The cognitive challenges of cooperation in humans and non-human animals

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Abstract

Cooperation is widespread in nature, occurring in every taxa on Earth. Nevertheless, the contexts in which cooperation occurs – and the forms it takes – vary widely. In this Review, we outline how cooperation can evolve in nature and the cognition needed to support cooperation in different scenarios. We argue that the cognitively simplest forms of cooperation are those where an organism does not need to individually recognise interaction partners and that do not depend upon individuals keeping track of their partners' actions and making contingent return investments. These simpler cooperative interactions occur most frequently among kin and among interdependent interaction partners and are relatively common in nonhuman species. Conversely, cooperation involving individual recognition of interaction partners and where benefits depend upon contingent responses levy greater cognitive demands and occur in limited nonhuman contexts.

[H1] Introduction

Cooperation is an interaction outcome that yields fitness benefits to all parties[1]. In addition, cooperation involves at least one party making an investment in the interaction by paying a temporary cost — for example by spending time or energy, by foregoing other profitable opportunities, or by increasing their risk of harm — either to help another party or to produce or contribute to the production of a public good (such as provision or protection of a shared resource).

In this Review, we first highlight the main pathways by which cooperation evolves in nature and then discuss the cognition needed to support cooperation in different scenarios, with a focus on cooperation in nonhuman species. One major fault line we highlight is whether cooperation requires individuals to recognise their interaction partners: in some simple cases, cooperation can emerge even without individual recognition. Another fault line concerns whether cooperation depends upon individuals keeping track of their partners' actions and making contingent return investments: we argue that where cooperation relies on contingent return investments, it will typically involve more sophisticated cognitive mechanisms (including partner-specific memory and the ability to tailor one's own behaviours to the behaviours of the partner). We conclude by discussing cooperation in humans, showing how uniquely human cognition supports a wider range of enforcement mechanisms, which give rise to distinctive and flexible forms of cooperation.

[H1] Evolutionary pathways to cooperation

In this section, we discuss the main evolutionary pathways by which individuals who invest in cooperative actions might reap fitness benefits (Fig. 1). To understand how a tendency to invest to help others could be favoured by evolution (that is, how such a tendency could be under positive selection), we must ask how such investments might ultimately be repaid. We show that the answer to this evolutionary question will depend on two factors: whom cooperative interactions occur with (kin, familiar non-relatives, or strangers) and whether investments are repaid via costly return investments from interaction partners[2]. We also differentiate cooperation among dyads (two interacting individuals) from collective action (cooperation occurring in larger groups), as cooperation in multi-player interactions might be supported by different evolutionary mechanisms and could also have different cognitive implications compared to dyadic interactions.

[H2]Kin Selection, Reciprocity and Pseudo-reciprocity

Individuals who invest in cooperative actions can derive direct (personal) and/or indirect (kin-selected) fitness benefits from their investments. The sum of direct and indirect fitness is commonly referred to as inclusive fitness[3]. In general, strategies resulting in cooperative behaviour will only be subject to positive selection if they increase an investor's inclusive fitness.

Cases where an individual invests to help a relative, and benefits because of the consequent increased reproductive success of the relative, fall under the framework of kin selection (Fig. 1a)[4–6]. Here, cooperative investments can also be described as altruistic, since the investor incurs lifetime personal fitness costs that are only repaid indirectly, via benefits to kin[2]. Examples of altruism include worker sterility in many social insect species, and contributions to rearing offspring observed in some cooperatively breeding species[7]. These altruistic strategies can be under positive selection because individuals who pay these costs (for example by developing as a sterile worker or by contributing to rearing offspring) benefit indirectly via benefits to kin.

Direct reciprocity occurs when an individual invests to help a partner and then benefits because the partner makes a reciprocal return investment (Fig. 1b)[8–10]. For example, pied flycatcher breeding pairs sometimes receive assistance from neighbours when repelling predators from their nest. Such help is then frequently reciprocated by the breeding pairs helping the same neighbours to repel any predators at the neighbours' own nest[11]. By contrast, indirect reciprocity occurs when investments are repaid by uninvolved bystanders rather than the original beneficiaries[12,13]. In nature, indirect reciprocity examples are rare, perhaps because indirect reciprocity is only evolutionarily stable when individuals within a group have a consensus over when individuals are expected to cooperate and when it is acceptable to withhold cooperation. Such consensus relies on social norms. For example, if a social norm dictates that it is acceptable to withhold cooperation from a defector (an individual who fails to cooperate) then individuals can safely withhold cooperation without damaging their own reputation by doing so[12]. There is no evidence for social norms outside of humans[14].

As well as reciprocating favours, individuals can also reciprocate harm: this is known as negative reciprocity or punishment[15,16]. Punishment, which involves an individual investing to harm a cheating partner, can enforce future cooperation (though it does not always have this effect[17]). Thus, one way that a punisher can derive a return on their investment is if the target (or a bystander[18]) subsequently behaves more cooperatively[16]. The interspecific mutualism between bluestreak cleaner wrasse and their reef-fish clients is a well-studied example. A cleaner wrasse provides a service to its client by eating ectoparasites found on the surface of the client's skin but prefers to feed on the client's mucus and scales instead. Cheating cleaners (those that feed on mucus or scales) risk being punished via aggressive chasing by the client — with such punishment causing cleaner fish to behave more cooperatively (by eating ectoparasites) in subsequent interactions[19]. Other work also suggests that vervet monkeys use punishment to encourage individuals to contribute to between-group aggression[20].

Pseudo-reciprocity occurs when an individual's investment allows a recipient of help (or a bystander) to perform a self-serving response, which benefits the investor as a by-product (Fig. 1a)[21]. Thus, the key difference between reciprocity and pseudo-reciprocity is that the latter does not require recipients of help to make contingent return investments. Various forms of farming in human and non-human societies provide examples of pseudo-reciprocity[22,23]. For instance, some ant species farm fungi, which involves the ants investing to nurture and defend the fungus. This investment allows the fungus to perform a self-serving response (growth and survival) that benefits the ants as a by-product (because the ants and their larvae can feed on the fungus)[23]. The act of choosing a partner for cooperative interactions — partner choice — can also be conceptualised as a form of pseudo-reciprocity. For instance, an individual can benefit from making cooperative investments if they are observed, and the observer makes a potentially self-serving decision to interact with the cooperative one (choosing them as a mating partner for example). Thus, partner choice is a way pseudo-reciprocity can facilitate the evolution of helping behaviour, whereby helpful individuals benefit from their cooperative investments because they are more likely to be chosen for future interactions[12].

