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A comparative approach to affect and cooperation

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ABSTRACT

A central premise of the science of comparative affect is that we can best learn about the causes and consequences of affect by comparing affective phenomena across a variety of species, including humans. We take as a given that affect is widely shared across animals, but a key challenge is to accurately represent each species' affective experience. A common approach in the comparative study of behavior and cognition is to develop standardized experimental paradigms that can be used across species, with the assumption that if the same task is being used, we can directly compare behavioral responses. This experimental approach rests on two underlying assumptions: first, that different species' perception of and affective response to these paradigms are the same; and second, that behavioral and physiological (including endocrine and neural) responses to these paradigms are homologous; if either of these assumptions is not true, then the comparison becomes much less straightforward. Our goal in the present paper is to summarize the dominant paradigms that have been used for such comparative research, with a particular focus on paradigms common in the cooperation literature, and to critically discuss dominant assumptions about what affective states these tasks can or should measure. We then consider the advantages and drawbacks of this experimental method, and consider alternatives that may improve our understanding. We hope that this will help scholars recognize and avoid pitfalls inherent in studying affect, and stimulate them to create novel, ecologically relevant paradigms for examining affect across the animal kingdom.

1. Introduction

The immense scale and plasticity of human cooperation is a defining feature of our species (Melis and Semmann, 2010). Human societies show a large variety of complex social configurations characterized by diverse cooperative relationships among multiple, often unrelated individuals (Hill et al., 2011; Kaplan et al., 2009). In general, our cooperative abilities are considered to be a major force in explaining humans' ecological dominance and biodemographic success (Kramer, 2010; Roberts and Stewart, 2018), and some argue it may have been a strong force driving the evolution of our intelligence (Vygotskian intelligence hypothesis: Vygotsky, 1978; Moll and Tomasello, 2007; but see González-Forero and Gardner, 2018). However, while extensive progress has been made in explaining the evolution of cooperative behavior across taxa (West et al., 2007), the evolution of complex human cooperation continues to pose explanatory challenges that, although debated for more than 50 years, remain unresolved (e.g. Burkart et al., 2009; Pinker, 2010; Silk and House, 2016; Taborsky et al., 2016a, b)

Whereas definitions for cooperation vary substantially between authors and scientific fields (Noë, 2006; West et al., 2007), all refer to benefits and costs for one or more social partners (often termed *players*). A key explanatory problem is that cooperation becomes prone to cheaters that reap the benefits, yet never pay the costs. Hamilton (1964) reconciled the problem of cooperation among genetically similar individuals with his inclusive fitness theory. Nevertheless, cooperation in animal societies often involves unrelated individuals, suggesting that direct fitness benefits must also play a central

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evolutionary role (Leimar and Hammerstein, 2010; Taborsky et al., 2016b). For example, cooperation between unrelated individuals may be explained when all parties immediately benefit from the action (i.e. byproduct mutualism, West et al., 2007), yet when possible, individuals are still expected to minimize their own cost at the expense of others (a.k.a. 'the tragedy of the commons', Lloyd, 1833) and cooperation can break down easily (e.g., Burton-Chellew and West, 2013; Kummerli et al., 2010).

This is particularly apparent for behaviors that do not reap immediate benefits for an actor. Trivers (1971) suggested that this could be resolved in situations in which individuals interact repeatedly and can differentiate cheaters from cooperators, as reciprocal altruism can evolve such that individuals engage in immediately costly behaviors that increase their probability of receiving future (greater) benefits from a partner. Originally, such iterated interactions were modeled using repeated prisoner's dilemma games, which suggested that reciprocity can be maintained through the evolution of decision rules reliant on a 'tit-for-tat' or similar strategy (Axelrod, 1984). Whereas there is a considerable amount of evidence for long-term exchange of commodities in social mammals (e.g., Kern and Radford, 2018; Schino and Aureli, 2008; Schino, 2007), and even for long-term memory for reciprocal interactions in birds (Müller et al., 2017), evidence for active 'bookkeeping' of the costs and benefits of reciprocity (a.k.a. calculated reciprocity, de Waal and Luttrell, 1988) is scarce (but see Dufour et al., 2009; Schweinfurth and Taborsky, 2018a). Furthermore, such calculated reciprocity may be too cognitive demanding for most animals (Stevens and Hauser, 2004).

Therefore, less cognitively demanding proximate mechanisms have been suggested to underpin reciprocity, such as symmetry-based reciprocity, attitudinal reciprocity and emotionally mediated reciprocity. Symmetry-based reciprocity describes simple decision rules reliant on symmetrical features of interaction partners: e.g. age, sex or mutual association (de Waal and Luttrell, 1988). Most relevant here, however, are attitudinal reciprocity, which describes decision rules based on short term attitudes towards specific cooperation partners, which in turn is based on recent interactions with that individual (Brosnan and de Waal, 2002), and/or emotionally mediated reciprocity, which describes decision rules based on long-term emotional appraisal of specific cooperation partners, which in turn is based on multiple interactions with that individual (Aureli and Schaffner, 2002; Schino and Aureli, 2009; Schino et al., 2007). Agent-based models (ABMs) have recently shown that over multiple generations, reciprocal altruism breaks down in populations that base partner choice solely on similarities with conspecifics, suggesting that symmetry-based reciprocity on its own is an evolutionarily unstable proximate mechanism for non-kin cooperation (Campennì and Schino, 2016). In contrast, several other studies using ABMs have generated evolutionary stable systems that represent actual social organizations (e.g. those of monkey groups) when individuals rely on emotionally mediated reciprocity (Campennì and Schino, 2016; Evers et al., 2016; Puga-Gonzalez et al., 2015). Note, however, that emotionally mediated reciprocity (or attitudinal reciprocity), and the more cognitively complex calculated reciprocity need not be mutually exclusive. In fact, human brain imaging studies support the notion that complex cognitive mechanisms and more 'basal' hormonal mechanisms may exist in parallel, and show that their employment depends on familiarity (Krueger et al., 2007); i.e. more hormonal/emotional areas are activated when cooperating with familiar individuals (cf. *emotionally mediated reciprocity* (Schino, and Aureli, 2009); and/or *attitudinal reciprocity* (Brosnan & de Waal, 2000)), whereas more cortical areas involved in mentalizing are activated while cooperating with unfamiliar individuals (cf. *calculated reciprocity* (de Waal, and Luttrell, 1988). Thus, the employment of these different mechanisms should be seen as a dynamic process that flexibly adjusts to the specific context in which it is needed (West et al., 2011a, b), and where the different components are also not independent— i.e. cognition can affect subsequent emotional appraisal, and emotions can affect cognitive decisions (cf. the componential view of emotions; Mendl et al., 2010; see below).

Given the ubiquity of cooperation in animals (Dugatkin, 1991; Clutton-Brock, 2009), biologists traditionally adopt a phylogenetic approach to trace the evolutionary history of cooperation (Huxley, 1923; Hamilton, 1964), comparing cooperation among different species. We now have evidence for non-kin cooperation in a growing number of species from different lineages, ranging from primates (e.g., Cronin et al., 2005; Melis, 2006; Mendres and de Waal, 2000; Miss and Burkart, 2018; Molesti and Majolo, 2016; Suchak et al., 2014) and other social mammals (e.g., Drea and Carter, 2009; Marshall-Pescini et al., 2017; Plotnik et al., 2011; Schmelz et al., 2017; Schweinfurth and Taborsky, 2048b) to birds (e.g., Massen et al., 2015; Schwing et al., 2016; Seed et al., 2008) and fish (e.g., Vail et al., 2013, 2014). However, while this approach is very useful for understanding how cooperation functions in response to a species' ecology, it has been less useful for identifying common cognitive and/or affective mechanisms underlying cooperation across species. Relevant to the current paper, while there have been some studies testing broad hypotheses about the evolution of cognition (Fitch et al., 2010; MacLean et al., 2012), fewer are explicitly comparative (but see Burkart et al., 2014) and even fewer have considered the emotional mediation of cooperation, despite its emerging prominence in explaining cooperation.

Emotional responses, specifically those of non-human animals, have been notoriously difficult to measure due to the subjective component of emotional experience, which per definition cannot be directly measured in another person, let alone in animals (Tinbergen, 1963). Yet, human emotions are considered to be multifaceted, comprising a subjective component as well as behavioral and physiological components (Izard, 1977). Indeed, most theoretical approaches to animal emotions assume that different components, including affect, interact and that emotions are either the sum of those parts (the componential view of emotions; Mendl et al., 2010; Paul et al., 2005; 2019) or are an emergent phenomenon of these parts (the constructivist view: Bliss-Moreau, 2017). While our message does not require discriminating further between these two views, we do emphasize the key point common to both for studying animals: emotions involve specific, measurable components and animal emotions, whatever they may be, should be studied by exploring each of these components and their interactions separately. Moreover, we support the view that, irrespective of whether animals can consciously experience feelings, it is important in this work not to make *a priori* assumptions about potential subjective experiences. Yet, to our knowledge, this approach has not been systematically imposed on questions regarding cooperation.

Therefore, in this review we aim to provide an overview of attempts to explore affective responses in the context of cooperation and consider ways in which related work informs our understanding of the affective components of cooperation. In particular, given the nascent state of the field, we will consider the limitations of experimental setups used thus far and how this constrains our understanding, and then provide our vision for future directions that the field can take.

2. Review of paradigms in light of "cognitive and/or emotional" cooperative decision making

2.1. Coordination paradigms

Animal cooperation studies have a long history, starting with the seminal work of Meredith Crawford in 1937 (Crawford, 1937). Crawford confronted two young chimpanzees with a tray filled with food with two ropes attached to it. The tray was too heavy for only one of the juvenile chimpanzees to pull into reach, so food could only be acquired when the two chimpanzees pulled the ropes simultaneously. Since then, several other studies have adopted this paradigm (Mendres and de Waal, 2000) or variations thereof (Fady, 1972; Suchak et al., 2014, 2016; Suchak et al., 2018). Similar paradigms that rely on coordinated

Table 1

Coordination paradigms used to study cooperation in animals, the species in which they were tested and several parameters tested.

Paradigm	Species	Study	Understanding the need of partner	Tolerance as constraint	Reward Equity as constrain	Physiological Measures	Other (affective) measures
Cooperative pulling task	*Primates*						
	Pan troglodytes	(Crawford, 1937; Suchak et al., 2014, 2016, 2018)	Y	Y	Y	–	–
			Y	Y	Y	–	–
	Macaca Mulatta & M. Tonkeana	(Petit et al., 1992)	N	Y	–	–	–
	Cebus Apella	(de Waal and Berger, 2000; de Waal and Davis, 2003; Mendres and de Waal, 2000)	Y	–	Y	–	
Coordinated pulling / pushing	*Primates*						
	Pan troglodytes	(Chalmeau and Gallo, 1996)	Y	–	–	–	–
	Pongo Pygmaeus	(Chalmeau et al., 1997a, b)	Y				
	Cebus apella	(Chalmeau et al., 1997a, b)	N	–	–	–	–
	Saguinus oedipus	(Cronin et al., 2005)	Y	–	–	–	–
	Other mammals						
	Crocutta Crocutta	(Drea and Carter, 2009)	Y	Y	–	–	–
	Tursiops truncatus	(Eskelinen et al., 2016; Jaakkola et al., 2018)	Y	–	–	–	Acoustic parameters: an increase in sound production while cooperating
Loose-string task	*Primates*						
	Pan troglodytes	(Hirata, 2003; Hirata and Fuwa, 2007; Melis, 2006; Melis et al., 2006)	Y	Y	–	–	A preference for efficient partners
	Pan paniscus	(Hare et al., 2007)	–	Y	–	–	–
	M. sylvanus	(Molesti and Majolo, 2016)	Y	Y	–	–	Similarity in boldness-shyness increased cooperation
	M. fascicularis	(Stocker et al., 2019)	–	N	–	Cortisol decreased while cooperating, but only when cooperating with a friend.	
	M. fuscata	(Kaigaishi et al., 2019)	± ; i.e. only one individual	Y	–	–	–
	Callithrix jacchus	(Martin et al., 2019)	± ; i.e., individual and/or dyadic learning was observed	Y	–	–	Prosociality increased cooperation
	Other mammals						
	Elephas maximus	(Plotnik et al., 2011)	Y	–	–	–	–
	Canis familiaris	(Sarah Marshall-Pescini et al., 2018; Sarah Marshall-Pescini et al., 2017; Ostojić and Clayton, 2014)	Y/N	Y	–	–	–
	Canis lupus	(Sarah Marshall-Pescini et al., 2017)	Y	Y	–	–	–
	Pteronura brasiliensis & Aonyx cinrea	(Schmelz et al., 2017)	N	–	–	–	–
	Birds						
	Corvus frugilegus	(Scheid and Noë, 2010; Seed et al., 2008)	N	Y	–	Cortisol related to boldness-shyness; i.e. higher in the latter after stressful event	Temperament; i.e. Bold individuals performed better in the cooperation task
	Psittacus erithacus	(Péron et al., 2011)	±	–	–	–	–
	Corvus corax	(Asakawa-Haas et al., 2016; Massen et al., 2015; 2019)	Y/N	Y	Y	–	–
	Nestor notabilis	(Heaney et al., 2017; Schwing et al., 2016)	Y/N	Y	Y	–	–
	Ara Glaucogularis	(Tassin du Montaigu, et al., 2019)	N	N	–	–	–
Complementary tasks							
	Callithrix jacchus	(Werdenich and Huber, 2002)	–	–	–	–	–
	Nestor notabilis	(Tebbich et al., 1996)	–	–	Y	–	Dominant kea manipulated their partners to produce.

(*continued on next page*)

Table 1 (*continued*)

Paradigm	Species	Study	Understanding the need of partner	Tolerance as constraint	Reward Equity as constrain	Physiological Measures	Other (affective) measures
	Plectropomus leopardus	(Vail et al., 2014)	Y	–	–	–	–
	Pan Paniscus	(Engelmann et al., 2015; Engelmann and Herrmann, 2016)	Y	Y	Y	–	–

action have been developed as well (e.g.: Cronin et al., 2005; Drea and Carter, 2009; Eskelinen et al., 2016; Jaakkola et al., 2018; Miss and Burkart, 2018; see Table 1 for a full overview), with the loose-string paradigm designed by Hirata (Hirata, 2003) being the most popular across a diversity of species (Table 1). Whereas much of human cooperation requires coordinated action, surprisingly few studies have experimentally tackled this phenomenon in humans, and those that do generally test children (Kagan and Madsen, 1970), or even infants (Ross and Lollis, 1987; Warneken et al., 2006)

Most of the studies employing coordination paradigms have concentrated on the cognitive underpinnings of the task, examining whether particular species (or age groups) do or do not understand the contingencies of the specific task. Recently, however, focus has also shifted to examining the influence of social context on task performance. Generally, in those species in which it has thus far been tested, social tolerance and relationship quality seem to be important constraints on the emergence of cooperation. Interspecific comparisons reveal that more socially tolerant species cooperate more (easily) (e.g., Petit et al., 1992; Hare et al., 2007; Joly et al., 2017). Intraspecific comparisons also show that populations with high tolerance outperform those with low tolerance on a cooperation task (Kaigaishi et al., 2019), and further demonstrate that dyads within a group cooperate more often and more successfully when they have good relationships and/or are socially tolerant to each other (see Table 1). Such individuals even select each other more often as cooperation partners when given the choice (e.g. Asakawa-Haas et al., 2016).

For our purposes, this is important because these patterns are consistent with animals utilizing emotionally mediated decision rules, yet specific emotional mechanisms are rarely considered. Friends, for example, tend to have similar personalities (Massen and Koski, 2014; Youyou et al., 2017; Ebenau et al., 2019), and it has been suggested that this phenotypic similarity increases cooperation through a better understanding of each other's behavior, subsequent increased trust, easier coordination of behavior, and the maintenance of a similar affective state while cooperating (Massen and Koski, 2014). Recent studies testing these hypotheses have indeed found that, at least among chimpanzees, friends tend to trust each other more than non-friends (Engelmann and Herrmann, 2016; but see Calcutt et al., 2019), and that for Barbary macaques, cooperative success is enhanced by personality similarity in animals (Molesti and Majolo, 2016).

