-fronted conures wait to pull a rope until their partner is present and stop pulling when the partner becomes inattentive [21–24,26]. Kea parrots can wait for a partner when cooperation is required to obtain food [38]. Rodents such as rats and mice also display waiting behavior [5,35].

Moreover, in the mutual cooperation task, mice engage in direct interaction by mutually poking their noses toward each other to coordinate their actions [5]. The increase in this mutual nose-to-nose interaction is accompanied by the increase in cooperation performance. Intriguingly, mice refine this mutual interaction as learning progresses, adopting a strategy that allows both animals to maintain visual and physical contact with their partner while simultaneously positioning themselves for efficient transition to cooperative action [5].

In primates, social gaze serves as a key strategy to gather partner information, analogous to the approach behavior seen in rodent cooperation. Monkeys are more likely to cooperate after viewing social cues, indicating that visual fixation on a partner's face or actions is a critical driver of cooperative learning [28]. Marmoset dyads use two distinct types of social monitoring based on social gaze, and the temporal precision between social gaze and partner's lever pulls is enhanced during successful cooperation, suggesting the use of social gaze to couple partner's behaviors [7]. In addition to the gaze-dependent strategy, marmosets employ a rhythmic strategy, coordinating their actions based on internal timing rather than visual cues alone.

### Leader-follower structure

Within the framework of mutualistic cooperation, leader-follower patterns are likely to emerge as an adaptive strategy to enhance coordination [6,34,39]. For instance, a more proficient cooperater who quickly

learns the task rules may take the lead to guide a less experienced partner toward successful outcomes. Moreover, because perfect symmetry in coordination is rarely achievable, the establishment of a stable leader-follower structure enables individuals to adopt complementary roles, thereby minimizing conflict and confusion in complex cooperative contexts. However, the formation of a stable leader-follower structure needs to be carefully distinguished from a fixed leader-follower relationship that reflects sequential following behavior as opposed to true cooperation.

### **Social relationships in cooperation**

Social relationships, such as kinship, familiarity, social status, and sex composition, profoundly influence cooperative interactions. Familiarity and kinship enhance cooperative performance, and strong social bonds facilitate the maintenance of cooperative interactions [7]. People preferentially cooperate with partners who have demonstrated cooperative tendencies in previous interactions [40]. Interestingly, mixed-sex marmoset pairs (female-male) often outperform same-sex male pairs, suggesting that sex composition functionally shapes cooperative dynamics [7].

Social status represents a natural hierarchical structure in many species and is distinct from the concept of leadership. In marmosets, dominant individuals can strategically follow the actions of subordinates, suggesting that dominant animals adopt adaptive roles to facilitate cooperative problem solving [7]. Moreover, marmosets with different dominance statuses exhibit distinct cooperative strategies: dominant individuals generally engage more actively and display higher overall social attention so that they can work with the subordinates to facilitate successful cooperation [7].

### **Neural mechanisms of cooperative behavior**

Mutualistic cooperation requires neural networks involved in social memory, partner recognition, decision-making, action coordination, and reward evaluation. By combining behavioral paradigms with genetic, circuit, and computational approaches, researchers have begun to identify the neuronal populations that encode and causally regulate these behavioral processes. We highlight recent advances, primarily from non-human primates and rodent studies, that elucidate the neural mechanisms underlying core building blocks of cooperation (Figures 2 and 3).

#### **Recognition and perception of partner**

While identity, familiarity, social status and sex composition all influence cooperative performance, recognizing and differentiating others is a fundamental prerequisite for initiating and maintaining cooperative

relationships [7,41,42]. In human cooperation, the right dorsolateral prefrontal cortex (dlPFC) shows increased activity when individuals encounter non-cooperative partners [40]. In non-human primates, partner recognition recruits brain regions specialized for encoding facial and identity information [43–45]. In rodents, neurons in the medial amygdala, the ventromedial hypothalamus, and the medial prefrontal cortex respond differentially to sex- and species-specific social stimuli [46–49], supporting categorical social recognition. The amygdala is also involved in social status perception in both non-human primates [50,51] and rodents [52].