Negative pseudo-reciprocity can promote or maintain cooperation when a cheating behaviour by one individual allows the partner to perform a self-serving response, which harms the cheating individual as a by-product[24]. Terminating an unprofitable interaction in response to a partner defecting is one simple example of such a self-serving response, as is seen in predator

inspection in Trinidadian guppies, where individuals use a 'walk away' strategy to abandon defecting partners[25]. Another example involves coral gobies evicting individuals who exceed a certain size threshold, a self-serving response that removes a competitor from the group[26]. Thus, positive and negative pseudo-reciprocity are involved in active partner choice and rejection, respectively.

Interdependence is another means by which pseudo-reciprocity can facilitate the evolution of cooperation. Interdependence occurs when interacting individuals have a stake in a partner's wellbeing or survival, such that investing in the partner (or in a public good that the partner can access) yields direct fitness benefits to the investor even in the absence of any return investment[27,28]. Individuals that live in stable groups or that work with an opposite sex partner to raise offspring, as is the case in many species, are often interdependent to varying degrees[29]. Interaction partners engaged in repeated reciprocal interactions can often become interdependent to some extent[30] which complicates attempts to tease apart mechanisms such as reciprocity and pseudo-reciprocity empirically[29].

All of the mechanisms described above can support human cooperation (Table 1)[31]. For example, humans help their relatives (where benefits could arise via kin selection[32]), and engage in direct reciprocity by helping individuals who helped them[33] and indirect reciprocity by preferentially helping individuals who have helped others[34,35]. Furthermore, humans form interdependent relationships (for example, romantic partnerships and friendships) where investments are favoured because it allows the partner to perform a self-serving response which benefits the investor as a by-product[28]. Humans also engage in other forms of pseudo-reciprocity, most notably by preferentially selecting good partners (and avoiding bad ones) for social interactions[12].

[H2] Investing in collective action

Individuals can also cooperate by investing in collective action to generate shared, or non-excludable, resources or benefits also known as public goods (Fig. 1c) (Table 1). Such benefits include increased mating success (generated when males form breeding aggregations, or leks, which attract females[36]), increased safety from neighbours and predators (achieved via individual investments in vigilance or in territorial aggression and mobbing of predators[20,37]) or the generation of food surpluses (achieved via hunting, foraging and storing food[38–40] or

when begging by offspring increases food delivery from adults[41]). Below we outline the mechanisms that can sustain investments in collective action and some cognitive implications of these mechanisms.

Unlike cooperation in dyads, cooperation in multi-player interactions cannot be so easily sustained by direct reciprocity because when individuals defect in response to a single defector in the group, this also harms any cooperative group members and might prompt these individuals to defect also. Nevertheless, many of the evolutionary mechanisms discussed above can support the evolution of cooperation in groups.

Cases where individuals invest to produce shared benefits can be by-product mutualisms, where the investment is immediately self-serving and the benefits to others arise as a by-product[42]. For example, scalefin anthias are a shoaling fish species that can be attacked by another fish species, saber-tooth blennies. Individual anthias invest to punish attacking blennies which generates a shared benefit for other anthias because punished blennies are more likely to switch to another species for their next attack[43]. Nevertheless, 'punisher' anthias personally benefit from their investment because blennies can apparently discriminate punishing from non-punishing individuals (and preferentially attack the latter). Thus, the shared benefit to non-punishing anthias arises as a by-product of the punisher's self-serving action.

Individuals might also benefit from collective action via kin selection. For example, acorn woodpeckers invest in the production and defence of large granaries, acorn stores which are amassed over winter and used as a food source for adults and nestlings in the spring[44]. Such investments in a public good generate both direct and indirect benefits: individuals can consume the acorns themselves, but stored acorns are also used to help raise the next generation of woodpeckers, who are typically relatives. Similarly, meerkats often collectively mob predators, driving these individuals away from the group. Individuals that invest in predator mobbing might benefit indirectly (if mobbing increases the survival of relatives) but it is also likely that mobbing yields direct benefits to the individuals involved, for example, by allowing individuals to learn about the predators in the environment or to benefit from living in a larger group[37,45].

In many other cases, the shared benefit of investing into collective action is likely to depend on whether other individuals also contribute because the investments of co-players can generate synergistic benefits. For instance, in chimpanzees, individual investments in hunting are thought to produce shared benefits for others in the group as a by-product of increased hunting success[46]. Although initiating a hunt might be a self-serving strategy for some individuals (and some key 'impact' hunters might hunt regardless of whether others join[46]), the benefits of hunting often increase as more individuals join[47,48], which may have selected for cognitive skills that allow individuals to coordinate their efforts[49].

Humans engage in collective action at many different scales, from cooperating in small groups (collaborating at work or volunteering at a community group) to investing in global public goods (by engaging in climate friendly behaviour or other large-scale collective action). Human collective action has been studied in laboratories using public goods games (experimental scenarios that mimic collective action problems in controlled settings, see[50–52]) but also in lab-in-the-field (controlled but naturalistic settings) and real-world settings[53–57]. Various factors can encourage individuals to contribute more to public goods, including interacting with familiar players (rather than strangers in each round), knowing that their contributions will be revealed to the others in the game[58] and knowing there is a threat of punishment for failing to contribute[59].

[H1] Cognition supporting cooperation

The different pathways to cooperation outlined above have implications for the evolution of the cognitive mechanisms supporting helping behaviour. We argue that recognising partners and keeping track of their previous actions will levy greater cognitive demands than interactions where recognition and long-term memory are not needed.

First, we address the possibility that individuals might need to identify appropriate cooperation partners, ensuring that they invest in individuals that should be helped or who are more likely to deliver return benefits. In some cases, this might entail being able to individually recognise partners. Next, we consider the cognitive implications when individuals who invest in cooperation rely upon return investments from their partner(s) or from bystanders in order to benefit. We discuss how this need for return investments selects for cognitive mechanisms allowing individuals to monitor their interaction partners and to remember their behaviour.