Cheating, on the other hand, seems to have negative effects on subsequent cooperation, and all studies that examined this effect to date report a loss of interest in the paradigm by the animal that was cheated (de Waal and Davis, 2003; Engelmann et al., 2015; Massen et al., 2015; Schwing et al., 2016) (see also Section 2.2.5 on inequity aversion). In human studies, participants are sometimes given the opportunity to punish defectors at a personal cost, and do so readily (Fehr and Gächter, 2002), although cultural differences in the tendency to punish are apparent (e.g., Henrich and Henrich, 2014). Interestingly, from our perspective, participants often report being angry when their partners 'defect', and this anger seems to mediate the amount of costly punishment in these games (Cubitt et al., 2011; Seip et al., 2014a). Moreover, when primed with anger prior to the experiment, humans punish defectors even more than normal (Seip et al., 2014a), again underlining the important mediating role of this emotion in dealing with defection. Whether the reported loss of motivation in animals that experience defection also reflects anger or is otherwise emotionally mediated remains unknown and is a promising avenue for further studies (see also Section 2.2.5 on inequity aversion).

2.2. Economic games

Original work on cooperation focused on more 'naturalistic' paradigms, such as the aforementioned barpull task, but more recently there has been interest in using economic games to explore cooperative decision-making across species. Although these games lack ecological

Table 2
Economic games tested in animals, type of game, purpose, species, and basic results within primates. Note that there are also results in species outside the primate order, particularly involving the Prisoner's dilemma game (Milinski, 1987; Dugatkin, 1991; Stephens et al., 2002; Wood et al., 2016), but for the sake of brevity and clarity chose to include only primates here.

Game	Purpose	Species	Studies	Result
Assurance Game (Stag Hunt)	Coordination game with two Nash equilibria (NE), one payoff dominant	Chimpanzees	(Brosnan et al., 2011; Bullinger et al., 2011; Duguid et al., 2014; Hall et al., 2019)	Chimpanzees can coordinate, and show evidence of a strategy, but do not always do so. Evidence of a leader/follower dynamic whereby the first player's choice affects the second player's strategy
		Rhesus monkeys	(Brosnan et al., 2012a; Parrish et al., 2014)	Rhesus coordinate whether or not they can see their partner's choice; mechanism appears to be *Stag* bias
		Capuchin monkeys	(Brosnan et al., 2011, 2012a, b; Smith et al., 2019)	Capuchins coordinate, but only when they can see their partner's choice; mechanism appears to be matching. There is no impact of oxytocin on decisions.
		Squirrel monkeys	(Vale et al., 2019)	Squirrel monkey females show a tendency to coordinate.
Snowdrift Game	Coordination game with a temptation to slack	Chimpanzees	(Sánchez-Amaro et al., 2016)	Chimpanzees coordinate, and their choices are influenced by the identity of their social partner.
Chicken Game (Hawk Dove)	Anti-coordination game	Chimpanzees	(Hall et al., 2019)	There is little evidence of anti-coordination, although this is a population that did not coordinate, either, indicating disinterest in the task.
		Rhesus monkeys	(Brosnan et al., 2017)	Rhesus monkeys play the NE, but only when they can see what their partner plays.
		Capuchin monkeys	(Brosnan et al., 2017; Smith et al., 2019)	Capuchin monkeys play the NE, but only when they can see what their partner plays. The second mover's choice is impacted by the first mover's decision. No impact of oxytocin on decisions.
		Squirrel monkeys	(Vale et al., 2019)	No evidence of NE play.
Matching pennies	Zero sum Anti-coordination game	Chimpanzees	(Martin et al., 2014)	Chimpanzees play the NE, but are faster at matching than anti-matching.
Prisoner's dilemma	Cooperation with temptation to defect	Chimpanzees	(Hall et al., 2019)	Little evidence of a consistent strategy, but over time second movers were less likely to *Defect* if the first mover did, suggesting they learned to avoid the worst outcome.
		Rhesus monkeys	(Haroush and Williams, 2015)	Mostly mutual defection, but cooperation was more common on trials subsequent to mutual cooperation
		Capuchin monkeys	(Smith et al., 2019)	Both mutual cooperation and mutual defection in different pairs. Subjects were more likely to defect after the partner defected. No impact of oxytocin on decisions.
		Squirrel monkeys	(Vale et al., 2019)	No evidence of NE play.
Ultimatum Game	Bargaining/ punishment game	Chimpanzees	(Jensen et al., 2007a, b; Kaiser et al., 2012; Proctor et al., 2013)	No evidence of refusals, but donors make more equitable choices when partners have the opportunity to refuse.
Trust Game			(Calcutt et al., 2019)	Subjects were more averse to social risk than in a non-social control. No influence of relationship on decisions.

validity, they are highly standardized and easy to use in (what we hope are) very similar ways across a variety of species and contexts (see Interpretations Section 4.1 for a further discussion of how animals interpret our tasks). This allows for developing and testing comparative hypotheses and deriving the underlying similarities and differences across species that can then be tested using more species-specific paradigms in more ecologically relevant contexts (Smith et al., 2018). These game scenarios are very simple. Two or more subjects are each given a choice, typically among only two options, and then rewards are distributed based on both what the subject and their partner(s) chose. The payoffs for outcomes can be adjusted so that researchers can test everything from coordination (Assurance game: both players benefit most if they choose the same outcome) to competition (Hawk Dove game: no coordinated outcome, players do best to play opposite their partner) and cooperation in the face of defection (Prisoner's Dilemma) (Table 2).

Thus far, these games indicate that both monkeys and apes can find the solutions to coordination games (Brosnan et al., 2011, 2012a). However, the mechanisms used to solve these games can differ across species. These mechanisms range from simple matching where the second player chooses the same option as their partner, a strategy that is often quite effective in these games even if it is not the highest paying outcome, to probability matching where the subjects play a strategy with the same frequency at which it is played in the environment, although not in a contingent manner (i.e., matching), to explicit strategy, in which the subject understands the rules of the game and makes decisions to maximize their overall benefit (Brosnan et al., 2011; Parrish et al., 2014). Early work also showed that chimpanzees used a leader-follower dynamic, whereby the second mover takes the first mover's choice into account (Bullinger et al., 2011), and recent studies suggest the same in at least some cases with monkeys as well (Smith et al., 2019; Vale et al., 2019).

In games that lack a mutually beneficial outcome, such as anti-coordination games, monkeys still find the Nash equilibrium (NE, or the choice for which they can do no better given what their partner is playing), although they find the NE in fewer contexts, indicating that it is either more difficult for them or that they only do so in specifics circumstances (Brosnan et al., 2017). Intriguingly, for our current focus on affect and relationship quality, in the closely related snowdrift game, where players have a conflict of interest over freeriding and cooperation, chimpanzees' choices are influenced by the identity of their social partner (Sánchez-Amaro et al., 2016). Finally, the only game in which substantial variation has been found across species is the prisoner's dilemma game. Early work on macaques found little evidence of mutual cooperation, although choosing the cooperation option was more common after mutual cooperation, suggesting that individual choices were influenced by the payoffs (Haroush and Williams, 2015). In capuchins, there was a tendency to defect after a partner's defection, also suggesting that choices were influenced by the game payoffs. More interestingly for our purposes, however, there were also substantial differences among pairs, with some showing high levels of mutual cooperation, some high levels of mutual defection, and some showing no discernable strategy (Smith et al., 2019). This variability suggests that the Prisoner's Dilemma may be a valuable game in which to explore how individual and social factors influence decision-making, including looking at how affect influences decision-making (Smith et al., 2019).

2.3. Reciprocity paradigms

Much of the evidence suggestive of animal cooperation stems from patterns of commodity exchange among individuals (e.g., Carter and Wilkinson, 2013; Jaeggi & Gurven, 2013; Schino and Aureli, 2008; Schino, 2007). The reciprocal nature of many of these exchanges is indeed suggestive of reciprocal altruism (Trivers, 1971), yet most of these studies consider correlational evidence only. Whereas some inferences about the nature of these exchanges can be made based on partner choice and the timeframe of reciprocity (Brosnan and de Waal, 2002; Schino et al., 2007), contextualizing specific motivations for reciprocal exchanges remains difficult. Experimental studies of reciprocity so far have mixed results. The initial absence of proof for contingent reciprocity in several species, including great apes (Amici et al., 2014; Brosnan et al., 2009; Melis et al., 2008; Stephens et al., 2002), supported the claim that cognitive constraints prevent the emergence of reciprocity in non-human animals (Stevens and Hauser, 2004). Since then, however, several studies have demonstrated contingent tit-for-tat reasoning in non-human animals (Dufour et al., 2009; Schweinfurth and Taborsky, 2018a), appropriate inhibition with regard to temporal discounting (Hayden, 2016), and the necessary memory for the nature of exchanges (Müller et al., 2017).

Moreover, the original experimental studies on reciprocity considered reciprocal altruism from a more cognitively mediated cost-benefit perspective only (cf. calculated reciprocity: de Waal and Luttrell, 1988), whereas there is now considerable theoretical evidence that emotional mediation can facilitate the evolution of reciprocity (Campennì & Schino, 2016; Evers et al., 2016; Puga-Gonzalez et al., 2015; see also attitudinal reciprocity: Brosnan and de Waal, 2002). These theoretical models make assumptions about emotional decision rules based on valence, arousal and the relatively slow feedback mechanisms of emotions (in comparison to purely calculated decision rules), yet do not precisely define what these emotions may be, nor how they directly influence decision rules. However, the timeframe of most reciprocal patterns (i.e. balanced over the long-term only), and the specificity of partner choice in reciprocal altruism, suggests that this phenomena is generally specific to long-term strong social bonds (Massen et al., 2010; Freiden et al., 2017), including in humans (Majolo et al., 2006). Consistent with this hypothesis, friendship has been found to increase trust in reciprocal interactions (Engelmann and Herrmann, 2016) and long-term stable relationships are correlated with a decrease in aversive reactions to inequity (Brosnan et al., 2005; Clark & Grote, 2003).

2.4. Inequity aversion

Inequity aversion, whereby individuals respond negatively to receiving less than a social partner (Adams, 1963), has been argued to be a way by which subjects can judge the value of their cooperation partners; subjects who consistently get less than their partners should seek out a new one (Brosnan and de Waal, 2014; Brosnan, 2006; Fehr and Schmidt, 1999). Although the first evidence for inequity responses in a non-human species was found relatively recently (Brosnan and Waal, 2003), since then there has been quite a lot of work in primates and other species using paradigms in which subjects receive different rewards than their partners for completing a task. Humans react very strongly when they receive fewer benefits than another for the same effort (Fehr and Schmidt, 1999), and tend to do so from an early age (Riedl et al., 2015). Humans also even react negatively when they receive more than another, albeit not as often or as strongly as they react to being disadvantaged (Blake et al., 2015; Loewenstein et al., 1989).

However, not every species responds negatively in these tasks, even within primates (see Table in Brosnan and de Waal, 2014 for details). Among those that do, it seems that whether a species routinely cooperates with non-kin is a better predictor of whether they respond to inequity than factors such as brain size, group size, or phylogeny (i.e., it is not a homology in either the primates more generally or the great apes specifically). This is true in primates as well as in corvids (Wascher, and Bugnyar, 2013) and canids (Essler et al., 2017), and recently some tentative evidence has been reported in parrots as well (Laumer et al., 2019). There are also individual differences in responses to inequity, sometimes substantial, and it is not yet clear what is underlying this variation. Although some factors show up consistently (i.e., dominance rank), it is clear that we do not yet have a full understanding of what other mechanisms may be contributing. Relevant to the current paper, affect is likely to be a component that strongly influences this response, although this possibility also remains currently unexamined. Finally, there is evidence that even species that respond negatively to inequity only do so in conditions in which the partner played a role in generating the inequity. For instance, species that respond negatively to inequity when partners are given different rewards for the same task do not do so when the rewards are simply handed out for "free" (reviewed in Brosnan and de Waal, 2014). Moreover, chimpanzees are not spiteful when they lose their food to a partner unless the partner actively steals it (Jensen et al., 2007a, b) and will not block their partner from receiving food (Jensen et al., 2006), although, interestingly, capuchin monkeys do show some evidence of spite (Leimgruber et al., 2016).

While the above findings support the link between cooperation and inequity at the phylogenetic level, there is also evidence that inequity directly impacts cooperative interactions within species. For instance, using the popular barpull task for cooperation (discussed in Section 2.1), researchers have found that subjects refuse to cooperate when the rewards are monopolizable (de Waal & Davis, 2003), and that whether subjects cooperate for unequal rewards (i.e., slices of apple vs. a more preferred grape) depends on their partner's behavior. If the partner dominates the better reward across most trials, cooperation ceases, whereas if subjects both benefit from the better reward on some trials, cooperation continues at high rates despite the short-term inequity (Brosnan et al., 2006). There is also an impact of social relationships, as chimpanzees prefer cooperative partners who tolerantly share food with them in other contexts (Melis et al., 2006).

Inequity aversion is a very likely candidate for being a behavior with a strong affective component. Responses to inequity are hypothesized to be driven by, at minimum, frustration, anger, and envy. In humans, negative emotions that have been consistently associated with inequity aversion are, among others, anger and guilt (Cubitt et al., 2011; Fehr and Gächter, 2002; Seip et al., 2014b), spite (Gummerum and Chu, 2014; McAuliffe et al., 2014), and jealousy (Matsuzawa and Tanimoto, 2018). Indeed, a very plausible hypothesis is that responses to inequity, in both humans and non-human animals, are emotionally mediated, rather than being underpinned by an explicit appraisal of their relative costs and benefits (even if such appraisal leads to an emotional response; Talbot et al., 2015), which, as in the case of reciprocity, may be so cognitively demanding as to be impossible for many species. Indeed, it may even be more parsimonious to assume a general state of frustration across experimental trials rather than a series of specific comparisons within trials. This suggests that we should explore the endocrine and sympathetic nervous system responses underlying individuals' decision to reject, which may indicate shifts in their arousal and valance following inequity. For example, one possible explanation for the individual variability mentioned above is that different subjects show different levels of arousal to being treated inequitably, which leads to different behavioral responses.

2.5. Prosocial motivations for cooperation

Given that cooperators are prone to exploitation by defectors, what motivates individuals to nonetheless start a cooperative interaction? Prosociality, here defined as behavior that is intended to benefit someone else (Jensen, 2016), has been suggested as important (motivational) driver for cooperative interactions (Silk, 2007; Jaeggi et al., 2010). Yet, few studies have tried to directly link these specific motivations to cooperative behavior. Indirect support for this hypothesis has been found in cross-species comparisons that link the varying natural cooperative tendencies of different species with the results of experimental prosociality tests of those same species (for reviews see Cronin, 2012; Marshall-Pescini et al., 2016). This work in turn motivated a central prediction of the cooperative breeding hypothesis (Burkart et al., 2014, 2009; Burkart et al., 2007), which argues that prosocial motivations enhance the ability to coordinate and cooperate, particularly in species that engage in cooperative breeding. Direct experimental evidence supports this hypothesis, demonstrating that intraspecific variation in prosociality among common marmosets predicts cooperative success (Martin et al. *in review*). This work suggests that prosociality may have been an important driver for the evolution of cooperation in these cooperative breeders or vice versa, although the benefits of prosociality need not be restricted to cooperative breeders.

A major drawback of interspecific comparisons of prosociality is the diversity of paradigms and procedures used (see Cronin, 2012). This is even more problematic if we wish to compare animals with humans, whose prosocial tendencies are often inferred from complex game-theoretical paradigms. There have been several attempts to make the human studies more comparable to those on animals, yet these simplified and more playful games are generally only tested on children (e.g. Burkart and Rueth, 2013; Horn et al., 2018; House et al., 2012). Such discrepancies in the developmental stages of the participants, and most importantly, the variety of paradigms used, make direct comparisons practically impossible (Leavens et al., 2017). In light of this limitation, Burkart and colleagues (Burkart et al., 2014) utilized the same experimental paradigm to study prosociality in 15 different primate species (including humans, albeit children only), finding that the amount of allomaternal care exhibited by a species predicts their prosocial tendencies. More recently, this paradigm has been converted to accommodate birds (Horn et al., 2016), and subsequently validated (Martin et al. *in review*) in one of the primate species from the original study by Burkart et al. (2014). This work has demonstrated a similar relationship between prosocial tendencies and social structure, at least in the cooperatively breeding azure-winged magpies, *Cyanopica cyanus* (Horn et al., 2016).