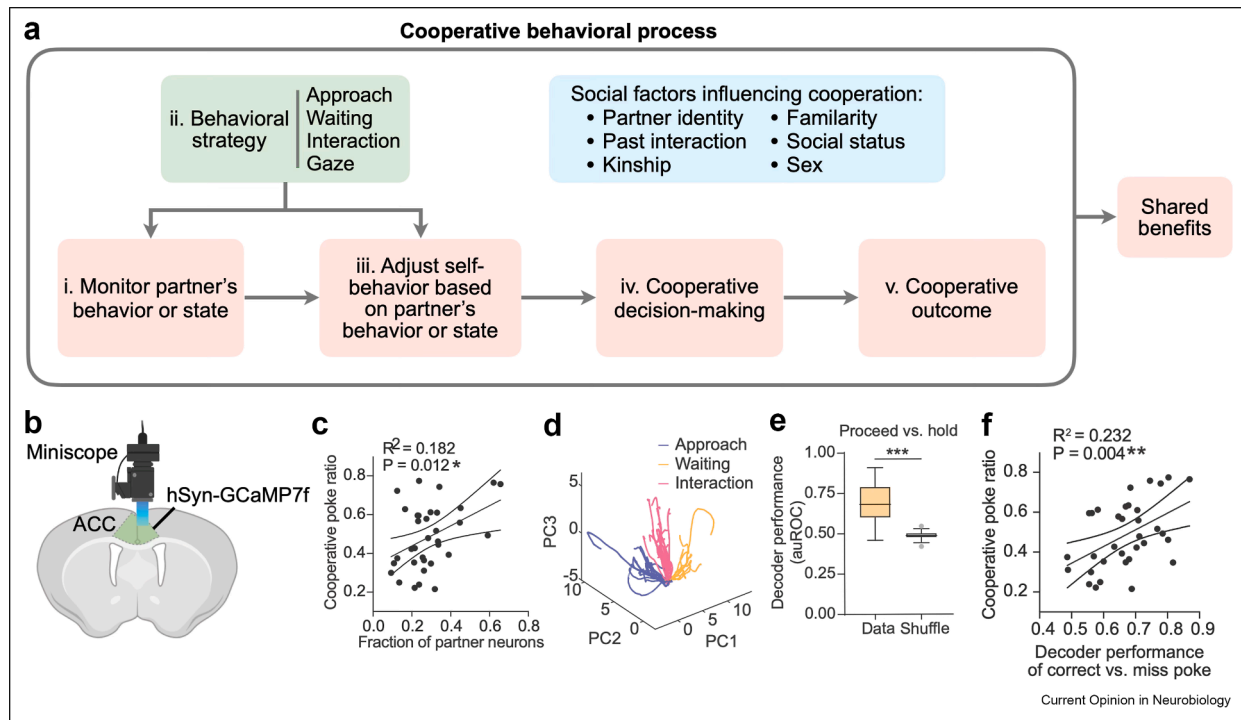
#### **Monitor and infer partner state**

The ability to actively monitor a partner's state and anticipate their intentions or future actions is critical for successful cooperation. A recent study in mice demonstrates that the anterior cingulate cortex (ACC) encodes partner's position and their relative distance to target locations relevant for cooperative behavior [5]. Notably, this partner-state encoding becomes stronger during key cooperative moments, and individuals with more robust partner representations exhibit better cooperative performance, suggesting that the ability to track and process partner-related information predicts cooperative capacity (Figure 3b and c). Beyond representations of others' positions, studies in primates have identified critical roles of the middle superior temporal sulcus (STS), amygdala and medial frontal cortex (MFC) played in inferring others' internal states and supporting adaptive social coordination. Specifically, neurons encoding predicted actions of a partner are more prevalent in the middle STS than in the anterior cingulate gyrus (ACCg) [17]. Neurons in the dorsal anterior cingulate cortex (dACC) encode other's unknown actions and can predict forthcoming choices [16]. Moreover, neurons in the amygdala accurately predict partner's decisions, enabling individuals to reconstruct other's internal states [53]. Within the MFC, neurons in the convexity preferentially encode other's actions and errors, whereas sulcus neurons are more closely associated with detecting others' errors and guiding subsequent action correction [54,55]. In addition, observing a partner increases spiking coordination between the midlevel visual cortex (V4) and dlPFC [28], and evaluating partner's reward engages a specific communication between ACC and the amygdala [56]. Together, these findings indicate that partner-dependent cooperative behaviors recruit a distributed network of neural nodes involved in social monitoring and inference.