Memory demands are likely to be larger over longer time periods or when several kinds of investment need to be integrated into a single assessment of the partner, and such complexities are also explored. Deriving return benefits via costly investments also implies that individuals might need to incentivise their interaction partners to behave appropriately which has cognitive implications. Finally, we ask whether individuals need to present themselves as attractive cooperation partners and what cognitive mechanisms might be involved in attracting others for cooperative interactions.

We note that the cognition involved in sustaining cooperation might differ according to the role individuals adopt in social interactions, particularly when these roles are asymmetrical, and that individuals involved in the same social interaction might therefore face different cognitive challenges.

[H2] Identifying appropriate partners

Cooperation will frequently rely on cognitive abilities that allow individuals to discriminate between partners that should and should not be helped. For example, where cooperation is supported by kin selection, individuals must ensure that any investments are directed towards kin and not towards unrelated individuals. Depending on the species' ecology, this can select for mechanisms allowing individuals to discriminate kin from non-kin[60,61], although such mechanisms might not be needed when non-relatives are infrequently encountered[62]. In kin-based interactions, individuals might also prioritise investments to the most valuable recipients of help. For example, ants are less likely to rescue injured or aged nestmates from danger because the benefits of helping these individuals are likely to be smaller[63,64]. Individuals might also discriminate between classes of partners. For example, cleaner fishes tailor their cleaning service according to several client characteristics, including whether the client has outside options (such as other cleaning stations it can visit), the client's ability to punish the cleaner and its ectoparasite load[65].

In some cases, individuals might additionally need to recognise interaction partners (Fig. 2). Such recognition is likely when the rounds of an interaction are temporally separated and individuals need to remember a partner's identity — as well as their previous behaviour, see below — to inform their current strategy. In shorter-term interactions the requirement to recognise interaction partners is likely to be less pronounced. For example, egg trading in

hermaphroditic hamlet fish is unlikely to involve partner recognition because each interaction takes place over a short-time period (in the evening, before sunset) and individual fish trade all their eggs with the current partner (over a series of reciprocal exchanges) before swimming away[66]. As such, it suffices for each fish to simply discriminate the current partner from others in the vicinity and there is little requirement for individual recognition.

For cooperation to occur, individuals might also need to assess and then preferentially choose or reject their interaction partners. In some simple cases, individuals might use 'walk away' strategies[67] where they simply leave defecting partners and associate with novel partners even if they lack information about them[25]. A capacity for active partner choice has been observed in chimpanzees who recruited the best collaborator for a cooperative pulling task[68] and in the interspecific mutualism involving coral trout and moray eels, who hunt cooperatively and increase their joint success by doing so[69,70]. To initiate a hunt, coral trout use stylised gestures aimed at recruiting a moray eel partner[40]. However, individual moray eels differ in their willingness to join a coral trout in a hunt, so the ability to recognise and remember the behaviour of moray eels could be advantageous for the coral trout. In an analogous laboratory study to the chimpanzee partner choice study[68], coral trout recruited the most responsive partner when choosing between two model moray eels[70]. As an important caveat of that study, the locations of the model moray eels were not counterbalanced, so fish could have been identifying 'good' partners based on a location cue rather than other identifying characteristics of individual fish.

Species as different as chimpanzees and coral trout choosing the best collaboration partners highlight the possibility that partner choice — which is an example of positive pseudo-reciprocity (Fig. 1b) — could support cooperation in many different contexts in nature. For partner choice to operate, individuals need only be able to identify good partners, although the exact content of what is encoded can vary across species. Partner choice is likely to be a relatively common self-serving strategy that can positively select for cooperative traits in partners[12]. The ability to identify and preferentially interact with good partners can also be used in the context of collective action (Fig. 1a). Group hunting is a collective action which occurs in many species including chimpanzees, lions, killer whales and wild dogs. In such species, it might be advantageous for individuals to contribute to a group hunt when there are other skilful or responsive hunters present. For example, 'impact hunters' tend to initiate hunts

more readily than other chimpanzees[46] and can be more skilful at making a kill[46]. Joining a hunt with an impact hunter could therefore carry a higher chance of success[71].

Cooperation can also be supported by reputation-based mechanisms, such as reputation-based partner choice and indirect reciprocity. In these cases, individuals that choose (or reward) partners must be able to distinguish cooperators from defectors without having previously interacted with them, either by witnessing third-party interactions or, in the case of humans, by hearing about these interactions via gossip[35]. In addition, chosen individuals might benefit from attending to the possibility of being observed and, if so, strategically adjusting their behaviour to further enhance their reputation for reliable cooperation.

In non-human animals, bystanders can learn through observation about the dominance status or fighting ability of others[72,73]. Evidence that bystanders evaluate others on the basis of prosocial behaviour is scarcer[14,74] with the exception of cleaner fish-client mutualism, where clients of the bluestreak cleaner wrasse are known to choose or avoid cleaners based on such observations[75]. Experimental studies in other species have typically addressed this issue by examining how individuals respond to a nice or a nasty human experimenter. For example, dogs avoided taking food from humans who refused to help the dog's owner[76], and chimpanzees and orangutans preferred approaching and sitting in proximity to a nice (food-sharing) rather than a nasty (non-food-sharing) experimenter after witnessing the nice and nasty individuals interact with a third neutral individual[77–79]. Similarly, capuchin monkeys preferred to accept food from a neutral rather than a nasty human experimenter[80,81]. By contrast, bonobos seemed to prefer antisocial over prosocial individuals[82]. In three different experiments, adult bonobos showed a preference for a hinderer that obstructed another individual's goal rather than for an individual that helped them achieve it. This preference could reflect an attraction to more dominant individuals[82].

Nevertheless, there are several methodological and conceptual limitations with these experimental studies. They all involve interactions with human experimenters, making it difficult to judge whether (and how) such abilities to evaluate potential interaction partners might be used in natural circumstances. For instance, in the dog studies[83,84], the procedure did not control for location of the experimenters, so it is possible that dogs were simply learning about the location associated with food rather than experimenter cooperativeness[85].