What constitutes or triggers these prosocial preferences remains, unfortunately, relatively unknown. Some authors, for example, have argued that chimpanzee prosocial preferences are in fact self-serving preferences that come about as a by-product of task design (Tennie et al., 2016), while others remain convinced that chimpanzees are truly willing to help others (Melis et al., 2018). One study has examined whether sympathy might motivate prosociality in great apes, as it does in humans (e.g. Vaish et al., 2009), but did not find evidence for the role of sympathetic concern in the prosocial behaviours of these apes (Liebal et al., 2014). Nevertheless, amidst other contextual features, the strength and nature of the relationship between donor and recipient does seem to have a strong influence on prosocial preferences in various species (reviewed in Cronin, 2012), suggesting a mediating role of emotions, as in emotionally mediated reciprocity. Social bonding is in part mediated by oxytocin (see also Section 3.5), so oxytocin levels may therefore be a valuable measure for further assessing the affective states involved in prosociality. In humans, the administration of oxytocin has been found to produce more generous donations to charity (Barraza et al., 2011), and also more coordinated cooperation, albeit at the expense of an out-group (Zhang et al., 2019). Studies using oxytocin in experimental prosociality paradigms in non-human animals are scarce and results are so far inconsistent. A recent study in Clark's nutcrackers, *Gymnorhinus cyanocephalus*, did corroborate a positive link between prosociality and the intranasal administration of mesotocin, the avian homologue of oxytocin (Duque et al., 2018), whereas a study on capuchin monkeys found that food-sharing was negatively impacted by the intranasal administration of oxytocin (possibly as a byproduct of oxytocin's anxiolytic effects; Brosnan et al., 2015a, b). Nevertheless, this line of research seems to be a promising avenue into the potential affective mediation of cooperative behaviours.

3. Affective correlates of cooperation

Since most studies only measure subjects' behavioral responses during cooperation games, inferences can only be made about behavioral decision-rules and little remains known about the underlying mechanisms. To tap into the proximate mechanisms underlying these decision rules, we need to understand the affective correlates of cooperation (which ultimately will help us to understand what emotions non-humans may or may not experience and how they might relate to our own). For this reason, several scientists have highlighted the need to include physiological parameters in studies on cooperation (e.g., Brosnan and Bshary, 2010; Bshary et al., 2011). However, in animal research the ability to include physiological measuring techniques is dependent on factors such as the species and the individual's level of training. Nonetheless, new techniques have made studies investigating such parameters more frequent. Here, we provide a broad overview of the most frequently applied non- or minimally invasive physiological measuring techniques in cooperation studies, first in humans and then, if applicable, in other animal species. Subsequently, we will also review assessments of affect possibly involved in cooperative interaction. Note that although research on brain activity can provide valuable insights into emotions and cooperation (e.g. Pan et al., 2016; Prochazkova et al., 2018), brain scanning technologies generally restrict social interactions between participants (Dulleck et al., 2014) and are difficult to apply in animals, particularly in the context of cooperation. Therefore, we do not discuss such techniques below.

3.1. *Physiological measures of affect*

3.1.1. *Cardiac function*

Researchers have been using different parameters of cardiac function to get information about the effect of specific (affective) stimuli on an organism's autonomic nervous system. Heart rate (HR), the number of heartbeats within a given period of time (usually per minute), is regulated by the sympathetic (fight and flight) as well as the parasympathetic system (rest and relax) and therefore represents a net effect of both systems' activity (Brownley et al., 2000). In order to disentangle the effects of the two systems, it is useful to determine heart rate variability (HRV), which refers to the fluctuation of the time interval between successive heartbeats (Berntson et al., 1997). Most of the HRV computations, such as the high frequency HRV or the root mean square of successive difference (RMSSD) represent parasympathetic activity. Specifically, if the high frequency band of a heartbeat is used for HRV calculations, then we are referring to the high frequency HRV, also called respiratory sinus arrhythmia (RSA) as it is associated with the breathing cycle, and since RSA is primarily controlled by vagal efferent pathways it can be used as an index of parasympathetic activity (Berntson et al., 1997). The low frequency HRV, in contrast, is thought to represent the sympathetic branch of the autonomic nervous system (Berntson et al., 1997).

Whereas heart rate (HR) measures thus provide information on the net effects of vagal (rest and relax) and sympathetic (fight and flight) activity, heart rate variability (HRV) reflects the balance between the two, making it a good indicator of psychosocial stress (von Borell et al., 2007). Cardiac activity and respiration rate can be measured with a single telemetry device, which has, for example, been used for measuring emotion responses in goats (*Capra hircus*) (Briefer et al., 2015). Such monitoring devices usually consist of a belt that is strapped around the thorax of the subject, which records the respective physiological signals, and a computer that receives these signals, making them both non-invasive and relatively easy to use for at least a subset of species (those without dexterous hands). Electrocardiograms (ECG) can also be recorded with electrodes attached to specific spots on the body, such as the inner forearm and inner leg. Using the latter method, Osumi and Ohira (2009) found that human participants' HR changes predicted their decision to accept or reject an offer in the ultimatum game, with initial HR decelerations preceding rejections. Note, however, that the act of measuring cardiac function in itself was found to promote giving in the trust game (Van Lange et al., 2011), suggesting that the method can influence the participant's behavior and the outcome of such a game, at least in humans.

Cardiac and respiratory parameters are often included in animal research because their respective measuring techniques can rather easily be adjusted to species-specific requirements (e.g. dogs, *Canis familiaris*, Kortekaas et al., 2013); sheep, *Ovis aries*, Reefmann et al., 2009). Early work using subcutaneously implanted telemetry devices in rhesus macaques, showed marked increases in HR when the macaques where in a risky situation, and notably, a decrease in HR when they received grooming, suggesting a tension reduction function of this cooperative behavior (Aureli et al., 1999). Most of the more recent studies using the less invasive belts have not investigated cooperation per se, yet many have focused on animal emotions. Sheep, for example, exhibit higher heart and respiration rates in response to a negative situation (presentation of unpalatable food) as compared to neutral or positive food-related situations (presentation of a desirable food; Reefmann et al., 2009). As the sheep's HRV (RMSSD) was not significantly affected, Reefmann et al. (2009) concluded that the sheep's reactions were mainly driven by the degree of sympathetic activity. Similar findings were reported for goats, who showed higher heart and respiration rates, yet also lower HRV (RMSSD) during situations that cause high arousal, irrespective of their valence (Briefer et al., 2015). However, using cardiac measures in rhesus macaques, Bliss-Moreau et al. (2013) did find differential responses of the sympathetic and parasympathetic system to the affective valence of social video stimuli. Due to the value of the information provided and the good acquisition possibilities in animals, we highly recommend greater use of cardiac measures for the study of cooperation in animals where it is feasible (review on the use of HRV in animals: von Borell et al., 2007).

3.1.2. *Skin conductance*

As the sympathetic tone briefly increases in response to most arousing stimuli, sweat glands are activated that produce more sweat, which reduces the electrical resistance of the skin and, hence, increases skin conductance (Boucsein, 2012). Electrodermal activity therefore reflects autonomic activity. In fact, it is often used to validate the success of a stimulus in eliciting the appropriate arousal response consistent with a specific affective valence or, in humans, emotion (e.g. fear, Phelps et al., 2001). Electrodermal activity can be measured by using a skin conductance amplifier, which amplifies the electric signal received from electrodes that are placed on specific spots of the subject's palm. /s00221-006-0346-5

van't Wout et al. (2006) were one of the first to include this parameter in the study of cooperation using an Ultimatum Game, demonstrating that participants' skin conductance activity was higher when they were confronted with an unfair offer. This suggests that unfair offers elicited stronger emotional arousal than fair offers (but see Osumi and Ohira, 2009). Elevated skin conductance levels have also been observed after opponent-directed negative emotions (e.g. anger) were induced in subjects who had to play a social decision-making game with the respective opponent (Eimontaite et al., 2013). Consequently, in the game itself, participants were more likely to defect against opponents they were angry at than against those whom they felt positive about (Eimontaite et al., 2013). Unfortunately, although skin conductance is a very informative parameter of affect in humans, it is quite difficult to measure in animals, which currently limits its applicability in the study of animal affect and cooperation.

3.1.3. *Facial skin temperature*

Another index of autonomic reactivity is the facial temperature, which shows specific patterns in response to different physical and psychological stimuli (see Panasiti et al., 2016). Facial skin temperature can be recorded with thermal infrared imaging. One major advantage of this method is that, in contrast to electrodermal and cardiovascular measurements, subjects are not influenced by the measuring technique as no device needs to be attached to them. There is an additional advantage for non-humans, for whom it may be dangerous, difficult or impossible to use a device that attaches to them in some way (cf. Ioannou et al., 2015). Changes of facial skin temperature are often measured in studies on deception, which generally counteracts any cooperation. Panasiti et al. (2016), for example, gave participants the choice of spontaneously deceiving someone in a setting where their reputation could potentially be harmed. Participants who deceived in the reputation-risk situation showed an increase in nose temperature (reflecting parasympathetic activation) during and after their decision to deceive (Panasiti et al., 2016). In another study, however, opposing results were found and nose and hand temperature decreased when participants called a significant person in their lives to tell an important lie (Moliné et al., 2017).

Facial temperature measurements can also be applied in a wide array of animal species, as the most frequently used target areas, the eyes and nose, are regions that are usually not covered by hair/feathers. The eye temperature and HR of dogs, for example, increases while individuals receive treats, a positively arousing situation (Travain et al., 2016). Proctor and Carder (2016) similarly investigated cows' (*Bos taurus*) responses using food rewards. Although the cows' nose temperature dropped when they experienced high arousal, they did not exhibit a change in temperature between positively and negatively valenced situations. Studies on rhesus macaques consistently show that a threatening stimulus induces a decrease in nasal temperature (Nakayama et al., 2005; Kuraoka, and Nakamura, 2011). Similarly, studies on chimpanzees show that playbacks of conspecifics fighting (Kano et al., 2016) or, more generally, aversive vocalisations of conspecifics (Dezecache et al., 2017) are associated with a decrease in nasal temperature. So far, facial skin temperature in animals has mostly been used as a tool to better understand whether individuals are experiencing heightened arousal, but there is also the potential for this technique to be very informative about more complex processes involved in cooperation. Given the small data set and relatively high inconsistency in responses, however, care will need to be taken until we have a better idea of what exactly these changes are measuring and are indicative of.

3.1.4. *Pupil mimicry*

Whereas facial skin temperature is regularly used in studies on deception, pupil mimicry is a physiological parameter that is of particular interest in the study of trust, a factor that promotes cooperation. Changes in pupil size are, like the parameters presented above, mediated by the autonomic nervous system, and can be measured with an eye-tracker. Recent findings suggest that the synchronized dilation of two persons' pupils recruits specific areas in the theory of mind network, resulting in individuals feeling 'mentally connected' and subsequently enhancing trust (Prochazkova et al., 2018). Kret and De Dreu (2017) showed that in a trust game, men trusted partners with dilating pupils even more after oxytocin treatment as compared to after placebo administration. In female participants, in contrast, oxytocin blunted the effect of pupil dilation on trust (Kret and De Dreu, 2017). Since collecting pupillometry data requires the subjects to keep their head still, there are only a few studies on this parameter in animals. Kret et al. (2014), for example, managed to investigate pupil mimicry in chimpanzees (*Pan troglodytes*) by using a binocular eye tracker, which allowed for relatively large head movements of the animals. They reported that chimpanzees exhibit stronger pupil mimicry with (unfamiliar) conspecifics than with humans, and found that chimpanzee mothers and their offspring exhibited the strongest effect (Kret et al., 2014). Several researchers have begun using creative ways to keep subjects' heads still, such as presenting the stimuli behind a wall that only allows animals to peek through a small slit (Ryan et al., 2019). Creative solutions like these will be key to the measurement of pupil mimicry in a much wider array of species, making it a promising factor for better understanding animal cooperation.

3.1.5. *Hormones*

Hormones are involved in many cooperative processes (reviewed by Soares et al., 2010; Trumble et al., 2015) and have a clear link to affect (Bos et al., 2012). They can be measured endogenously or actively manipulated by, for example, administering hormones or blocking receptors (e.g., Bird et al., 2018; Bos et al., 2010; Brosnan et al., 2015a, b; Rilling et al., 2012; Soares et al., 2014). Although this is a promising and popular technique, it is not without challenges. Not only circulating hormone levels, but also neural responses to them, can be influenced by several different factors (illustrated by Trumble et al., 2015), and most fluctuate substantially. Levels also differ depending on how they are measured. Endogenous hormones and/or their metabolites can be extracted from different organic materials, such as blood, saliva, urine, feces and hair/feathers. Which of these should be used depends on the hormone and the time frame to be investigated. All of these materials reflect hormone levels on different time scales, from minutes (e.g. in saliva) to months (in hair/feathers), hence not all of them are suitable for the investigation of emotions, which are considered to have a short time frame (for non-invasive monitoring of endocrine markers in primates see Behringer and Deschner, 2017). The hormones oxytocin and testosterone, as well as glucocorticoids such as cortisol, have been the most studied in relation to cooperation.

Oxytocin plays an important role in social bonding, trust and generosity. In preschoolers, for example, salivary oxytocin measured directly before a dictator game was associated with how much chocolate the children allocated to others (Fujii et al., 2016). In boys, oxytocin levels were negatively correlated with allocations; in girls, levels before and after the game were positively correlated when playing with a class mate (ingroup member), but no effect was found when playing with an outgroup member (Fujii et al., 2016). This emphasizes an important emerging point—the effects of oxytocin are highly dependent on sex (see Feng et al., 2015) and on context (Shamay-Tsoory et al., 2009; Ne'eman et al., 2016), and there may be opposite effects for ingroup and outgroup members (De Dreu et al., 2012; De Dreu and Kret, 2016; Zhang et al., 2019; for a review see Shamay-Tsoory, and Abu-Akel, 2016). Results are perhaps even more variable in non-human species, although this may be in part due to a combination of less research effort and less ability to control the parameters of the study. In general, endogenous oxytocin has been positively associated with food sharing, intergroup conflict, and cooperative hunting in chimpanzees (Samuni et al., 2019, 2018a; Samuni et al., 2017; 2018b; Wittig et al., 2014), grooming in capuchins (Benítez et al., 2018), and, more generally, to influence social cognition, behavioral synchrony, and prosociality across a variety of non-human primates (Chang and Platt, 2014; Finkenwirth et al., 2015; Jiang and Platt, 2018; Wittig et al., 2014; but see Staes et al., 2015). Recent work has also identified the importance of endogenous oxytocin in social bonding and cooperation among female bonobos (Moscovice et al., 2019). However, the effects of *exogenously* administered OT have been far less consistent (Brosnan et al., 2015a, b; Duque et al., 2018; 2019; Mustoe et al., 2016; Proctor et al., 2016). Note however, that as oxytocin is primarily involved in social bonding, the mediating effects of this hormone on cooperation may, as with humans, be highly dependent on the dyad tested, and this should be accounted for in future tests. Clearly more work is needed to determine the complex influences of oxytocin on behavior.

Popular belief dictates that steroid hormones should inhibit cooperation, yet recent research shows that the picture is far more intricate. Specifically, the hormones testosterone and cortisol seem highly dependent on each other with regard to behavior related to social status (cf. dual-hormone hypothesis: Mehta and Josephs, 2010; Mehta and Prasad, 2015), and as such may influence decision-making in economic games (Mehta and Prasad, 2015). Social status or rank, in turn, seem to have effects on cooperation (e.g. Horn et al., 2018; Massen et al., 2015; Suchak et al., 2014), thus making the interplay of these two hormones particularly interesting for the study of affect and cooperation. Unfortunately, little work has been done on cooperation while considering both hormones in parallel; generally, studies consider only one of these hormones.