#### **Behavioral strategies**

To effectively monitor partner information and position themselves for flexible coordination, animals use several preparatory behavioral strategies, including approach, waiting, interaction, and social gaze. The ACC and PFC

Figure 3



#### A model of cooperative process between two individuals.

(a) During cooperation, individuals continuously monitor their partner's state, actively adjust their own behavior and decision making based on partner's behavior or state (e.g., whether to hold or proceed), and execute task-related actions such as poking or pressing. During this process, individuals may use multiple behavioral strategies, including approach, waiting, interaction, and gaze, to facilitate social coordination. Successful coordination leads to shared benefits, which may reinforce the motivational drive to sustain cooperation over time. Cooperation involves recognition of partner's identities, social memory (past interactions), as well as additional social factors such as kinship, familiarity, social status, and sex.

(b) Schematic illustrating *in vivo* calcium imaging in mice using a miniature microendoscope (Miniscope) in the anterior cingulate cortex (ACC).

(c) Correlation between the fraction of neurons encoding partner position and cooperative poke ratio in individual animals.

(d) Principal component (PC) projections of ACC population activity associated with approach, waiting, and interaction behaviors, showing distinct neural trajectories for each behavioral strategy.

(e) Performance of decoders in classifying proceed versus hold decisions.

(f) Correlation between decoder performance for classifying correct versus miss pokes and animals' cooperative performance. Animals with better neural discrimination of trial outcomes exhibited higher cooperative performance.

Panels in **b–f** are adapted from Jiang *et al.* 2025 *Science*.

play central roles in organizing these preparatory behaviors [5,28], with distinct neuronal subpopulations selectively encoding specific behavioral components. In mice, separate ensembles of ACC neurons encode approach, waiting, and interaction behaviors (Figure 3d), and the strength of these neural representations is positively correlated with cooperative performance [5]. In macaques, both V4 and dIPFC encode social gaze-related activity—whereas most V4 neurons respond exclusively to social gaze, dIPFC neurons encode both social gaze and action-related variables [28], suggesting integrative processing of visual and action information during social coordination. Moreover, interactive social gaze variables are widely represented in the prefrontal-amygdala circuits of primates, supporting an integrative role of social gaze in these brain areas central to social cognition [57].

#### Social decision-making

Decision-making occurs in the brief moment preceding action execution, when participants make an internal choice to proceed with or withhold the cooperative action based on other's actions. Cortical regions such as the PFC, ACC, and amygdala are implicated in this process [5,28,58]. In mice, ACC neurons can differentiate the decisions to hold or to execute the cooperative action (Figure 3e), and the fraction of neurons encoding these decision-making processes is positively correlated with cooperative performance, suggesting that a stronger representation of social decision-making process is associated with cooperative efficiency [5]. Moreover, in freely moving marmoset pairs, the dmPFC carries out a gaze-dependent social evidence accumulation process to guide cooperative decisions [58], illustrating one

specific manner by which social monitoring directly guides cooperative decision-making.

### **Action execution and outcome**

Animals can distinguish whether their actions are performed individually or jointly, indicating strong context dependence in motor representations. The prelimbic cortex (PRL) and nucleus accumbens (NAc) exhibit increased delta/theta activity, whereas the basolateral amygdala (BLA) shows decreased delta/theta activity when rats stay together on a platform, compared to when they jump onto it individually [33,34]. At the single neuron level, neurons in the rat orbitofrontal cortex (OFC) and PRL respond differently to the same actions depending on whether they occur during individual or cooperative performance [6], suggesting that these regions encode the contextual state of an action rather than the action itself. In mice, the ACC shows a similar encoding pattern, differentiating actions that lead to successful or unsuccessful cooperation and signaling whether partner-related information is available during action execution (Figure 3f) [5]. Importantly, inhibition of ACC activity in mice disrupts the coordination of actions between partners without affecting the general ability to execute actions, underscoring its specific role in mediating cooperative coordination rather than basic motor output [5].