Furthermore, the different preferences exhibited by chimpanzees and orangutans on the one hand[77,79] and bonobos on the other[82], suggest that context could affect non-human great apes' preferences for prosocial versus dominant (or antisocial) individuals. An attraction to both prosocial and dominant partners could explain these mixed results. More research is needed to unequivocally demonstrate nonhumans animals can evaluate conspecifics for their cooperativeness. By contrast, human children can identify (and preferentially help) prosocial over antisocial partners from around two years old[86,87].Whether children exhibit such preferences at younger ages is currently a matter of debate, with some studies finding supportive evidence[88,89] whereas other studies do not[90–93].

[H2] Monitoring partners

The cognition supporting cooperation will also depend on the route by which individuals reap the downstream benefits from their investments in others. Where benefits arise via self-serving responses of recipients of help (pseudo-reciprocity) or where partners are less incentivised to exploit one another (for example, because they are genealogically related or are interdependent), then the requirement to monitor the actions of others will be less pronounced (Fig. 2). For example, meerkats who invest to help raise offspring do not need to monitor whether and how the beneficiary converts the donated food resource into growth and survival. Although the requirement to monitor others' responses will be less pronounced in such cases, this does not completely obviate the need for individuals to monitor and identify those partners whose self-serving responses might generate higher return benefits. In addition, males and females who jointly raise offspring are interdependent to some extent but can still monitor and respond to one another's contributions to parenting[94].

In interactions where the benefits to investors are contingent on receiving return investments from their partners, then individuals might need to monitor the partner's behaviour. For contingent cooperation, individuals need to minimally condition their own behaviour on the previous behaviour of their partner, which, depending on the social ecology of the system where the interaction occurs, does not always involve long-term memory. For example, hamlet fish find a single partner and reciprocally exchange eggs before nightfall, so long-term memory of the partner's actions is not required: instead, it suffices to remember how the partner behaved in any previous interactions that evening (rounds) and respond accordingly. Therefore, cases in which individuals exchange goods and services almost concurrently or over short time-scales

(allogrooming in many species, predator inspection in fishes) need not involve long-term memory nor the ability to recognise other individuals[95].

In cases where interaction bouts are temporarily separated, monitoring the partner's behaviour over a longer period can be necessary, placing greater demands on memory. In some cases, this can simply involve an individual remembering how a partner behaved in a specific context over an extended period. For example, pied flycatchers are more likely to help to mob a predator at a neighbour's nest if those neighbours had helped them one hour before in a similar predator encounter, but not otherwise[11]. Thus, one interpretation is that pied flycatchers use their memory of neighbours' previous actions to inform their own cooperative behaviour. Furthermore, in experiments with 'reliable' and 'unreliable' human partners, ravens can remember (and preferentially interact with) the reliable individual for up to one month[96,97]. However, these experiments cannot reveal what exactly individual ravens remember about their human partners' previous behaviours, and it is possible that reciprocity emerged from emotion-based processes such as the tendency to affiliate with partners associated with prior positive experiences.

In species that live in stable social groups, such as many primate species, enduring reciprocal patterns of exchange have also been documented (see[98] for a review), which likely involve the ability to remember how a partner behaved over the longer term — and potentially remembering several separate interactions involving different currencies. It is unclear whether such long-term cooperative exchange is supported by precise bookkeeping strategies or by emotional bookkeeping (see[9] for a review). Exchangeable units often occur in different currencies. For example, grooming could be exchanged for coalitionary support, food and / or infant handling opportunities[33,98] (see also[99,100] for evidence of commodity exchange in rats). These different currencies and the long-term relationships these animals have with many different partners present additional cognitive challenges that require individuals to keep track of who did what and how often. The different currencies also pose problems for a precise bookkeeping account since it is not clear how individuals ought to convert units from one currency into another.

Moreover, when individuals have stable long-term relationships, they might need to integrate information from several encounters, adding further complexity to the problem of monitoring

a partner's behaviour. Several studies have explored the possibility for reciprocal exchange in rats, a species that lives in complex social groups of up to 200 individuals but lacks 'social' bonds[101]. Perhaps because they do not form such enduring bonds with other individuals, rats base their decision to cooperate on the last encounter with their partner (using tit-for-tat like strategies) and not on the partner's overall level of cooperation[102]. Great apes remember past events for long periods of time[103,104], but it is less clear how well and for how long they remember the social component of past events[105,106]. More studies requiring animals to encode social and non-social components of an event (especially a cooperative interaction) will further reveal the psychological basis of contingent cooperation in non-human animals.

Given the complexity in encoding who did what and when, it seems likely that many species, including humans[107], often use cognitively simpler strategies to facilitate social exchange such as attitudinal (or emotion-based) reciprocity (see[9] for a review). Moreover, when individuals have stable long-term relationships, a strict bookkeeping strategy could be less effective at sustaining cooperation than a more flexible approach. Attitudinal reciprocity implies that individuals encode their partner's past behaviour in terms of an emotional or social predisposition, which predicts their future behaviour towards that partner. Although attitudinal reciprocity relies on partner-specific memory, there is evidence for individual recognition skills and long-term memory of past events in primates[103,104,108–111]; and empirical evidence suggests that social bonds do predict future cooperation in many non-human primate species[112–114]. Attitudinal reciprocity has been argued to support cooperative interactions over both the short-term and long-term[115,116], although this does not solve the problem of 'fuzzy score-keeping' (how individual investors avoid being exploited by their partners if they don't keep track of exact cooperative exchanges)[117]. One possible explanation is that single episodes of defection or failed reciprocation have negligible costs to partners, particularly when interactions occur among partners who have stable, interdependent relationships with one another[33].

[H2] Incentivising partners

In addition to monitoring how partners behave, individuals might need to modify their own behaviour to encourage or enforce cooperation. Individuals can encourage partners to cooperate by changing the benefits associated with cooperating and defecting, by abandoning[25], evicting[26] or avoiding[75] uncooperative partners for example. In other cases, individuals might invest to punish defectors[16], which requires individuals to keep track of their

partners' behaviour and sometimes even their intentions. For example, chimpanzees distinguish between scenarios where a conspecific steals food versus where a human transfers food to the conspecific, being more likely to punish — by collapsing the conspecific's food tray — when the conspecific steals[118]. Other work suggests that some non-human animals use redirected aggression (aimed at an aggressor's kin) to deter the aggressor repeating the harmful actions in future[119,120]. Although it is not obvious that reduced aggression necessarily constitutes 'cooperation', this highlights the possibility for individuals to use harmful actions to incentivise partners to behave in ways that produce benefits for them.