Testosterone is often associated with aggressiveness and competition (Eisenegger et al., 2010), but recent results show that testosterone also mediates parochial altruism (Reimers and Diekhof, 2015) and prosociality (Dreher et al., 2016; Eisenegger et al., 2010). For example, male soccer fans who participated in a Prisoner's Dilemma Game exhibited increased salivary testosterone while cooperating with other fans of their team (Reimers and Diekhof, 2015). Cortisol, on the other hand, is often associated with stress. Social interactions can be very stressful, and indeed tend to lead to an increase in glucocorticoid hormones, such as cortisol and corticosterone. Jäschke et al. (2016), for instance, reported that playing a cooperative game generally seems to increase the participants' salivary cortisol levels, while playing with a cooperative partner of higher social status leads to a faster recovery of cortisol levels. Similarly, salivary cortisol in long-tailed macaques (*Macaca fascicularis*) has been found to decrease when participating in a cooperation task with closely bonded individuals, irrespective of the dyad's cooperative performance (Stocker, Loretto, Sterck, Bugnyar, & Massen, *in review*). Moreover, glucocorticoid excretion patterns have also been connected to personality traits, such as boldness, which in turn affect cooperative behavior (e.g. in rooks, *Corvus frugilegus,* Scheid and Noë, 2010). For non-invasive glucocorticoid measurements see Palme (2019). Despite the promise of endocrine measures as important indicators of affect, care is warranted, as these hormones interact intensively with each other; i.e. not only amongst other steroid hormones (Mehta and Josephs, 2010), but also with oxytocin (Ziegler and Crockford, 2017). Therefore, systematic studies that investigate cooperation and measure, at minimum, these three hormones in parallel, are needed.

3.2. Behavioral measures of affect

3.2.1. Cognitive Bias paradigms

One often used behavioral measure of affect is a cognitive bias paradigm. Cognitive bias paradigms (Harding et al., 2004; Mendl et al., 2009; Paul et al., 2019) present an exciting and relatively untapped resource for measuring consistent individual differences in affect. Originally, these paradigms were mostly used to study the effect of husbandry procedures on animals' affective states (Bateson, and Matheson, 2007; Bateson et al., 2011; Bethell et al., 2012). Using this approach, however, Bateson and Nettle (2015) also provided tentative evidence for consistent moods in chimpanzees. Notably, Schino et al. (2016) showed that in tufted capuchin monkeys, *Sapajus [Cebus]* sp., the amount of grooming received was positively correlated to 'optimistic' responses in this paradigm, albeit based only on overall grooming received and not on grooming received immediately before the cognitive bias test (Schino et al., 2016). This work, along with other studies using bias paradigms to investigate the effects of (chronic) stress in, for example, capuchin monkeys (Boggiani et al., 2018), rats (Chaby et al., 2013) and starlings (Gott et al., 2019), suggests the feasibility of these methods for incorporating rigorous measures of affective dispositions into experimental studies of animal cooperation. Importantly, inter-individual differences in cognitive bias need to be taken into account, in both these experimental and observational studies of cooperation. Therefore, some knowledge about individuals 'base-line' cognitive bias is required as a reference point for the cognitive bias of the same individual after the cooperation manipulation, be it experimental (cf. Adriaense et al., 2019) or observed cooperative behaviors (cf. PC/MC method by de Waal, and Yoshihara, 1983).

3.2.2. Vocalizations

Communication can be an important aid in coordination while cooperating. Not surprisingly, humans cooperate more when they are able to converse with each other (Wichman, 1970; Cooper et al., 1992), and some argue that communication as a coordination tool has been the key selection pressure for the evolution of human language (David-Barrett and Dunbar, 2016). Cross-species comparisons have revealed that among non-human animals, cooperative breeding influences communicative complexity, namely the number and type of vocalizations in birds (Leighton, 2018) and mammals (Manser et al., 2014), which supports the idea that communicative complexity is predicted by social complexity and cooperation. Within a species and within an actual cooperative context, there is some evidence that animals use vocalizations to coordinate cooperation (e.g. lunge feeding in humpback whales, *Megaptera novaeangliae*: D'Vincent et al., 1985), recruit conspecifics to a food-source, either in the prosocial context of sharing food with fledged offspring (e.g. pied babblers, *Turdoides bicolor*: Radford, and Ridley, 2006), or friends in the group (e.g. chimpanzees: Schel et al., 2013), or recruit befriended conspecifics whose help is needed to acquire a food source (e.g. common ravens: Sierro et al., 2019). Animals may also communicate information about their inner state; for example, pied babblers negotiate how much time they will spend performing sentinel behavior based on their hunger state (Bell et al., 2010), rats communicate their need to those who can provide (Schweinfurth, and Taborsky, 2018c), and many animal species react to increased begging from offspring with increased help (Bee, and Miller, 2016). Although vocalizations can inform the receiver about the inner state of the sender, it remains unclear whether and how that may be emotionally mediated.

A recent study showed that humans are able to detect arousal in the calls of animals from all classes of terrestrial vertebrates, suggesting that vertebrates, at least for contexts with high arousal, share fundamental mechanisms of vocal expression (Filippi et al., 2017). Highly arousing states like being trapped do indeed elicit distress or alarm calls in animals which may lead to conspecifics helping their distressed group member (chimpanzees: Boesch, and Boesch, 1989; Amati et al., 2008; rats: Bartal et al., 2011), although these instances are often too rare to study systematically and unethical to invoke experimentally. What is needed is an extensive library of vocalizations characterized by both their valence and arousal, as well as the context, if known, to consider possible affectively mediated modulations that can be actively linked to cooperation and subsequently coded during cooperation experiments, or even manipulated in such an experiment. An experiment on humans found that priming participants with vocal expressions of joy increased their cooperative tendencies in an assurance game, whereas vocal expressions of anger decreased cooperative tendencies in comparison to a neutral vocal stimulus (Caballero Meneses, and Menez Díaz, 2017). To our knowledge, the only study that used a similar framework in a non-human animal is a study on rats by Łopuch and Popik (2011), which not only showed that allowing communication between rats benefits cooperation, but also that the number of 50 kHz calls, a call-type that was previously validated as an indicator for positive emotions (Burgdorf et al., 2008), positively influenced cooperative behavior (Łopuch, and Popik, 2011). Although studies on the role of vocalizations in cooperative interactions among animals are still rare, given the right framework this field may be very informative about the mediating role of affect on cooperation.

3.2.3. Facial displays and body language

Communication does not necessarily involve vocalizations. Many species, including most non-human primates, in fact seem restricted in their use of vocal signals (but see Fitch et al., 2016). On the other hand, there are often consistent changes in facial displays, often interpreted as facial expressions, which seem very potent as emotional indicators, especially with regard to affect, something Darwin already noticed while describing homologies in the facial expressions of humans and other animals (Darwin, 1872; see also Kret et al., 2019). Primates, for example, show clear, often ritualized, facial displays that have been linked to both negative and positive emotional states (e.g. van Hooff, 1971, 1976). These are often used in social contexts to display benign intent, or to appease prior conflicts (e.g. de Waal, 1988), and could thus potentially also be involved in initiating cooperative actions. The play-face, for example, is a clear example of an affective facial expression that also helps facilitating play between interaction partners (e.g. Waller, and Cherry, 2012). In humans, there are several studies showing that a smile can initiate cooperation and/or increase cooperative investments (e.g. Stouten, and de Cremer, 2010; Scharlemann et al., 2001), yet so far similar studies in non-human animals are missing. The development of the Facial Action Coding Systems (FACS) for multiple animal species (see Waller et al., 2019) allows for more rigorous testing of affective correlates in animal facial expressions, and would subsequently allow experimental testing of the effect of affective facial expressions on cooperation.

As with facial displays, many animal species also show clear, often ritualized, bodily displays to communicate with each other (e.g. van Hooff, and Wensing, 1987). Dominance and subordinance displays are probably the best-known examples. Unfortunately, however, little work has been done on whether and how this ‘body-language’ relates to potential underlying affective responses. One exception are studies on displacement activities, which have now been consistently shown to indicate stress (e.g. Maestripieri et al., 1992; Troisi, 2002) and as such are suggested to have a communicative function as well. Indeed, Barbary macaques do attend to scratching in others, yet this seems rather to avoid re-directed aggression from these others than to facilitate cooperative efforts (Whitehouse et al., 2016). Nevertheless, informed decisions about, for example, with whom not to cooperate, can be as valuable as knowing with whom to cooperate. Therefore, assessing the body-language of test-subject during cooperation experiments/observations, as well as more generally, might be a valuable tool to investigate possible affective correlates.

4. Interpretation of results

4.1. How comparable are the paradigms?

There may be more paradigms to test for cooperation than there are species tested within those paradigms. More critically, perhaps, it is extremely difficult to compare human studies with those involving other species due to differences in procedure. Human paradigms largely consist of social dilemmas that often rely on elaborate explanations to the participants, whereas animals must learn the structure of the game through repeated exposure. Moreover, the often complex game structures used to study human economic decision-making may be too challenging for non-human animals. Aside from the fact that null results are not proof of absence, in some cases null results are a consequence of the experimental set-up used. To address this challenge, researchers often test a specific species in multiple different paradigms. As a consequence, particularly within the animal literature, the number of different paradigms employed has increased drastically. Even when the same paradigm is used (e.g. loose-string paradigm, see Section 2.1 & Table 1), the procedures used to test the specific paradigm may differ across labs, so that results may differ even within a species. Consequently, particular caution is needed in the interpretation of comparisons based on a different procedure, albeit using the same experimental set-up (cf. Massen et al., 2019).

Recently, there have been several attempts to study animal decision-making using the same set-ups *and* procedures in multiple species (e.g. MacLean et al., 2014; see also Bohn et al., 2019), including studies on socio-cognitive traits like prosociality (Burkart et al., 2014). Moreover, the paradigms and procedures originally used to investigate prosociality in primates have now been successfully translated to birds (Horn et al., 2016). These phylogenetically broad comparisons are key if we are to understand the core mechanisms driving decision-making across species, but they still rely on strong assumptions: firstly, that the perception of and response to these paradigms are the same for all species; and secondly, that behavioral and physiological (including endocrine and neural) responses to these paradigms are homologous or sufficiently analogous. If either of these assumptions is not true, then the comparison becomes much less straightforward.

Indeed, we know that in many cases these assumptions are false. For example, work on the assurance game finds that many primate species can find the payoff dominant coordinated outcome (coordinated Stag play; Brosnan et al., 2011; Brosnan et al., 2012a, b). However, we also know that these primates are using different mechanisms to reach these outcomes (Parrish et al., 2014; reviewed in Smith et al., 2018). Capuchin monkeys, a New World monkey species, appear to be matching their partner’s play, albeit with a (strong) bias towards the payoff dominant outcome. However, they cannot maintain it when they cannot see their partners’ choices. Of course, capuchins also live in relatively small, cohesive groups, so there may have been little selection pressure to coordinate when they cannot see their partners. Humans probability match, but, interestingly, rhesus monkeys, who probability match in other contexts, do not do so in this task; instead they simply show a preference for the outcome that generally pays the best. Chimpanzees sometimes show evidence of understanding that there is a strategy to the game, extrapolating their choices from one situation to a new one. That being said, this is highly context dependent, as indicated by the fact that some chimpanzees play randomly despite hundreds of trials of exposure (Hall et al., 2019). This may be due to their level of experience and/or disinterest in the game, but in either case shows very clearly that even *within* the same species, using the same procedure (within practical constraints), there is substantial variability.

As this detailed summary shows, null results must be taken within the context of the study, and just because an animal is known to show some mechanism in one context does not mean that they will show it in another, even in a context in which other species are known to use that mechanism. What, then, do we do as researchers? First, we recognize that any research program will involve numerous studies, first documenting outcomes and then trying to tease apart underlying mechanisms. Second, we must keep in mind the distinction between function and mechanism, and be careful not to conflate the two, or assume one from the other (Tinbergen, 1963). Third, it is clear that a comparative program must start by testing multiple species using the same paradigm, or as close as we can get to the same paradigm, but we must also give every species multiple opportunities using different approaches. For instance, subjects who do poorly on a manual version of a task may do quite well on a computerized version (Brosnan et al., 2012a). Fourth, once we have some idea of how the species are similar and different, we must “back test” those species on more species-specific paradigms to see if the predictions from our tightly controlled comparisons yielded correct hypotheses. If not, then we tweak the paradigms and iterate towards a better understanding of how species’ unique abilities and evolutionary history have influenced a behavior (Smith et al., 2018).

In the case of comparative affective science, this presumably means starting by testing animals on situations in which we know affect influences decision-making in humans. Of course, it may not – and often will not – be the case that the same situations lead to the same responses, but it is a reasonable starting point (Williams, Brosnan & Clay, 2019). Next, we need to compare across a variety of species in order to determine which outcomes are species-specific and which are more general (Shettleworth, 2012; Andics and Miklósi, 2018; Kret and Tomonaga, 2016; MacLean et al., 2012). Finally, we should try, when possible, to simultaneously measure several physiological parameters to get a more nuanced view of animals’ responses (Dunn et al., 2012; Osumi and Ohira, 2009; Reefmann et al., 2009; Travain et al., 2016).

We also emphasize the importance of actually measuring affect, rather than simply assuming it after priming, or from subjects’ behavior. As these above examples illustrate, it is very common for different species to reach the same outcomes through entirely different mechanisms (and the same may be true for different animals within a species). Likewise, they may show different behavioral manifestations of the same affective response, or the same behavioral manifestation for different affective responses. It is critically important to provide further objective evidence of assumed similarities (or differences), in the form of a physiological parameter, endocrine measure, cognitive bias or, ideally, multiple responses taken together.

One final note is in order about the challenge of understanding animal decision-making from captive studies. While captive settings allow for tight experimental control, they are also an artificial environment for the development and expression of normal adaptive decision-making processes (Boesch, 2007), particularly in the context of cross-species comparisons (Leavens et al., 2017). For instance, as previously mentioned, while prosocial behavior has been surprisingly difficult to demonstrate in captive studies of primates, field workers have consistently documented behaviors such as food sharing and group hunting in wild populations (Samuni et al., 2018a). Even the presence of a physical barrier, comparable to barriers common in research with captive apes, impedes dogs' success in an imperative pointing task (Kirchhofer et al., 2012), suggesting that work in apes may be underestimating their abilities. This difference between captive and wild studies could be particularly important in understanding affect. For instance, research has demonstrated increased pessimism biases in animals raised in impoverished captive environments (e.g., Harding et al., 2004).

Captive research clearly is important in determining underlying mechanisms, and there are a few steps researchers can take to ensure that results are as generalizable as possible. Animals should be socially housed, for example, and when feasible, testing can be done within social groups (e.g., Martin et al., in review; Massen et al., 2015). Unfortunately, although relatively non-invasive, many physiological measures require specific set-ups that often inhibit testing in ecologically relevant complex social configurations. Thus, if early experiments require more tightly controlled social situations, subsequent studies can be done in group situations, allowing for both the interpretation of messy results in the context of the more controlled studies, as well as the ability to document behaviors that may correlate with emotional responses that are impossible to measure in group situations. Similarly, tests with human experimenters as social partners should be avoided as much as possible as this is an artificial social situation without any ecological relevance and prohibits the measurement of the potentially intricate socio-emotional interplay between two cooperating conspecifics. Finally, ideally field experiments can also be used to validate laboratory results, as well as to better probe the developmental plasticity of the proximate mechanisms hypothesized to influence task performance (Morand-Ferron et al., 2016).

4.2. Impact of social and individual factors on decision-making

Another likely source of individual differences that is often ignored in experimental studies is social relationships. Humans can flexibly adjust among different proximate mechanisms to meet the requirements of specific cooperative contexts (Melis and Semmann, 2010; West et al., 2011a, b). In particular, as previously noted, human brain imaging studies support the notion that complex cognitive mechanisms and more 'basal' hormonal mechanisms may exist in parallel, and show that their employment depends on familiarity (Krueger et al., 2007), such that more emotional areas are activated when cooperating with familiar individuals (i.e., emotionally based bookkeeping, Schino and Aureli, 2009; attitudinal reciprocity, Brosnan and de Waal, 2002), whereas more cortical areas involved in mentalizing are activated while cooperating with unfamiliar individuals (i.e., calculated reciprocity, de Waal and Luttrell, 1988). This is a key dichotomy that must be resolved, but studies examining this dualism in decision rules in non-human animals have so far been lacking, and consequently any conclusions about the uniqueness of this phenomenon for humans are premature.