Beyond action execution, the OFC, NAc, and caudate nucleus exhibit increased activity following mutual cooperation in humans [59,60]. These regions process outcome-related signals in a context-dependent manner. In primates, OFC neurons predominantly encode rewards received by oneself, whereas the ACCg encodes reward outcomes not only for oneself but also for the partner. In contrast, neurons in the anterior cingulate sulcus (ACCs) preferentially respond to rewards delivered to others [61]. The amygdala also encodes reward information for both self and other [53,62], and specific communication patterns between ACCg and amygdala are associated with prosocial preference [63] and vicarious reward [56]. Within the dmPFC, distinct populations of self-type and other-type neurons modulate their activity according to the reward magnitude received by oneself or a social partner, respectively [64]. These studies underscore the importance of the prefrontal cortex in processing action and reward outcomes for self and other that are important for the reciprocal aspects of cooperation.

### **Future direction: understanding cooperation across scales, contexts, and systems**

While rodent and primate studies highlight key regions such as the OFC, PRL, dmPFC, ACC, and amygdala in encoding social and cooperative information, brain-wide dynamics linking these regions remain elusive. Large-scale, high-density recording techniques such as

Neuropixels probes will allow simultaneous monitoring of distributed neural activity to reveal how sensory, motor, and social signals are integrated for coordinated action. Beyond dyadic interactions, real-world cooperation often involves groups, yet how neural and computational mechanisms scale from pairs to collectives remains largely unknown. Understanding how multiple individuals cooperate to achieve shared goals will illuminate the neural basis of collective behavior and inform strategies for improving group decision-making. Finally, balancing cooperation and competition represents a fundamental social dilemma. Identifying the underlying mechanisms will advance our understanding of social decision-making in complex social settings.

### **Artificial intelligence as a model system for cooperation**

Recent advances in artificial intelligence (AI), particularly multi-agent reinforcement learning (MARL), have opened new avenues for understanding cooperative behavior among AI agents and for investigating the computational principles underlying cooperation [5,65]. By training artificial agents with recurrent neural networks to cooperate in simulated environments that mirror biological paradigms used for mice, researchers revealed striking parallels between artificial and biological systems [5]. Like their biological counterparts in mice, artificial agents develop behavioral strategies such as waiting and active coordination based on partner information, and their neural networks encode both self and partner positions [5]. A defining feature of the multi-agent environment is full access to each agent's neural network, which allows for precise manipulations. Indeed, selective ablation of task-relevant neurons in artificial networks disrupts specific aspects of cooperation, demonstrating functionally distinct subpopulations that causally regulate cooperative behavior [5]. This convergence between biological and artificial systems not only reveals key computational principles of cooperation but also positions AI as a tractable platform for testing mechanistic hypotheses that remain technically challenging in animal models, while simultaneously informing the design of more sophisticated collaborative AI architectures for real-world applications. Exploring cooperation between humans or animals and AI agents also represents a promising frontier, where adaptive AI partners can advance human-AI collaboration in domains such as education and companionship.

### **Concluding remarks**

Over the past few decades, research on cooperation has progressed from qualitative behavioral observations to quantitative, mechanistic investigations that span species, scales, and methodologies. These advances have begun to establish an integrative framework that links behavior, neural circuitry, and computational principles

underlying cooperative interactions. Moving forward, the integration of innovative behavioral paradigms with next-generation, brain-wide neural recordings and computational approaches promises to uncover how cooperation emerges from the coordinated activity of distributed neural networks. Such efforts will ultimately deepen our understanding of the mechanisms that enable cooperative behavior across species, help improve human lives, and inform the development of better social AI. Impaired cooperation is a hallmark of several mental conditions, including autism spectrum disorder and schizophrenia. Understanding the underlying neural mechanisms will elucidate the causes of disrupted social behavior and inform translational approaches for diagnosis and treatment.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Data availability

No data was used for the research described in the article.

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- \* of special interest
- \*\* of outstanding interest

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