Effective punishment often requires the target of punishment to learn to change their behaviour in future interactions (but see[59] for other explanations of the possible role of punishment). This learning requirement has several cognitive implications. For instance, punishment must be administered in close temporal sequence to the undesirable behaviour for the target of punishment to learn the connection between their action and the negative consequence. Similarly, punishment is also more likely to evolve in response to an individual performing an undesirable action (such as in the case of a cheating cleaner fish biting a client[121,122]) than when an individual fails to perform a cooperative action. This is because an individual who is punished for failing to perform the cooperative action cannot easily infer (without an explanation) the desired behaviour[16]. However, although this general rule typically holds, a study revealed that male vervet monkeys received aggression from females when they failed to participate in inter-group conflict[20], and punished males were more likely to participate thereafter. How males inferred the appropriate behaviour after receiving aggression from females remains unclear.

Punishment is used much more frequently in humans compared to non-human animals[16]. Evidence from both laboratory studies[123] and field settings[55] shows that humans will act to punish individuals that cheat, even in scenarios where the punisher was not directly harmed by the transgression (third-party punishment)[124]. The threat of punishment appears to incentivise cooperation in such settings[59]. As with reputation-based cooperation, punishment in humans is often supported by social norms[125] or collectively agreed standards of behaviour that are followed and enforced from a very young age[126]. No evidence of anything similar supporting punishment exists in non-human animals[12,17].

Similarly, cases where individuals reward cooperators outside the context of direct reciprocal interactions (such as indirect reciprocity and rewarding contributions to collective action) are also relatively uncommon in non-human animals. Indirect reciprocity relies on individuals within a population agreeing on which behaviours ought to be rewarded; in other words, the evolution of indirect reciprocity relies on the ability of individuals to create and follow social norms[12,14]. This requirement might help account for the relative scarcity of indirect reciprocity and other reward-based strategies among non-human animals in nature. Nevertheless, a handful of examples exist, suggesting that under certain circumstances the emergence of rewarding mechanisms is possible without social norms. For example, dwarf mongooses who invested more in sentinel duty during the day received more grooming from others at the end of the day[127], whereas male vervet monkeys who contributed to intergroup conflict were also rewarded with increased grooming from females and were subsequently more likely to contribute in the future[20]. The proximate cognitive mechanisms supporting contingent cooperation in these examples is not clear. In the case of the dwarf mongooses, it is unclear whether individuals keep track of who contributes to sentinel duty, how long for, and whether this is a larger or smaller contribution than others in the group – or whether they use attitudinal-based processes to keep track. For the vervet monkeys, increased grooming of individuals who contribute to intergroup aggression could occur due to proximity and increased social tolerance following a stressful encounter rather than as a reward for contributing to the conflict.

Rewarding individual contributions might be particularly important to stabilise cooperation in the context of collective action. Cooperative hunting is an example of collective action seen in many species that creates the potential for conflict between partners over the shared benefits from the resources gained. One problem that arises is that unless participating individuals receive downstream benefits, and thus stay motivated to contribute, cooperation will break down[128]. In some cases, individuals will facilitate cooperation by keeping track of their partners' contributions to collective action and instigating mechanisms to facilitate equitable sharing between partners. However, such mechanisms are not always necessary. For example, moray eels and groupers do not share their prey on any given successful hunt, but who gets the prey varies randomly from hunt to hunt, so that the moray eel and the grouper both benefit in the long-term[69]. In the case of group hunting in chimpanzees, it has been suggested that an equitable distribution and a greater per capita caloric intake may not be necessary because

important micronutrients are already present in small quantities of meat, so that any scrap of meat could be beneficial for individuals[129].

In other species, high social tolerance between individuals might facilitate the sharing of benefits following cooperation[130,131]. For example, in experimental settings where two individuals must work together to pull a reward-bearing tray, more socially tolerant bonobos succeed more readily than chimpanzees when the rewards are clumped in one dish and the potential for conflict between partners increases[131] (although see[132] for different findings regarding tolerance in bonobos). Another possibility is that joint action itself increases social tolerance between individuals[133,134]. For example, brown capuchin monkeys passively share food by tolerating other monkeys who reach for the crumbs they drop, and they do this more after collaborative than individual effort[135]. Although the psychological mechanisms underpinning this so-called 'facilitated taking' are unclear, it is possible that social tolerance increases after individuals work together - and that increased tolerance results in lowered aggression towards partners taking some of the food reward.

Some authors describe chimpanzees in the wild participating in highly collaborative group hunts, with individuals taking different but complementary roles (for example driver, ambusher, or blocker)[136]. After the collective action, chimpanzees frequently share meat from the hunt, and it has been argued that individuals who participated in the hunt get more meat compared to individuals who were simply in the vicinity or who arrived later[136–138]. This assertion implies that chimpanzees might be able to keep track of individuals' contributions to the hunt and that individuals are motivated to meritocratically reward contributors. Nevertheless, these interpretations are not universally supported[71]. Experimental studies suggest that proximity to the food, rather than participation in the cooperation task, predicts how much food individuals get[139,140]. Importantly, proximity to food and participation in the hunt are frequently confounded in the wild[141]. Another, non-mutually exclusive possibility is that individuals participating in group hunts are hungrier or more motivated to get a share of the meat, meaning that they beg more and ultimately receive more once the hunt ends[140,142] (although see[138], who report that, in chimpanzees, hunters receive more food than non-hunters independent of how much they beg for food).

There is no conclusive evidence that non-human animals strategically incentivise their partners' investments in collective action. However, simpler mechanisms, such as increased social tolerance (maybe mediated by an increase in oxytocin after coordinated activities[134,138]), proximity, or their partners' behaviour, can lead to increased sharing of benefits after collaboration in collective action. By contrast, human children as young as three years old already share more after collaborative effort than individual effort[143,144], showing that the abilities to monitor partners and incentivise partner contributions emerge early in human development. Furthermore, conclusive evidence is also missing in non-human animals that individuals expect to receive fair compensation for their contributions to collective action as experimental studies have yielded mixed results regarding non-human animals' responses to inequity. However, an unpublished meta-analysis suggests that, where non-human animals exhibit a tendency to reject poor offers, this stems from disappointment rather than fairness preferences (Ritov et al. under review).