These results also indicate that caution should be used in interpreting existing results. Human cooperation research using experimental games rarely takes such proximate mechanisms into account, and many behavioral economic studies rely on games played by anonymous dyads/duos (e.g. in Prisoner's dilemmas) and/or groups of individuals that did not know each other prior to the game (e.g. in Public goods games). Similarly, cooperation research in animals generally tests experimentally determined dyads (Table 1), inhibiting subjects' capacity for partner choice. However, individuals of social species are typically surrounded by multiple individuals, and these multiple partners are generally *known* individuals that interact within their group. This suggests that we may be getting very different (affective) responses in the experiments than in wild observations, or their natural interactions, because we fail to take into account the impact of social context on their decision-making.

Moreover, while these experiments often focus on just two individuals, cooperation in the daily lives of most animals is a dynamic process within a multi-player field in which relationships differ substantially. Indeed, in such 'biological markets' (Hammerstein and Noë, 2016), individuals often have their choice of cooperative partner (Bull and Rice, 1991; Noë and Voelkl, 2013), and pay-off structures may differ dramatically among different partners (Taborsky et al., 2016a). For example, long-term positive relations or 'friendships' can create mutual trust that increases the benefits of cooperation and the costs of partner-switching. Empirical evidence in chimpanzees indeed shows that friendship increases trust (Engelmann and Herrmann, 2016; but see Kaburu and Newton-Fisher, 2016), and studies allowing for partner choice find that animals prefer to cooperate with their friends (e.g. Asakawa-Haas et al., 2016; Massen et al., 2015; Molesti and Majolo, 2016). Additionally, interdependence of pair-bonds through investment in mutual offspring may also inhibit partner-switching for the parents during critical periods of offspring development (Johnstone and Rodrigues, 2016), as do other forms of interdependence, such as inter-household food sharing and commodity exchange in nonindustrial human societies (Ember et al., 2018; Jaeggi et al., 2016). Much more attention needs to be paid to relationships and how they interact with the affective components of cooperation.

Personality, or consistent individual differences in behavioral responses (Gosling, 2001; Réale et al., 2007), also influences decision-making. Over a century of research has demonstrated the importance of human personality for determining physical and psychological health (Ozer and Benet-Martínez, 2006), social relationships (Asendorpf and Wilpers, 1998; Robins et al., 2002), and reproductive success (Alvergne et al., 2010; Berg et al., 2014; Gurven et al., 2014), and recent work indicates that personality is influencing animals in similar ways. For instance, personality influences cooperation and responsiveness to punishment in public goods games (Schroeder et al., 2015), sensitivity to inequity (Brosnan et al., 2015a, b), and patterns of social learning in experimental tasks (Barrett et al., 2017), which can lead to population-level inferences deviating appreciably from the behavior observed for most individuals (Barrett et al., 2017). There is less known about how personality is influenced by or influences affect, but this literature could help us understand the affective components of animal cooperation. Monoamine systems, for instance, are highly conserved across animals (Edsinger and Dölen, 2018; Gruber, 2014) and have been linked to dispositional affect (Aluja et al., 2018; Chester et al., 2015; DeYoung, 2013), and variation in the functionality of these systems influences personality in rhesus macaques (McCormack et al., 2009), great tits (Fidler et al., 2007), and crickets (Abbey-Lee et al., 2018), among other taxa. Similarly, regulatory patterns of the HPA axis influence personality in numerous species (Carere et al., 2010). Given the deep homology of these systems, which play a crucial role in the adaptive regulation of social behavior, it is plausible that similar affective phenomena accompany their activity in non-human animals.

5. Future directions and conclusions

It is an exciting time in the study of affective science, as we are at a threshold where we can begin to get objective, consistent measures of affect that are comparable across multiple species. Technology has advanced to the degree that we can measure sympathetic and endocrine responses in a non-invasive way, often even in group situations. Given that cooperation research necessarily involves a group (of at least two!), these advances are essential to develop a comparative affective science of cooperation.

We have a few recommendations to allow us to fully benefit from our ability to measure affect. First, and most obviously, we need to be cautious in how we interpret what we measure. In most cases, we are not measuring affect *per se*. We are measuring physiological responses that we *interpret* as determining or being determined by affect. As we cannot ask our subjects how they feel, this is what we have. To its benefit, this objective measurement approach is arguably less biased than self-report and is directly comparable across species. Nonetheless, this caveat must be kept in mind when interpreting our results. We encourage researchers to not depend on just one measure, but to triangulate affect by looking at physiology, behavior and cognition (e.g. cognitive bias tests) in parallel whenever possible (cf. Izard, 1977; Mendl et al., 2010; Paul et al., 2005; 2019). Similarly, we encourage the incorporation of *multiple* physiological measures whenever possible, to see if they are consistent. Second, it is important to compare results across species, and when contradictions emerge, consider carefully what might have caused them. Our ability to interpret physiological responses is only increasing, but failing to recognize the intricacies of how these responses interact with each other and how they compare across species will slow the advancement of our knowledge.

Second, keeping animals in atypical social configurations or stressful circumstances will influence their affective state and alter results. Of course, captive work is important to perform the carefully controlled behavioral studies that are needed to determine the role of affect in decision-making. Nonetheless, it is important to keep animals in social groups that are as close to species-typical as is possible, and moreover, to run studies that include more than two individuals. While we have gained immense knowledge from even dyadic studies of cooperation, extending these results to larger groups provides a better understanding of how social dynamics influence cooperation (Fruteau et al., 2013; Massen et al., 2015; Suchak et al., 2016).

Relatedly, we want to stress the importance of animal training. By designing and following training protocols using positive reinforcement training (e.g. Kemp et al., 2017), one can facilitate the use of measuring devices, reduce unwanted effects of testing procedures, which potentially influence the outcome of the study (e.g. Lambeth et al., 2006), and improve animal welfare (Prescott and Buchanan-Smith, 2003). Clearly, ecologically valid and psychologically informed experiments will be more instructive as to the proximate mechanisms and evolution of cooperation (McAuliffe & Thornton, 2015).

Scientists have been discussing the possibility of emotions in animals since at least Darwin (1872), if not before. Scholars have, however, often rejected the idea, as they argued that it was solely based on anthropomorphism (but see de Waal, 1999; Williams, Brosnan & Clay, 2019), and that non-human species lack the phenomenological experience so typical of human emotions. Contemporary science, however, does not view emotions as solely based on subjective feelings, but considers it as a multifaceted construct that includes some combination of affect, behavior, physiology and cognitive elements (Mendl et al., 2010; Paul et al., 2005; 2019; Bliss-Moreau, 2017). With recent developments, we now finally also have the tools to be able to measure what is going on physiologically in ways that previous scientists could not, and sophisticated behavioral experiments are disclosing the underlying cognition. This provides us with the ability to more objectively validate conjectures about affect in general, but particularly in animals, and to explore influences that we may not have even considered, given that other species' affect may be considerably different from our own (Bliss-Moreau, 2017). Aside from providing a better understanding of the evolution of affect, and, thereby, emotion, these new tools may also allow us to recognize new and exciting ways in which other species interact with the world. Much theoretical work has assumed a mediating role for affect in cooperation, yet this has so far mainly been based on assumptions. With the recent methodological developments reviewed above now in place, and the framework we aimed to provide here, we are at the dawn of gaining a much more comprehensive insight into the proximate, affective mechanisms underlying cooperation, as well as the evolutionary history of these mechanisms across the animal kingdom.

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References

Abbey-Lee, R.N., Uhrig, E.J., Garnham, L., Lundgren, K., Child, S., Løvlie, H., 2018. Experimental manipulation of monoamine levels alters personality in crickets. Sci. Rep. 8 (1), 16211. https://doi.org/10.1038/s41598-018-34519-z.

Adams, J.S., 1963. Toward an understanding of inequity. J. Abnorm. Psychol. 67, 422–436.

Adriaense, J.E.C., Martin, J.S., Schiestl, M., Lamm, C., Bugnyar, T., 2019. Negative emotional contagion and cognitive bias in common ravens (*Corvus corax*). Proc. Natl. Acad. Sci. U. S. A. 116, 11547–11552.

Aluja, A., Balada, F., Blanco, E., Fibla, J., Blanch, A., 2018. Twenty candidate genes predicting neuroticism and sensation seeking personality traits: a multivariate analysis association approach. Pers. Individ. Dif. https://doi.org/10.1016/j.paid.2018.03.041.

Alvergne, A., Jokela, M., Lummaa, V., 2010. Personality and reproductive success in a high-fertility human population. Proc. Natl. Acad. Sci. 107 (26), 11745–11750. https://doi.org/10.1073/pnas.1001752107.

Amati, S., Babweteera, F., Wittig, R.M., 2008. Snare removal by a chimpanzee of the Songo community, Budongo Forest (Ugande). Pan Afr. News 15, 6–8.

Amici, F., Aureli, F., Mundry, R., Amaro, A.S., Barroso, A.M., Ferretti, J., Call, J., 2014. Calculated reciprocity? A comparative test with six primate species. Primates 55 (3), 447–457. https://doi.org/10.1007/s10329-014-0424-4.

Andics, A., Miklósi, Á., 2018. Neural processes of vocal social perception: dog-human comparative fMRI studies. Neurosci. Biobehav. Rev. 85, 54–64. https://doi.org/10.1016/J.NEUBIOREV.2017.11.017.

Asakawa-Haas, K., Schiestl, M., Bugnyar, T., Massen, J.J.M., 2016. Partner choice in raven (Corvus corax) cooperation. PLoS One 11 (6), e0156962. https://doi.org/10.1371/journal.pone.0156962.

Asendorpf, J.B., Wilpers, S., 1998. Personality effects on social relationships. J. Pers. Soc. Psychol. 74 (6), 1531–1544. https://doi.org/10.1037/0022-3514.74.6.1531.

Aureli, F., Schaffner, C.M., 2002. Relationship assessment through emotional mediation. Behaviour 139 (2/3), 393–420.

Aureli, F., Preston, S.D., de Waal, F.B.M., 1999. Heart rate responses to social interactions in free-moving rhesus macaques *(macaca mulatto):* a pilot study. J. Comp. Psychol. 113, 59–65.

Axelrod, R., 1984. The Evolution of Cooperation. Basic Books, New York, NY.

Barraza, J.A., McCullough, M.E., Ahmadi, S., Zak, P.J., 2011. Oxytocin infusion increases charitable donations regardless of monetary resources. Horm. Behav. 60 (2), 148–151. https://doi.org/10.1016/j.yhbeh.2011.04.008.

Barrett, B.J., 2017. Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. Proceedings of the Royal Society B: Biological Sciences 284, 20170358.

Bartal, I.B., Decety, J., Mason, P., 2011. Empathy and pro-social behavior in rats. Science 334, 1427–1430.

Bateson, M., Nettle, D., 2015. Development of a cognitive bias methodology for measuring low mood in chimpanzees. PeerJ 3, e998.

Bateson, M., Matheson, S.M., 2007. Performance on a categorisation task suggests that removal of environmental enrichment induces 'pessimism' in captive European starlings (*Sturnus vulgaris*). Anim. Welf. 16, 33–36.

Bateson, M., Desire, S., Gartside, S.E., Wright, G.A., 2011. Agitated honeybees exhibit pessimistic cognitive biases. Curr. Biol. 21, 1070–1073.

Bee, M.A., Miller, C.T. (Eds.), 2016. Psychological Mechanisms in Animal Communication Vol. 5 Springer International Publishing., Cham, Switzerland.

Behringer, V., Deschner, T., 2017. Non-invasive monitoring of physiological markers in primates. Horm. Behav. https://doi.org/10.1016/j.yhbeh.2017.02.001.

Bell, M.B.V., Radford, A.N., Smith, R.A., Thompson, A.M., Ridley, A.R., 2010. Bargaining babblers: vocal negotiations of cooperative behaviour in a social bird. Proc. R. Soc. B 277, 3223–3228.

Benítez, M.E., Sosnowski, M.J., Tomeo, O.B., Brosnan, S.F., 2018. Urinary oxytocin in capuchin monkeys: validation and the influence of social behavior. Am. J. Primatol. 80 (10), e22877. https://doi.org/10.1002/ajp.22877.

Berg, V., Lummaa, V., Lahdenperä, M., Rotkirch, A., Jokela, M., 2014. Personality and long-term reproductive success measured by the number of grandchildren. Evol. Hum. Behav. 35 (6), 533–539. https://doi.org/10.1016/j.evolhumbehav.2014.07.006.

Berntson, G.G., Bigger, J.T., Eckberg, D.L., Grossman, P., Kaufmann, P.G., Malik, M., Nagaraja, H.N., Porges, S.W., Saul, J.P., Stone, P.H., van der Molen, M.W., 1997. Heart rate variability: origins, methods, and interpretive caveats. Psychophysiology 34, 623–648.

Bethell, E.J., Holmes, A., MacLarnon, A., Semple, S., 2012. Cognitive bias in a non-human primate: husbandry procedures influence cognitive indicators of psychological well-being in captive rhesus macaques. Anim. Welfare UFAW J. 21 (2), 185.

Bird, B.M., Geniole, S.N., Procyshyn, T.L., Ortiz, T.L., Carré, J.M., Watson, N.V., 2018. Effect of exogenous testosterone on cooperation depends on personality and time pressure. Neuropsychopharmacology 1. https://doi.org/10.1038/s41386-018-0220-8.

Blake, P.R., McAuliffe, K., Corbit, J., Callaghan, T.C., Barry, O., Bowie, A., et al., 2015. The ontogeny of fairness in seven societies. Nature 528 (7581), 258–261. https://doi.org/10.1038/nature15703.

Bliss-Moreau, E., 2017. Constructing nonhuman animal emotion. Curr. Opin. Psychol. 27, 184–188.

Bliss-Moreau, E., Machado, C.J., Amaral, D., 2013. Macaque cardiac physiology is sensitive to the valence of passively viewed sensory stimuli. PLoS One 8, e71170.

Boesch, C., 2007. What makes us human (Homo sapiens)? The challenge of cognitive cross-species comparison. J. Comp. Psychol. 121 (3), 227–240. https://doi.org/10.1037/0735-7036.121.3.227.

Boesch, C., Boesch, H., 1989. Hunting behavior of wild chimpanzees in the Taï national park. Am. J. Phys. Anthropol. 78, 547–573.

Boggiani, L., Addessi, E., Schino, G., 2018. Receiving aggression triggers attention bias in tufted capuchin monkeys. Anim. Behav. 146, 173–180.

Bohn, M., Schmitt, V., Sanchez-Amaro, A., Keupp, S., Hopper, L., Völter, C., et al., 2019. Establishing an Infrastructure for Collaboration in Primate Cognition Research. PsyArXiv preprinthttps://doi.org/10.31234/osf.io/3xu7q.

Bos, P.A., Panksepp, J., Bluthé, R.-M., Honk, J., 2012. Acute effects of steroid hormones and neuropeptides on human social–emotional behavior: a review of single administration studies. Front. Neuroendocrinol. 33 (1), 17–35. https://doi.org/10.1016/J.YFRNE.2011.01.002.

Bos, P.A., Terburg, D., van Honk, J., 2010. Testosterone decreases trust in socially naive humans. Proc. Natl. Acad. Sci. U. S. A. 107 (22), 9991–9995. https://doi.org/10.1073/pnas.0911700107.

Boucsein, W., 2012. Electrodermal activity, second edition. Electrodermal Activity: Second Edition Vol. 9781461411https://doi.org/10.1007/978-1-4614-1126-0.

Briefer, E.F., Tettamanti, F., McElligott, A.G., 2015. Emotions in goats: mapping physiological, behavioural and vocal profiles. Anim. Behav. 99, 131–143. https://doi.org/10.1016/J.ANBEHAV.2014.11.002.

Brosnan, S.F., de Waal, F.B.M., 2014. Evolution of responses to (un)fairness. Science 346 (6207), 1251776. https://doi.org/10.1126/science.1251776.