Finally, we note an additional difference in how humans and nonhuman species incentivise interaction partners to cooperate. In humans, some instances of reciprocity are supported by the capacity to anticipate the future benefits of cooperating, allowing investments to help others to be strategically motivated[145]. Prospective or future-oriented reciprocity requires individuals to discount immediate costs in pursuit of downstream rewards in future. The capacities to anticipate the future benefits of current investments and to plan to achieve them likely have a key role in allowing humans to cooperatively solve a wide range of problems. Prospective reciprocity might help to foster the emergence of large-scale cooperation in our species, contributing to many of our societal and economical arrangements. But computing how one's actions might influence the future behaviour of another individual is more cognitively demanding than simply responding to a partner's previous behaviour; and evidence suggests that human children only begin to reason in this way at around the age of five[146–148]. By contrast, children as young as three years old can keep track of and respond contingently to their partner's previous behaviour[149,150], suggesting that is less cognitively demanding. Whether non-human animals are capable of such future-oriented reciprocity is a question that deserves further study, but the current evidence does not suggest so[146,151].

[H2] Attracting partners

When cooperators benefit because they are rewarded or chosen by others for interactions, they might exhibit sensitivity to audience presence, behaving differently when observed compared to when potential partners are absent. Such sensitivity to audience presence has been observed in cleaner fish[152] but there is scant further evidence that non-human animals behave more cooperatively in the presence of bystanders. The socio-ecology of the cleaner fish-client mutualism might especially lend itself to the emergence of audience effects as cleaner fish have thousands of interactions with clients in a day[153]. Thus, cleaner fish have ample opportunities to learn through trial and error how their own behaviour affects the behaviour of current clients and bystander reef-fish (potential future clients). In other words, cleaner fish can learn that cheating results in immediate negative outcomes (current clients swimming away) without needing to attribute mental states to their clients. Where the socio–ecology allows, we might expect to also observe similar audience effects in other species, although we are not aware of any cases. However, socio-ecology might also explain the lack of audience effects in other species. For example, unlike cleaner fish, chimpanzees do not behave more prosocially when observed by others compared to when they are unobserved[154]. It could be the case that there is little selection pressure for such audience effects in chimpanzee societies, since (unlike cleaner fish) chimpanzees do not routinely engage in cooperative interactions with strangers. Thus, chimpanzees own personal experience might be more informative than third-party observations when it comes to interactions with known individuals.

In contrast to cleaner fish, humans seem to use more complex cognitive strategies to strategically manage their reputation. Namely, individuals take the perspective of an observer and infer how the observer's impression of them would change after witnessing their different social behaviours[14]. Perhaps for this reason, humans only begin to strategically manage their prosocial reputation when they are around five years old, which is when these kinds of mental abilities begin to emerge[14,154,155].

The challenges of cooperation — identifying appropriate partners, monitoring and keeping track of their behaviour, incentivising them to cooperate (via punishment or/and reward) and attracting them as partners — are faced by different species to different degrees. In some cases, the socio-ecology of the system reduces the cognitive challenges, such as when individuals interact with only one partner in concurrent exchanges (hamlet fish, for example). By contrast,

when individuals interact with the multiple partners over extended periods of time, the cognitive challenges of cooperation are increased.

[H1] Uniquely human cooperation

In the previous sections we mainly focused on cooperation mechanisms in non-human animals. However, humans are clear outliers in the scale, frequency and variety of contexts in which their cooperative interactions occur (Table 1)[31,156,157]. Whereas cooperation in most other species is limited to one or a handful of contexts, humans do it all.

The differences in the scale and frequency of cooperation and the cognition that supports it between humans and other species could stem from historical selection pressures associated with the occupation of a highly interdependent collaborative foraging niche[31,158,159]. This evolutionary history, which placed a huge premium on successful cooperation and egalitarianism, is thought to have given rise to a suite of specific and complex cognitive abilities that underpin the many forms of cooperation, including at larger scales, that are exclusively observed in humans.

We discussed how an ability to anticipate downstream benefits might encourage individual investments in cooperation and how an ability to explain actions to others (using language) might render cooperation-enforcement mechanisms, like punishment, more efficient. But there is clearly more to it than this. Humans are endowed with a unique ability to see the world from another individual's perspective and, specifically, to understand and formally represent another individual's knowledge states, beliefs and goals (see[14,160] for reviews). These cognitive abilities allow individuals to understand how their actions might affect others' impressions of them (allowing humans to strategically manage our reputations). They can also be involved in empathy, where humans both affectively and cognitively represent other individuals' emotional states, providing a motivational foundation for some instances of helping behaviour (Box 1). In addition to representing others' intentions, humans are capable of shared intentionality — an understanding that individuals are solving a problem together and are committed to supporting each other[161]. Shared intentionality, in combination with a general proclivity for fairness, can help to foster the successful collaboration observed in a wider range of contexts[143,162,163]. Language enables humans to communicate information about other individuals' reputations[35], to explain the rationale behind their actions and to describe and

enforce social norms. Moreover, humans can generate and enforce social norms with the whole array of mechanisms reviewed above, from non-costly partner choice to rewarding, gossiping and punishing. Although we acknowledge that elements of these cognitive abilities may be present in non-human animals, there is no doubt that humans outperform other species in all of these major socio-cognitive domains. Many of the abilities we described do not emerge until middle childhood and continue to develop into adolescence[164–167], coinciding with the development of core cognitive traits, including a larger working memory, likely to underpin many aspects of complex social cognition in humans[14,168].

Humans are also uniquely able to design rules, norms and institutions to obtain preferred mutual outcomes when faced with social dilemmas [146,169,170]. This ability allows cooperation to transition from small-scale interactions involving intensive monitoring of identifiable partners to large-scale settings where humans cooperate unconditionally, often with strangers, and where cooperative investments don't seem to be as clearly monitored or enforced by others[171]. Humans create, follow and internalize social norms[172–175], meaning that cooperating is often subjectively rewarding[176–178]. When cooperation becomes subjectively rewarding it acts as a psychological shortcut that removes some of the cognitive obstacles to cooperating when costs are paid upfront but rewards are delayed or uncertain. It is not yet known whether non-human animals experience a similar subjective reward from helping others, but we believe this would be a promising avenue for future research. A similar shortcut to cooperation might be the emotional contagion response experienced by animals exposed to the suffering or distress from others. This aversive reaction might motivate individuals to perform actions that help distressed partners as a by-product of relieving one's own subjective distress (Box 1).

[H1] Summary and future directions

Cooperation need not always involve complex cognitive abilities[179,180]. Where cooperative investments are repaid via self-serving responses of beneficiaries (Fig. 1), individuals do not necessarily need to recognise partners or track the outcome of interactions; and the cognition needed to support cooperation can often be quite simple. This is the case in the many examples of kin selection, pseudo-reciprocity, and interdependence we described above and can perhaps help to explain why such interactions seem to be especially widespread in nature.

The requirement for recognising interaction partners differentiates cooperation examples observed in nature (Fig. 2) and the need to recognise partners is likely to be higher when interactions take place over longer time scales. We have highlighted examples where the need to recognize partners is shaped by the species' socio-ecology, which can help to reduce the cognitive burden that cooperating over longer time scales — and having to remember a specific partner's identity — would otherwise create. Thus, in the simplest cases of contingent cooperation found in non-human animals, socio-ecology can constrain the cognitive complexity of a cooperative interaction. However, in other cases where cooperative interactions involving contingent cooperation take place over longer time scales, individuals might need to recognise interaction partners and even to have partner-specific memory about previous interactions. Contingent cooperation might also involve the anticipation of downstream benefits rather than immediate reward and it is an open question whether such psychological abilities are unique to humans. Where partners are monitored, we believe that cognitive mechanisms are also likely to vary according to whether cooperation occurs only within dyads or whether there is collective action in a larger group. Collective action implies that individuals can track — and perhaps even compare — investments in multi-player interactions and that they are able to respond accordingly.

Although various examples of dyadic contingent cooperation in non-human species exist, our survey of the literature suggests that cooperation supported by reputation-based mechanisms and / or by social norms is relatively rare or non-existent. Very few examples of reputation-based cooperation exist in non-human species, and we are not aware of any examples of cooperation supported by social norms. It is possible that these forms of cooperation rely on the ability to communicate about norms and the behaviour of others using language[12]. Such mechanisms might also be involved in monitoring and incentivising contributions to collective action, which might help to explain why examples of successful collective action involving contingent investments in non-human animals are scarce[181].

Based on this review, more studies should investigate the proximate mechanisms supporting cooperation in non-human animals to better understand if this could explain why they cooperate in relatively narrow and constrained contexts. Such investigations could aim to reveal what cognitive skills are necessary for strategic, future-oriented reciprocal cooperation,

which non-human animals have long-term memory about 'who did what and when'; and what, precisely, different species encode about their past interactions with others.

Little, if anything, is known about whether non-human animals can keep track of a partner's relative contributions to collective action. Similarly, except for the cleaner fish-client mutualism, almost no evidence exists for non-human animals having the capacity to identify and choose cooperative partners based on others' observations. Thus, other species might typically rely on first-hand experience when choosing partners. In the case of the cleaner fish-client example, clients still evaluate the cleaner fish by observing the interaction themselves, rather than being informed about it by a third-party; and we are aware of no evidence for gossip or transmission of reputations among individuals in non-human animals. In general, more studies that assess non-human animals' capacity to learn about others' cooperativeness based on third-party observations are necessary; including studies that assess whether non-human animals manage their reputation, and, if so, the cognition involved.

Given the theoretical importance of punishment, partner switching or sanctions to enforce cooperation, studies are also necessary that investigate how individuals interpret punishment (or being rejected by a social partner) and whether individuals learn to change their behaviour in future. Furthermore, the findings with vervet monkeys showing that they participate more in intergroup encounters after punishment also raise the question of how animals can infer that the punishment or sanction was because of their inaction or failure to cooperate. Finally, we believe it would be interesting to ask whether there is any evidence for proximate mechanisms akin to subjective warm glow among non-humans, and how we might measure these if they exist.

We look forward to seeing more work on non-human species that identifies the cognition supporting cooperation – especially in naturalistic or ecologically valid settings. By tapping more precisely into the cognition supporting cooperation in non-humans, especially forms of cooperation where temptation for free-riding is high and that rely on partner recognition and return investments, we will be able to identify what, if anything, sets human cooperation apart from what is observed elsewhere in nature.

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Table 1: Representative examples of cooperation in non-human animals and humans

Cooperation form	Non-primates	Non-human primates	Humans
Altruism	Individuals invest to help kin, particularly in cooperatively breeding and eusocial species[182,183]	Cooperative breeding in species such as ring-tailed lemurs, cotton-top tamarins and common marmosets[184]	Altruistic investments to help kin are commonplace and can involve reproductive sacrifice such as the evolution of menopause and grandmothers[32,185]
Interdependence[a]	Parents working together to raise young[94]; social species where individuals benefit from living in larger groups [22]	Similar examples as reported for non-primate animals	Forms the basis of friendships and mutual exchange partnerships in small-scale, non-industrial societies such as osotua in Maasai, hxaro exchange in Hadza[28,186].
Partner choice[a]	Limited evidence. Coral trout recruitment of the best moray eel partner for hunting[70]; reef-fish clients of the bluestreak cleaner wrasse avoid uncooperative cleaners[75]	Chimpanzees select the best partner for a cooperative pulling task[68]; partner choice could also have a role in reciprocal cooperation.	Key mechanism supporting cooperation in humans[12,14]
Reciprocal cooperation	Mostly in concurrent exchanges like predator inspection in sticklebacks and egg trading in hamlet fish[187,188]; rats have tit-for-tat like reciprocity in experimental settings[99,100]	Limited evidence for strict tit-for-tat reciprocity in experimental settings; evidence for longer-term exchange of services and goods in many species[9,107,114]	Key mechanism supporting cooperation in humans that occurs in several domains (food sharing, exchange of goods and services)[189]; but may only infrequently be based on strict tit-for-tat principles[33,107]
Punishment	Limited evidence. Clients of cleaner fish punish cheating individuals; cleaner fish also punish cheating conspecifics [19,122]	Limited evidence. Vervet monkeys punish individuals that don't contribute to territorial disputes; chimpanzees punish conspecifics who steal food [20,118]	Humans willingly punish others especially in lab settings and even when individuals weren't personally harmed by the transgression; however, the real-world prevalence and consequence of punishment are not well understood[59,190]
Investment in public goods	Scalefin anthias produce a public good in the form of deterrence against a parasite[43]; contributions to cooperative hunting and predator detection in group-living species[127,191]	Chimpanzees contribute to cooperative hunting and territory defence[137,192]	Key part of the human behavioural repertoire and can occur at both local and global scales[31]
Reputation management	Limited evidence. Cleaner fish sensitivity to the presence of an audience when providing cleaning service[75]	No evidence that non-human primates strategically manage their reputation[154].	Observability or the potential that an individual's behaviour will be revealed to others impacts human prosocial and punitive behaviour[193]
Rewarding and meritocratic sharing	No evidence in non-primates.	Limited but suggestive evidence that chimpanzees might reward those who contributed to group	Many examples although concepts and notions of fairness differ substantially across societies[194]