Brosnan, S.F., Parrish, A., Beran, M.J., Flemming, T., Heimbauer, L., Talbot, C.F., et al., 2011. Responses to the Assurance game in monkeys, apes, and humans using equivalent procedures. Proc. Natl. Acad. Sci. 108 (8), 3442–3447. https://doi.org/10.1073/pnas.1016269108.

Brosnan, S.F., Schiff, H.C., de Waal, F.B.M., 2005. Tolerance for inequity may increase with social closeness in chimpanzees. Proc. R. Soc. B Biol. Sci. 272 (1560), 253–258. https://doi.org/10.1098/rspb.2004.2947.

Brosnan, S.F., Wilson, B.J., Beran, M.J., 2012a. Old World monkeys are more similar to humans than New World monkeys when playing a coordination game. Proc. R. Soc. B Biol. Sci. 279 (1733), 1522–1530. https://doi.org/10.1098/rspb.2011.1781.

Brosnan, S.F., Wilson, B.J., Beran, M.J., 2012b. Old World monkeys are more similar to humans than New World monkeys when playing a coordination game. Proc. R. Soc. B: Biol. Sci. 279 (1733), 1522–1530. https://doi.org/10.1098/rspb.2011.1781.

Brosnan, S.F., 2006. Nonhuman species' reactions to inequity and their implications for fairness. Soc. Justice Res. 19 (2), 153–185. https://doi.org/10.1007/s11211-006-0002-z.

Brosnan, S.F., Bshary, R., 2010. Cooperation and deception: from evolution to mechanisms. Philos. Trans. R. Soc. Lond. B Biol. Sci. 365 (1553), 2593–2598.

Brosnan, S.F., de Waal, F.B.M., 2002. A proximate perspective on reciprocal altruism. Hum. Nat. 13 (1), 129–152. https://doi.org/10.1007/s12110-002-1017-2.

Brosnan, S.F., Freeman, C., De Waal, F.B.M., 2006. Partner's behavior, not reward distribution, determines success in an unequal cooperative task in capuchin monkeys. Am. J. Primatol. 68 (7), 713–724. https://doi.org/10.1002/ajp.20261.

Brosnan, S.F., Hopper, L.M., Richey, S., Freeman, H.D., Talbot, C.F., Gosling, S.D., et al., 2015a. Personality influences responses to inequity and contrast in chimpanzees. Anim. Behav. 101, 75–87. https://doi.org/10.1016/j.anbehav.2014.12.019.

Brosnan, S.F., Price, S.A., Leverett, K., Prétôt, L., Beran, M., Wilson, B.J., 2017. Human and monkey responses in a symmetric game of conflict with asymmetric equilibria. J. Econ. Behav. Organ. 142, 293–306. https://doi.org/10.1016/j.jebo.2017.07.037.

Brosnan, S.F., Talbot, C.F., Essler, J.L., Leverett, K., Flamming, T., Dougall, P., et al., 2015b. Oxytocin reduces food sharing in capuchin monkeys by modulating social distance. Behaviour. https://doi.org/10.1163/1568539X-00003268.

Brosnan, S.F., Waal, F.B.M., 2003. Monkeys reject unequal pay. Nature 425 (6955), 297–299. https://doi.org/10.1038/nature01963.

Brosnan, S.F., Silk, J.B., Henrich, J., Mareno, M.C., Lambeth, S.P., Schapiro, S.J., 2009. Chimpanzees (Pan troglodytes) do not develop contingent reciprocity in an experimental task. Anim. Cogn. 12 (4), 587–597. https://doi.org/10.1007/s10071-009-0218-z.

Brownley, K.A., Hurwitz, B.E., Schneiderman, N., 2000. Cardiovascular psycho- physiology. In: Cacioppo, J.T., Tassinary, L.G., Berntson, G.G. (Eds.), Handbook of Psychophysiology, 2nd edition. Cambridge University Press, New York, pp. 224–264.

Bshary, R., Oliveira, R.F., Grutter, A.S., 2011. Short-term variation in the level of cooperation in the cleaner wrasse Labroides dimidiatus: implications for the role of potential stressors. Ethology 117 (3), 246–253. https://doi.org/10.1111/j.1439-0310.2010.01872.x.

Bull, J.J., Rice, W.R., 1991. Distinguishing mechanisms for the evolution of co-operation. J. Theor. Biol. 149 (1), 63–74. https://doi.org/10.1016/S0022-5193(05)80072-4.

Bullinger, A.F., Wyman, E., Melis, A.P., Tomasello, M., 2011. Coordination of chimpanzees (Pan troglodytes) in a stag hunt game. Int. J. Primatol. 32 (6), 1296–1310. https://doi.org/10.1007/s10764-011-9546-3.

Burgdorf, J., Kroes, R.A., Moskal, J.R., Pfaus, J.G., Brudzynski, S.M., Panksepp, J., 2008. Ultrasonic vocalizations of rats (*Rauuts norvegicus*) during mating, play, and aggression: behavioural concomitants, relationship to reward, and self-administration of playback. J. Comp. Psychol. 122, 357–367.

Burkart, J.M., Allon, O., Amici, F., Fichtel, C., Finkenwirth, C., Heschl, A., et al., 2014. The evolutionary origin of human hyper-cooperation. Nat. Commun. 5, 4747. https://doi.org/10.1038/ncomms5747.

Burkart, J.M., Hrdy, S.B., Van Schaik, C.P., 2009. Cooperative breeding and human cognitive evolution. Evol. Anthropol. Issues News Rev. 18 (5), 175–186. https://doi.org/10.1002/evan.20222.

Burkart, J.M., Fehr, E., Efferson, C., van Schaik, C.P., 2007. Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. Proc. Natl. Acad. Sci. 104 (50), 19762–19766. https://doi.org/10.1073/pnas.0710310104.

Burkart, J.M., Rueth, K., 2013. Preschool children fail primate prosocial game because of attentional task demands. PLoS One 8 (7), e68440. https://doi.org/10.1371/journal.pone.0068440.

Burton-Chellew, M.N., West, S.A., 2013. Prosocial preferences do not explain human cooperation in public-goods games. Proc. Natl. Acad. Sci. 110 (1), 216–221. https://doi.org/10.1073/pnas.1210960110.

Caballero Meneses, J.A., Menez Díaz, J.M., 2017. Vocal emotion expression effects on cooperation behavior. Psicolgica 38, 1–24.

Calcutt, S.E., Proctor, D., Berman, S.M., de Waal, F.B.M., 2019. Chimpanzees (*Pan troglodytes*) are more averse to social than nonsocial risk. Psychol. Sci. 30 (1), 105–115. https://doi.org/10.1177/0956797618811877.

Campennì, M., Schino, G., 2016. Symmetry-based reciprocity: evolutionary constraints on a proximate mechanism. PeerJ 4, e1812. https://doi.org/10.7717/peerj.1812.

Carere, C., Caramaschi, D., Fawcett, T.W., 2010. Covariation between personalities and individual differences in coping with stress: converging evidence and hypotheses. Curr. Zool. 56, 728–740.

Carter, G.G., Wilkinson, G.S., 2013. Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. Proc. R. Soc. B 280, 20122573.

Chaby, L., Cavigelli, S., White, A., Wang, K., Braithwaite, V., 2013. Long-term changes in cognitive bias and coping response as a result of chronic unpredictable stress during adolescence. Front. Hum. Neurosci. 7, 328.

Chalmeau, Raphael, Gallo, A., 1996. What chimpanzees (Pan troglodytes) learn in a cooperative task. Primates 37 (1), 39–47. https://doi.org/10.1007/BF02382918.

Chalmeau, R., Lardeux, K., Brandibas, P., Gallo, A., 1997a. Cooperative problem solving by orangutans. Int. J. Primatol. 18, 23–32.

Chalmeau, R., Visalberghi, E., Gallo, A., 1997b. Capuchin monkeys,Cebus apellafail to understand a cooperative task. Anim. Behav. 54 (5), 1215–1225. https://doi.org/10.1006/anbe.1997.0517.

Chang, S.W.C., Platt, M.L., 2014. Oxytocin and social cognition in rhesus macaques: implications for understanding and treating human psychopathology. Brain Res. 1580, 57–68. https://doi.org/10.1016/j.brainres.2013.11.006.

Chester, D.S., DeWall, C.N., Derefinko, K.J., Estus, S., Peters, J.R., Lynam, D.R., Jiang, Y., 2015. Monoamine oxidase a (MAOA) genotype predicts greater aggression through impulsive reactivity to negative affect. Behav. Brain Res. 283, 97–101. https://doi.org/10.1016/j.bbr.2015.01.034.

Clark, M.S., Grote, N.K., 2003. Close relationships. In: Millon, T., Lerner, M.J. (Eds.), Handbook of Psychology: Personality and Social Psychology. Wiley, Ne York, pp. 447–461.

Clutton-Brock, T., 2009. Cooperation between non-kin in animal societies. Nature 462 (7269), 51–57. https://doi.org/10.1038/nature08366.

Cooper, R., DeJong, D.V., Forsythe, R., Ross, T.W., 1992. Communication in coordination games. Q. J. Econ. 107, 739–771.

Crawford, M.P., 1937. The cooperative solving of problems by young chimpanzees. Comp. Psychol. Monogr. 14, 1–88.

Cronin, K.A., 2012. Prosocial behaviour in animals: the influence of social relationships, communication and rewards. Anim. Behav. 84 (5), 1085–1093. https://doi.org/10.1016/j.anbehav.2012.08.009.

Cronin, K.A., Kurian, A.V., Snowdon, C.T., 2005. Cooperative problem solving in a cooperatively breeding primate (Saguinus oedipus). Anim. Behav. 69 (1), 133–142. https://doi.org/10.1016/j.anbehav.2004.02.024.

Cubitt, R.P., Drouvelis, M., Gächter, S., 2011. Framing and free riding: emotional responses and punishment in social dilemma games. Exp. Econ. 14 (2), 254–272. https://doi.org/10.1007/s10683-010-9266-0.

Darwin, C., 1872. The Expressions of Emotions in Man and Animals. John Murray. .

David-Barrett, T., Dunbar, R.I.M., 2016. Language as a coordination tool evolves slowly. R. Soc. Open Sci. 3, 160259.

De Dreu, C.K.W., Greer, L.L., Handgraaf, M.J.J., Shalvi, S., Van Kleef, G.A., 2012. Oxytocin modulates selection of allies in intergroup conflict. Proc. of the R. Soc. B Biol. Sci. 279 (1731), 1150–1154. https://doi.org/10.1098/rspb.2011.1444.

De Dreu, C.K.W., Kret, M.E., 2016. Oxytocin conditions intergroup relations through upregulated in-group empathy, cooperation, conformity, and defense. Biol. Psychiatry 79 (3), 165–173. https://doi.org/10.1016/j.biopsych.2015.03.020.

De Waal, F.B.M., 1988. The communicative repertoire of captive bonobos, Pan paniscus., compared to that of chimpanzees. Behaviour 106, 183–251.

de Waal, F.B.M., 1999. Anthropomorphism and anthropodenial: consistency in our thinking about humans and other animals. Philos. Top. 27 (1), 255–280.

de Waal, F.B.M., Berger, M.L., 2000. Payment for labour in monkeys. Nature 404 (6778), 563. https://doi.org/10.1038/35007138.

de Waal, F.B.M., Davis, J.M., 2003. Capuchin cognitive ecology: cooperation based on projected returns. Neuropsychologia 41 (2), 221–228. https://doi.org/10.1016/S0028-3932(02)00152-5.

de Waal, F.B.M., Luttrell, L.M., 1988. Mechanisms of social reciprocity in three primate species: Symmetrical relationship characteristics or cognition? Ethol. Sociobiol. 9 (2–4), 101–118. https://doi.org/10.1016/0162-3095(88)90016-7.

de Waal, F.B.M., Yoshihara, D., 1983. Reconciliation and redirected affection in rhesus monkeys. Behaviour 85, 224–241.

DeYoung, C.G., 2013. The neuromodulator of exploration: a unifying theory of the role of dopamine in personality. Front. Hum. Neurosci. 7. https://doi.org/10.3389/fnhum.2013.00762.

Dezecache, G., Zuberbühler, K., Davila-Ross, M., Dahl, C.D., 2017. Skin temperature changes in wild chimpanzees upon hearing vocalizations of conspecifics. R. Soc. Open Sci. 4 (1), 160816.

Drea, C.M., Carter, A.N., 2009. Cooperative problem solving in a social carnivore. Anim. Behav. 78 (4), 967–977. https://doi.org/10.1016/j.anbehav.2009.06.030.

Dreher, J.C., Dunne, S., Pazderska, A., Frodl, T., Nolan, J.J., O'Doherty, J.P., 2016. Testosterone causes both prosocial and antisocial status-enhancing behaviors in human males. Proc. Natl. Acad. Sci. 113, 11633–11638.

Dufour, V., Pele, M., Neumann, M., Thierry, B., Call, J., 2009. Calculated reciprocity after all: computation behind token transfers in orang-utans. Biol. Lett. 5 (2), 172–175. https://doi.org/10.1098/rsbl.2008.0644.

Dugatkin, L.A., 1991. Dynamics of the TIT FOR TAT strategy during predator inspection in the guppy (Poecilia reticulata). Behav. Ecol. Sociobiol. 28, 243–246.

Duguid, S., Wyman, E., Bullinger, A.F., Herfurth-Majstorovic, K., Tomasello, M., 2014. Coordination strategies of chimpanzees and human children in a Stag Hunt game. Proc. R. Soc. B: Biol. Sci. 281 (1796), 20141973. https://doi.org/10.1098/rspb.2014.1973.

Dulleck, U., 2014. Heartbeat and Economic Decisions: Observing Mental Stress among Proposers and Responders in the Ultimatum Bargaining Game. PLoS ONE, e108218.

Dunn, B.D., Evans, D., Makarova, D., White, J., Clark, L., 2012. Gut feelings and the reaction to perceived inequity: the interplay between bodily responses, regulation, and perception shapes the rejection of unfair offers on the ultimatum game. Cogn. Affect. Behav. Neurosci. 12 (3), 419–429. https://doi.org/10.3758/s13415-012-0092-z.

Duque, J.F., Leichner, W., Ahmann, H., Stevens, J.R., 2018. Mesotocin influences pinyon jay prosociality. Biol. Lett. 14 (4), 20180105. https://doi.org/10.1098/rsbl.2018.0105.

Duque, J.F., Rasmussen, T., Rodriguez, A., Stevens, J.R., 2019. The role of mesotocin on social bonding in pinyon jays (in press). Ethology.

D'Vincent, C.G., Nilson, R.M., Hanna, R.E., 1985. Vocalization and coordinated feeding behavior of the humpback whale in southeastern Alaske. Sci. Rep. Whales Res. Inst. 36, 41–47.

Ebenau, A., von Borell, C., Penke, L., Ostner, J., Schülke, O., 2019. Personality homophily affects male social bonding in wild Assamese macaques, Macaca assamensis. Anim. Behav. 155, 21–35.

Edsinger, E., Dölen, G., 2018. A conserved role for serotonergic neurotransmission in mediating social behavior in Octopus. Curr. Biol. 28 (19), 3136–3142. https://doi.org/10.1016/j.cub.2018.07.061. e4.

Eimontaite, I., Nicolle, A., Schindler, I., Goel, V., 2013. The effect of partner-directed emotion in social exchange decision-making. Front. Psychol. 4, 469. https://doi.org/10.3389/fpsyg.2013.00469.

Eisenegger, C., Naef, M., Snozzi, R., Heinrichs, M., Fehr, E., 2010. Prejudice and truth about the effect of testosterone on human bargaining behaviour. Nature 463 (7279), 356–359. https://doi.org/10.1038/nature08711.

Ember, C.R., Skoggard, I., Ringen, E.J., Farrer, M., 2018. Our better nature: Does resource stress predict beyond-household sharing? Evol. Hum. Behav. 39 (4), 380–391. https://doi.org/10.1016/j.evolhumbehav.2018.03.001.

Engelmann, J.M., Herrmann, E., Tomasello, M., 2015. Chimpanzees trust conspecifics to engage in low-cost reciprocity. Proc. R. Soc. B: Biol. Sci. 282 (1801), 20142803. https://doi.org/10.1098/rspb.2014.2803.

Engelmann, J.M., Herrmann, E., 2016. Chimpanzees trust their friends. Curr. Biol. 26 (2), 252–256. https://doi.org/10.1016/j.cub.2015.11.037.

Eskelinen, H.C., Winship, K.A., Jones, B.L., Ames, A.E.M., Kuczaj, S.A., 2016. Acoustic behavior associated with cooperative task success in bottlenose dolphins (Tursiops truncatus). Anim. Cogn. 19 (4), 789–797. https://doi.org/10.1007/s10071-016-0978-1.

Essler, J.L., Marshall-Pescini, S., Range, F., 2017. Domestication does not explain the presence of inequity aversion in dogs. Curr. Biol. 27 (12), 1861–1865 e3.

Evers, E., de Vries, H., Spruijt, B.M., Sterck, E.H.M., 2016. Intermediate-term emotional bookkeeping is necessary for long-term reciprocal grooming partner preferences in an agent-based model of macaque groups. PeerJ 4, e1488. https://doi.org/10.7717/peerj.1488.

Fady, J.C., 1972. Absence de cooperation de type instrumental en milieu naturel chez Papio papio. Behaviour 43 (1/4), 157–164.

Fehr, E., Gächter, S., 2002. Altruistic punishment in humans. Nature 415, 137–140. https://doi.org/10.1038/415137a.

Fehr, E., Schmidt, 1999. A theory of fairness, competition, and cooperation. Q. J. Econ. 52.

Feng, C., Hackett, P.D., DeMarco, A.C., Chen, X., Stair, S., Haroon, E., et al., 2015. Oxytocin and vasopressin effects on the neural response to social cooperation are modulated by sex in humans. Brain Imaging Behav. 9 (4), 754–764. https://doi.org/10.1007/s11682-014-9333-9.

Fidler, A.E., van Oers, K., Drent, P.J., Kuhn, S., Mueller, J.C., Kempenaers, B., 2007. Drd4 gene polymorphisms are associated with personality variation in a passerine bird. Proc. R. Soc. B: Biol. Sci. 274 (1619), 1685–1691. https://doi.org/10.1098/rspb.2007.0337.

Filippi, P., Congdon, J.V., Hoang, J., Bowling, D.L., Reber, S.A., Pašukonis, A., et al., 2017. Humans recognize emotional arousal in vocalizations across all classes of terrestrial vertebrates: evidence for acoustic universals. Proc. R. Soc. B 284 (1859), 20170990.

Finkenwirth, C., van Schaik, C., Ziegler, T.E., Burkart, J.M., 2015. Strongly bonded family members in common marmosets show synchronized fluctuations in oxytocin. Physiol. Behav. 151, 246–251. https://doi.org/10.1016/j.physbeh.2015.07.034.

Fitch, W.T., Huber, L., Bugnyar, T., 2010. Social cognition and the evolution of language: constructing cognitive phylogenies. Neuron 65 (6), 795–814. https://doi.org/10.1016/j.neuron.2010.03.011.

Fitch, W.T., de Boer, B., Mathur, N., Ghazanfar, A.A., 2016. Monkey vocal tracts are speech-ready. Sci. Adv. 2, e1600723.

Freiden, E., 2017. Direct reciprocity in animals: The roles of bonding and affective processes. Int. J. Psychol. 52, 163–170.

Fruteau, C., van Damme, E., Noë, R., 2013. Vervet monkeys solve a multiplayer "Forbidden circle game" by queuing to learn restraint. Curr. Biol. 23 (8), 665–670. https://doi.org/10.1016/j.cub.2013.02.039.

Fujii, T., Schug, J., Nishina, K., Takahashi, T., Okada, H., Takagishi, H., 2016. Relationship between salivary oxytocin levels and generosity in preschoolers. Sci. Rep. 6, 38662. https://doi.org/10.1038/srep38662.

González-Forero, M., Gardner, A., 2018. Inference of ecological and social drivers of human brain-size evolution. Nature 557 (7706), 554–557. https://doi.org/10.1038/s41586-018-0127-x.

Gosling, S.D., 2001. From mice to men: What can we learn about personality from animal research? Psychol. Bull. 127 (1), 45–86. https://doi.org/10.1037//0033-2909.127.1.45.

Gott, A., Andrews, C., Bedford, T., Nettle, D., Bateson, M., 2019. Developmental history and stress responsiveness are related to response inhibition, but not judgement bias, in a cohort of European starlings (*Sturnus vulgaris*). Anim. Cogn. 22, 99–111.

Gruber, C.W., 2014. Physiology of invertebrate oxytocin and vasopressin neuropeptides. Exp. Physiol. 99 (1), 55–61. https://doi.org/10.1113/expphysiol.2013.072561.

Gummerum, M., Chu, M.T., 2014. Outcomes and intentions in children's, adolescents', and adults' second- and third-party punishment behavior. Cognition 133 (1), 97–103. https://doi.org/10.1016/j.cognition.2014.06.001.

Gurven, M., Von Rueden, C., Stieglitz, J., Kaplan, H., Rodriguez, D.E., 2014. The evolutionary fitness of personality traits in a small-scale subsistence society. Evol. Hum. Behav. 35 (1). https://doi.org/10.1016/j.evolhumbehav.2013.09.002.

Hall, K., Smith, M., Russell, J.L., Lambeth, S.P., Schapiro, S.J., Brosnan, S.F., 2019. Chimpanzees rarely settle on consistent patterns of play in the hawk dove, assurance, and prisoner's dilemma games, in a token exchange task. Anim. Behav. Cogn. 6 (1), 48–70. https://doi.org/10.26451/abc.06.01.04.2019.

Hamilton, W.D., 1964. The genetical evolution of social behaviour. I. J. Theor. Biol. 7 (1), 1–16. https://doi.org/10.1016/0022-5193(64)90038-4.

Hammerstein, P., Noë, R., 2016. Biological trade and markets. Philos. Trans. Biol. Sci. 371, 20150101.

Harding, E.J., Paul, E.S., Mendl, M., 2004. Cognitive bias and affective state: animal behaviour. Nature 427 (6972), 312. https://doi.org/10.1038/427312a.

Hare, B., Melis, A.P., Woods, V., Hastings, S., Wrangham, R., 2007. Tolerance allows bonobos to outperform chimpanzees on a cooperative task. Curr. Biol. 17 (7), 619–623. https://doi.org/10.1016/j.cub.2007.02.040.

Haroush, K., Williams, Z.M., 2015. Neuronal prediction of opponent's behavior during cooperative social interchange in Primates. Cell 160 (6), 1233–1245. https://doi.org/10.1016/j.cell.2015.01.045.

Hayden, B.Y., 2016. Time discounting and time preference in animals: a critical review. Psychon. Bull. Rev. 23 (1), 39–53. https://doi.org/10.3758/s13423-015-0879-3.

Heaney, M., Gray, R.D., Taylor, A.H., 2017. Keas perform similarly to chimpanzees and elephants when solving collaborative tasks. PLoS One 12 (2), e0169799. https://doi.org/10.1371/journal.pone.0169799.

Henrich, J., Henrich, N., 2014. Fairness without punishment: behavioral experiments in the yasawa Island, Fiji. In: Ensminger, J., Henrich, J. (Eds.), Experimenting With Social Norms: Fairness and Punishment in Cross-Cultural Perspective. Russell Sage Foundation, New York, NY, pp. 225–258.

Hill, K.R., Walker, R.S., Božičević, M., Eder, J., Headland, T., Hewlett, B., et al., 2011. Co-residence patterns in hunter-gatherer societies show unique human social structure. Science 331 (6022), 1286–1289. https://doi.org/10.1126/science.1199071.

Hirata, S., 2003. Cooperation in chimpanzees. Hattatsu 95, 103–111.

Hirata, S., Fuwa, K., 2007. Chimpanzees (Pan troglodytes) learn to act with other individuals in a cooperative task. Primates 48 (1), 13–21. https://doi.org/10.1007/s10329-006-0022-1.

Horn, L., Hungerländer, N.A., Windhager, S., Bugnyar, T., Massen, J.J.M., 2018. Social status and prenatal testosterone exposure assessed via second-to-fourth digit ratio affect 6–9-year-old children's prosocial choices. Sci. Rep. 8 (1), 9198. https://doi.org/10.1038/s41598-018-27468-0.

Horn, L., Scheer, C., Bugnyar, T., Massen, J.J.M., 2016. Proactive prosociality in a cooperatively breeding corvid, the azure-winged magpie (*Cyanopica cyana*). Biol. Lett. 12 (10), 20160649. https://doi.org/10.1098/rsbl.2016.0649.

House, B.R., Henrich, J., Brosnan, S.F., Silk, J.B., 2012. The ontogeny of human prosociality: behavioral experiments with children aged 3 to 8. Evol. Hum. Behav. 33 (4), 291–308. https://doi.org/10.1016/j.evolhumbehav.2011.10.007.

Huxley, J., 1923. Biology and sociology. Sociol. Rev. 15, 53–55.

Ioannou, S., Chotard, H., Davila-Ross, M., 2015. No strings attached: physiological monitoring of rhesus monkeys (Macaca mulatta) with thermal imaging. Front. Behav. Neurosci. 9, 160.

Izard, C., 1977. Human Emotions. Springer.

Jaakkola, K., Guarino, E., Donegan, K., King, S.L., 2018. Bottlenose dolphins can understand their partner's role in a cooperative task. Proc. R. Soc. B 285 (1887), 20180948. https://doi.org/10.1098/rspb.2018.0948.

Jaeggi, A.V., Burkart, J.M., Van Schaik, C.P., 2010. On the psychology of cooperation in humans and other primates: combining the natural history and experimental evidence of prosociality. Philos. Trans. R. Soc. B: Biol. Sci. 365, 2723–2735.

Jaeggi, A.V., Hooper, P.L., Beheim, B.A., Kaplan, H., Gurven, M., 2016. Reciprocal exchange patterned by market forces helps explain cooperation in a small-scale society. Curr. Biol. 26 (16), 2180–2187. https://doi.org/10.1016/j.cub.2016.06.019.

Jäschke, J.P.M., Primes, G., Windhager, S., Fieder, M., Wallner, B., 2016. Effects of socioeconomic status and fairness on salivary cortisol. Evol. Psychol. 14 (2), 1474704916653487. https://doi.org/10.1177/1474704916653487.

Jensen, K., 2016. Prosociality. Curr. Biol. 26, R748–R752.

Jensen, K., Call, J., Tomasello, M., 2007a. Chimpanzees are rational maximizers in an ultimatum game. Science 318 (5847), 107–109.

Jensen, K., Call, J., Tomasello, M., 2007b. Chimpanzees are vengeful but not spiteful. Proc. Natl. Acad. Sci.(1286), 0705555104.

Jensen, K., Hare, B., Call, J., Tomasello, M., 2006. What's in it for me? Self-regard precludes altruism and spite in chimpanzees. Proc. R. Soc. B: Biol. Sci. 273, 1013–1021.

Jiang, Y., Platt, M.L., 2018. Oxytocin and vasopressin flatten dominance hierarchy and enhance behavioral synchrony in part via anterior cingulate cortex. Sci. Rep. 8 (1), 8201. https://doi.org/10.1038/s41598-018-25607-1.

Johnstone, R.A., Rodrigues, A.M.M., 2016. Cooperation and the common good. Philos. Trans. Biol. Sci. 371 (1687), 20150086. https://doi.org/10.1098/rstb.2015.0086.

Joly, M., Micheletta, J., Marco, A.D., Langermans, J.A., Sterck, E.H.M., Waller, B.M., 2017. Comparing physical and social cognitive skills in macaque species with different degrees of social tolerance. Proc. R. Soc. B 284 (1862), 20162738. https://doi.org/10.1098/rspb.2016.2738.

Kaburu, S.S.K., Newton-Fisher, N.E., 2016. Bystanders, parcelling, and an absence of trust in the grooming interactions of wild male chimpanzees. Sci. Rep. 6 (1). https://doi.org/10.1038/srep20634.

Kagan, S., Madsen, M.C., 1970. Cooperation and Competition of Mexican, Mexican-American, and Anglo-American Children of Two Ages Under Four Instructional Sets. Retrieved from. https://eric.ed.gov/?id=ED042532.

Kaigaishi, Y., Nakamichi, M., Yamada, K., 2019. High but not low tolerance populations of japanese macaques solve a novel cooperative task. Primates online first.

Kaiser, I., Jensen, K., Call, J., Tomasello, M., 2012. Theft in an ultimatum game: chimpanzees and bonobos are insensitive to unfairness. Biol. Lett. 8 (6), 942–945. https://doi.org/10.1098/rsbl.2012.0519.

Kano, F., Hirata, S., Deschner, T., Behringer, V., Call, J., 2016. Nasal temperature drop in response to a playback of conspecific fights in chimpanzees: a thermo-imaging study. Physiol. Behav. 155, 83–94.

Kaplan, H.S., Hooper, P.L., Gurven, M., 2009. The evolutionary and ecological roots of human social organization. Philos. Trans. Biol. Sci. 364 (1533), 3289–3299. https://doi.org/10.1098/rstb.2009.0115.

Kemp, C., Thatcher, H., Farningham, D., Witham, C., MacLarnon, A., Holmes, A., et al., 2017. A protocol for training group-housed rhesus macaques (*Macaca mulatta*) to cooperate with husbandry and research procedures using positive reinforcement. Appl. Anim. Behav. Sci. 0 (0). https://doi.org/10.1016/j.applanim.2017.08.006.

Kern, J.M., Radford, A.N., 2018. Experimental evidence for delayed contingent cooperation among wild dwarf mongooses. Proc. Natl. Acad. Sci. https://doi.org/10.1073/pnas.1801000115. 201801000.

Kirchhofer, K.C., Zimmermann, F., Kaminski, J., Tomasello, M., 2012. Dogs (Canis familiaris), but not chimpanzees (Pan troglodytes), understand imperative pointing. PLoS One 7 (2), e30913. https://doi.org/10.1371/journal.pone.0030913.

Kortekaas, K., Range, F., Virányi, Z., Kotrschal, K., 2013. Heart rate and heart rate variability of dogs (Canis lupus familiaris) during physical and mental activities. J. Vet. Behav. Clin. Appl. Res. 8 (4), e45–e46. https://doi.org/10.1016/J.JVEB.2013.04.070.

Kramer, K.L., 2010. Cooperative breeding and its significance to the demographic success of humans. Annu. Rev. Anthropol. 39 (1), 417–436. https://doi.org/10.1146/annurev.anthro.012809.105054.

Kret, M.E., De Dreu, C.K.W., 2017. Pupil-mimicry conditions trust in partners: moderation by oxytocin and group membership. Proc. R. Soc. B: Biol. Sci. 284.

Kret, M.E., Tomonaga, M., 2016. Getting to the bottom of face processing. species-specific inversion effects for faces and behinds in humans and chimpanzees (Pan Troglodytes). PLoS One 11 (11), e0165357. https://doi.org/10.1371/journal.pone.0165357.

Kret, M.E., Tomonaga, M., Matsuzawa, T., 2014. Chimpanzees and humans mimic pupil-size of conspecifics. PLoS One 9 (8), e104886. https://doi.org/10.1371/journal.pone.0104886.

Kret, M.E., Prochazkova, E., Sterck, E.H.M., Clay, Z., 2019. Emotional expressions in humans and non-human great apes (this issue). Neurosci. Biobehav. Rev.

Krueger, F., McCabe, K., Moll, J., Kriegeskorte, N., Zahn, R., Strenziok, M., et al., 2007. Neural correlates of trust. Proc. Natl. Acad. Sci. 104 (50), 20084–20089.

Kummerli, R., Burton-Chellew, M.N., Ross-Gillespie, A., West, S.A., 2010. Resistance to extreme strategies, rather than prosocial preferences, can explain human cooperation in public goods games. Proc. Natl. Acad. Sci. 107 (22), 10125–10130. https://doi.org/10.1073/pnas.1000829107.

Kuraoka, K., Nakamura, K., 2011. The use of nasal skin temperature measurements in studying emotion in macaque monkeys. Physiol. Behav. 102 (3–4), 347–355.