		hunting success; but alternative explanations are also possible[129,138,140,142].	

[a]Interdependence and partner choice both fit the concept of pseudo-reciprocity, whereby an individual's investments allow the partner(s) to perform a self-serving response which benefits the investor as a by-product.

Fig. 1 |Pathways by which investments might yield benefits to an individual and their partner(s). In each scenario, blue arrows denote investment and red arrows denote by-product benefits. By-product benefits simply refer to benefits that arise for the investor due to a self-serving response of the recipient or arise in collective action at least in part due to the actions of another individual. **a |** Depicts kin selection and pseudo-reciprocity, where an individual invests to help a recipient(s) and the investor either accrues indirect benefits (via the increased fitness of the relative) or direct benefits as a by-product of the recipient's self-serving response which directly benefits the investor. **b |** Depicts reciprocity, where an individual invests to help another individual(s) and the benefits arise because of a return investment from the recipient(s) of help. **c |** Individuals invest in collective action to produce shared benefits or a public good. Individual investments can benefit others, even individuals who do not contribute to the collective action. The size of the benefit produced can be a linear or non-linear function of their investments[195]; and some collective actions will have threshold dynamics, whereby benefits are either produced in full or not produced at all. Where shared benefits are affected by the contributions of other individuals, then individuals might be sensitive to the presence and/or behaviour of others when deciding whether or how much to invest in collective action. We do not show the possibility that in collective action and reciprocity the by-product benefits and return investments respectively could come from bystanders rather than the recipients of the original investment to maintain the figure's clarity.

Fig. 2 | Cooperative interactions categorized by how cognitive challenges are solved. The cognitive challenges posed during cooperative interactions can be used to categorise them, with the first major differentiation being whether individuals must individually recognise interaction partners. Recognition implies that individuals remember the current interaction partner and could identify them again even when the current interaction ends. A second major differentiation concerns whether interactions involve contingent investments, so that individuals must condition their own behaviour on the behaviour of their interaction partner(s). Interactions involving contingent investments are most likely to involve reciprocity in dyads or collective action in groups. By contrast, most interactions not involving conditional investments will fall under the banners of kin selection, interdependence, by-product mutualism and pseudo-reciprocity and are relatively common in nonhuman species.

Cooperative interactions involving individual recognition where benefits also depend upon contingent responses levy greater cognitive demands and occur in limited contexts outside humans. Whereas we have framed partner choice and rejection as not involving contingent return investments from the partner, we acknowledge that partners can be chosen for subsequently reciprocal interactions or to contribute to collective action – so in that case the benefit of choosing a partner might depend upon the partner returning the investment or investing in the collective good.

Box 1: Same outcome, different cognition

Although similar functional outcomes can evolve independently across taxa, they frequently arise via different proximate mechanisms. One example concerns helping behaviour, which is a form of cooperative investment. The willingness to help conspecifics is observed in ants, rats and chimpanzees, but the processes underpinning such helpful behaviour are probably very different in the three species[196–203]. To show that the helper's motivation is to improve a recipient's welfare requires control conditions demonstrating that the following criteria are met: helpers do not immediately selfishly benefit from the action itself; the same helping behaviour is not exhibited when the recipient's needs or goals change; and the helper's response is instrumental and flexibly deployed to increase the recipient's welfare[204].

In ants, the rescue behaviour of injured conspecifics does not fit the above criteria and is likely to be a highly context-specific and programmed behaviour, triggered by pheromones[199]. For example, ants will also rescue healthy individuals that are covered with pheromone, even when the healthy individuals try to free themselves from the carriers. Moreover, individuals will only rescue injured ants if they are met after a raid (the very specific context in which the behaviour probably evolved)[199].

By contrast, laboratory rats learn to open a door to free a trapped cagemate[196], although individuals are only likely to act when seeing or hearing the vocalisations of the trapped cagemate means that they experience a negative emotion themselves and cannot escape from the distressing situation. In a study where the free rats could escape to another room, the free rats were less likely to release the cagemate[198]. Thus, it is possible that rats perceive the ultrasonic distress calls of the trapped cagemate and act to stop this aversive and distressing call, either by releasing the conspecific or by removing themselves from the situation[196,205]. If this is the case, rats' behaviour would also not meet the criteria mentioned above.

Helping behaviour among chimpanzees seems to be supported by cognitive skills that allow individuals to assess others' goals. The experimental paradigms used with chimpanzees have not elicited distress vocalizations in the targets of helping, so emotional contagion can probably be ruled out as a proximate mechanism. Chimpanzees help others achieve various goals, such as reaching an out-of-reach object, releasing stuck food or opening a door[206–209]. Several

control conditions showed that the helping behaviour was not rewarding for the individual or a carry-over effect from the familiarization sessions[206,207], and that the same behaviour was not exhibited when the partner's goals changed[206]. Helpers select the appropriate tool for the specific problem the partner is struggling with[209], suggesting that their behaviour is intentional, flexible and instrumental to supporting the partner's goals[203], so that it would fit the criteria mentioned above. However, whether chimpanzee helping behaviour is also supported by affective perspective-taking or sympathy is unclear.