Lambeth, S.P., Hau, J., Perlman, J.E., Martino, M., Schapiro, S.J., 2006. Positive reinforcement training affects hematologic and serum chemistry values in captive chimpanzees (Pan troglodytes). Am. J. Primatol. 68 (3), 245–256. https://doi.org/10.1002/ajp.20148.

laumer, I.B., Massen, J.J.M., Wakonig, B., Lorck-Tympner, M., Carminito, C., Auersperg, A.M.I., 2019. Tentative evidence for inequity aversion to unequal work-effort but not to unequal reward distribution in Goffin's cockatoos. in press. Ethology.

Leavens, D.A., Bard, K.A., Hopkins, W.D., 2017. The mismeasure of ape social cognition. Anim. Cogn. https://doi.org/10.1007/s10071-017-1119-1.

Leighton, G.M., 2018. Cooperative breeding influences the number and type of vocalizations in avian lineages. Proc. R. Soc. Lond. B 284, 20171508.

Leimar, O., Hammerstein, P., 2010. Cooperation for direct fitness benefits. Philos. Trans. Biol. Sci. 365 (1553), 2619–2626. https://doi.org/10.1098/rstb.2010.0116.

Leimgruber, K.L., Rosati, A.G., Santos, L.R., 2016. Capuchin monkeys punish those who have more. Evol. Hum. Behav. 37, 236–244.

Liebal, K., Vaish, A., Haun, D., Tomasello, M., 2014. Does sympathy motivate prosocial behaviour in great apes? PLoS One 9 (1), e84299.

Loewenstein, G.F., Thompson, L., Bazerman, M.H., 1989. Social utility and decision making in interpersonal contexts. J. Pers. Soc. Psychol. 57 (3), 426–441. https://doi.org/10.1037/0022-3514.57.3.426.

Łopuch, S., Popik, P., 2011. Cooperative behavior of laboratory rats (*Rattus norvegicus*) in an instrumental task. J. Comp. Psychol. 125, 250–253.

Lloyd, W.F., 1833. Two Lectures on the Checks to Populations. Oxford University Press.

MacLean, E.L., Hare, B., Nunn, C.L., Addessi, E., Amici, F., Anderson, R.C., et al., 2014. The evolution of self-control. Proc. Natl. Acad. Sci. 111 (20), E2140–E2148. https://doi.org/10.1073/pnas.1323533111.

MacLean, E.L., Matthews, L.J., Hare, B.A., Nunn, C.L., Anderson, R.C., Aureli, F., et al., 2012. How does cognition evolve? Phylogenetic comparative psychology. Anim. Cogn. 15 (2), 223–238. https://doi.org/10.1007/s10071-011-0448-8.

Majolo, B., Ames, K., Brumpton, R., Garratt, R., Hall, K., Wilson, N., 2006. Human friendship favours cooperation in the iterated prisoner's dilemma. Behaviour 143 (11), 1383–1395.

Maestripieri, D., Schino, G., Aureli, F., Troisi, A., 1992. A modest proposal: displacement activities as an indicator of emotions in primates. Anim. Behav. 2, 967e979.

Manser, M.B., Jansen, D., Graw, B., Hollén, L.I., Bousquet, C.A., Furrer, R.D., le Roux, A., 2014. Vocal complexity in meerkats and other mongoose species. Adv. Study Behav. 46, 281–310.

Marshall-Pescini, S., Dale, R., Quervel-Chaumette, M., Range, F., 2016. Critical issues in experimental studies of prosociality in non-human species. Anim. Cogn. 19 (4), 679–705. https://doi.org/10.1007/s10071-016-0973-6.

Marshall-Pescini, S., Basin, C., Range, F., 2018. A task-experienced partner does not help dogs be as successful as wolves in a cooperative string-pulling task. Sci. Rep. 8 (1). https://doi.org/10.1038/s41598-018-33771-7.

Marshall-Pescini, S., Schwarz, J.F.L., Kostelnik, I., Virányi, Z., Range, F., 2017. Importance of a species' socioecology: wolves outperform dogs in a conspecific cooperation task. Proc. Natl. Acad. Sci. 114 (44), 11793–11798. https://doi.org/10.1073/pnas.1709027114.

Martin, J.S., Koski, S.E., Bugnyar, T., Jaeggie, A.V., Massen, J.J.M., 2019. Prosociality Enhances Cooperation in Common Marmosets (Callithrix Jacchus) (in review). .

Martin, C.F., Bhui, R., Bossaerts, P., Matsuzawa, T., Camerer, C., 2014. Chimpanzee choice rates in competitive games match equilibrium game theory predictions. Sci. Rep. 4. https://doi.org/10.1038/srep05182.

Massen, J.J.M., Koski, S.E., 2014. Chimps of a feather sit together: chimpanzee friendships are based on homophily in personality. Evol. Hum. Behav. 35 (1), 1–8. https://doi.org/10.1016/j.evolhumbehav.2013.08.008.

Massen, J.J.M., Ritter, C., Bugnyar, T., 2015. Tolerance and reward equity predict cooperation in ravens (Corvus corax). Sci. Rep. 5 (1). https://doi.org/10.1038/srep15021.

Massen, J.J.M., Sterck, E.H.M., De Vos, H., 2010. Close social associations in animals and humans: functions and mechanisms of friendship. Behaviour 147 (11), 1379–1412. https://doi.org/10.1163/000579510X528224.

Massen, J.J.M., Schaake, W.A.A., Bugnyar, T., 2019. A comparison of cooperative cognition in corvids, chimpanzees, and other animals. in press In: Hopper, L., Ross, S. (Eds.), Chimpanzees in Context. University of Chicago Press, Chicago, USA.

Matsuzawa, R., Tanimoto, J., 2018. Sanctions triggered by jealousy help promote the cooperation in spatial prisoner's dilemma games. Chaos Solitons Fractals 110, 239–243. https://doi.org/10.1016/j.chaos.2018.03.029.

McAuliffe, K., Blake Peter, R., Warneken, F., 2014. Children reject inequity out of spite. Biol. Lett. 10 (12), 20140743. https://doi.org/10.1098/rsbl.2014.0743.

McAuliffe, K., 2015. The psychology of cooperation in animals: an ecological approach. J. Zool. 295, 23–35.

McCormack, K., Newman, T.K., Higley, J.D., Maestripieri, D., Sanchez, M.M., 2009. Serotonin transporter gene variation, infant abuse, and responsiveness to stress in rhesus macaque mothers and infants. Horm. Behav. 55 (4), 538–547. https://doi.org/10.1016/j.yhbeh.2009.01.009.

Mehta, P.H., Josephs, R.A., 2010. Testosterone and cortisol jointly regulate dominance: evidence for a dual-hormone hypothesis. Horm. Behav. 58 (5), 898–906. https://doi.org/10.1016/j.yhbeh.2010.08.020.

Mehta, P.H., Prasad, S., 2015. The dual-hormone hypothesis: a brief review and future research agenda. Curr. Opin. Behav. Sci. 3, 163–168. https://doi.org/10.1016/j.cobeha.2015.04.008.

Melis, A.P., 2006. Chimpanzees recruit the best collaborators. Science 311 (5765), 1297–1300. https://doi.org/10.1126/science.1123007.

Melis, A.P., Engelmann, J.M., Warneken, F., 2018. Correspondence: chimpanzee helping is real, not a byproduct. Nat. Commun. 9 (1), 615. https://doi.org/10.1038/s41467-017-02321-6.

Melis, A.P., Hare, B., Tomasello, M., 2006. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. Anim. Behav. 72 (2), 275–286. https://doi.org/10.1016/j.anbehav.2005.09.018.

Melis, A.P., Hare, B., Tomasello, M., 2008. Do chimpanzees reciprocate received favours? Anim. Behav. 76 (3), 951–962. https://doi.org/10.1016/j.anbehav.2008.05.014.

Melis, A.P., Semmann, D., 2010. How is human cooperation different? Philos. Trans. Biol. Sci. 365 (1553), 2663–2674. https://doi.org/10.1098/rstb.2010.0157.

Mendl, M., Burman, O.H., Parker, R.M., Paul, E.S., 2009. Cognitive bias as an indicator of animal emotion and welfare: emerging evidence and underlying mechanisms. Appl. Anim. Behav. Sci. 118, 161–181.

Mendl, M., Burman, O.H.P., Paul, E.S., 2010. An integrative and functional framework for the study of animal emotion and mood. Proc. R. Soc. B: Biol. Sci. 277 (1696), 2895–2904. https://doi.org/10.1098/rspb.2010.0303.

Mendres, K.A., de Waal, F.B.M., 2000. Capuchins do cooperate: the advantage of an intuitive task. Anim. Behav. 60 (4), 523–529. https://doi.org/10.1006/anbe.2000.1512.

Milinski, M., 1987. Tit for tat in sticklebacks and the evolution of cooperation. Nature 325, 433–435.

Miss, F.M., Burkart, J.M., 2018. Corepresentation during joint action in marmoset monkeys (Callithrix jacchus). Psychol. Sci., 0956797618772046. https://doi.org/10.1177/0956797618772046.

Molesti, S., Majolo, B., 2016. Cooperation in wild Barbary macaques: factors affecting free partner choice. Anim. Cogn. 19 (1), 133–146. https://doi.org/10.1007/s10071-015-0919-4.

Moliné, A., Gálvez-García, G., Fernández-Gómez, J., De la Fuente, J., Iborra, O., Tornay, F., et al., 2017. The pinocchio effect and the cold stress test: lies and thermography. Psychophysiology 54 (11), 1621–1631. https://doi.org/10.1111/psyp.12956.

Moll, H., Tomasello, M., 2007. Cooperation and human cognition: the Vygotskian intelligence hypothesis. Philos. Trans. R. Soc. Lond. B Biol. Sci. 362 (1480), 639–648. https://doi.org/10.1098/rstb.2006.2000.

Morand-Ferron, J., Cole, E.F., Quinn, J.L., 2016. Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. Biol. Rev. 91, 367–389.

Moscovice, L.R., Surbeck, M., Fruth, B., Hohmann, G., Jaeggi, A.V., Deschner, T., 2019. The cooperative sex: sexual interactions among female bonobos are linked to increases in oxytocin, proximity and coalitions. Horm. Behav. 116, 104581.

Müller, J.J.A., Massen, J.J.M., Bugnyar, T., Osvath, M., 2017. Ravens remember the nature of a single reciprocal interaction sequence over 2 days and even after a month. Anim. Behav. 128, 69–78. https://doi.org/10.1016/j.anbehav.2017.04.004.

Mustoe, A.C., Harnisch, A.M., Hochfelder, B., Cavanaugh, J., French, J.A., 2016. Inequity aversion strategies between marmosets are influenced by partner familiarity and sex but not by oxytocin. Anim. Behav. 114, 69–79. https://doi.org/10.1016/j.anbehav.2016.01.025.

Nakayama, K., Goto, S., Kuraoka, K., Nakamura, K., 2005. Decrease in nasal temperature of rhesus monkeys (Macaca mulatta) in negative emotional state. Physiol. Behav. 84 (5), 783–790.

Ne'eman, R., Perach-Barzilay, N., Fischer-Shofty, M., Atias, A., Shamay-Tsoory, S.G., 2016. Intranasal administration of oxytocin increases human aggressive behavior. Horm. Behav. 80, 125–131.

Noë, R., 2006. Cooperation experiments: coordination through communication versus acting apart together. Anim. Behav. 71 (1), 1–18. https://doi.org/10.1016/j.anbehav.2005.03.037.

Noë, R., Voelkl, B., 2013. Cooperation and biological markets: the power of partner chocie. In: Sterelny, K., Joyce, R., Calcott, B., Fraser, B. (Eds.), Cooperation and Its Evolution. MIT Press, Cambridge, MA, pp. 131–151.

Ostojić, L., Clayton, N.S., 2014. Behavioural coordination of dogs in a cooperative problem-solving task with a conspecific and a human partner. Anim. Cogn. 17 (2), 445–459. https://doi.org/10.1007/s10071-013-0676-1.

Osumi, T., Ohira, H., 2009. Cardiac responses predict decisions: an investigation of the relation between orienting response and decisions in the ultimatum game. Int. J. Psychophysiol. 74 (1), 74–79. https://doi.org/10.1016/j.ijpsycho.2009.07.007.

Ozer, D.J., Benet-Martínez, V., 2006. Personality and the prediction of consequential outcomes. Annu. Rev. Psychol. 57 (1), 401–421. https://doi.org/10.1146/annurev.psych.57.102904.190127.

Palme, R., 2019. Non-invasive measurement of glucocorticoids: advances and problems. Physiol. Behav. 199, 229–243. https://doi.org/10.1016/J.PHYSBEH.2018.11.021.

Pan, Y., Cheng, X., Zhang, Z., Li, X., Hu, Y., 2016. Cooperation in lovers: an fNIRS-based hyperscanning study. Hum. Brain Mapp. https://doi.org/10.1002/HBM.23421.

Panasiti, M.S., Cardone, D., Pavone, E.F., Mancini, A., Merla, A., Aglioti, S.M., 2016. Thermal signatures of voluntary deception in ecological conditions. Sci. Rep. 6 (1), 35174. https://doi.org/10.1038/srep35174.

Parrish, A., Brosnan, S.F., Wilson, B.J., Beran, M.J., 2014. Differential responding by rhesus monkeys (Macaca mulatta) and humans (Homo sapiens) to variable outcomes in the assurance game. Anim. Behav. Cogn.

Paul, E.S., Harding, E.J., Mendl, M., 2005. Measuring emotional processes in animals: the utility of a cognitive approach. Neurosci. Biobehav. Rev. 29 (3), 469–491. https://doi.org/10.1016/j.neubiorev.2005.01.002.

Paul, E.S., Sher, S., Tamietto, M., Winkielman, P., Mendl, M.T., 2019. Towards a comparative science of emotion: affect and consciousness in humans and animals (this issue). Neurosci. Biobehav. Rev.

Péron, F., Rat-Fischer, L., Lalot, M., Nagle, L., Bovet, D., 2011. Cooperative problem solving in African grey parrots (Psittacus erithacus). Anim. Cogn. 14 (4), 545–553. https://doi.org/10.1007/s10071-011-0389-2.

Petit, O., Desportes, C., Thierry, B., 1992. Differential Probability of "Coproduction" in two Species of Macaque (Macaca tonkeana, M. mulatta). Ethology 90 (2), 107–120. https://doi.org/10.1111/j.1439-0310.1992.tb00825.x.

Phelps, E.A., O'Connor, K.J., Gatenby, J.C., Gore, J.C., Grillon, C., Davis, M., 2001. Activation of the left amygdala to a cognitive representation of fear. Nat. Neurosci. 4 (4), 437–441. https://doi.org/10.1038/86110.

Pinker, S., 2010.). The cognitive niche: coevolution of intelligence, sociality, and language. Proc. Natl. Acad. Sci. 107 (Supplement 2), 8993–8999. https://doi.org/10.1073/pnas.0914630107.

Plotnik, J.M., Lair, R., Suphachoksahakun, W., de Waal, F.B.M., 2011. Elephants know when they need a helping trunk in a cooperative task. Proc. Natl. Acad. Sci. 108 (12), 5116–5121. https://doi.org/10.1073/pnas.1101765108.

Prescott, M.J., Buchanan-Smith, H.M., 2003. Training nonhuman primates using positive reinforcement techniques. July 4. J. Appl. Anim. Welf. Sci. 6 (3), 157–161. https://doi.org/10.1207/S15327604JAWS0603_01.

Prochazkova, E., Prochazkova, L., Giffin, M.R., Scholte, H.S., De Dreu, C.K.W., Kret, M.E., 2018. Pupil mimicry promotes trust through the theory-of-mind network. Proc. Natl. Acad. Sci. 115 (31), E7265–E7274. https://doi.org/10.1073/pnas.1803916115.

Proctor, D., Williamson, R.A., de Waal, F.B.M., Brosnan, S.F., 2013. Chimpanzees play the ultimatum game. Proc. Natl. Acad. Sci. 110 (6), 2070–2075. https://doi.org/10.1073/pnas.1220806110.

Proctor, D., Calcutt, S., Burke, K., de Waal, F., 2016. Intranasal oxytocin failed to affect chimpanzee (Pan troglodytes) social behavior. Anim. Behav. Cogn. 3 (3), 150–158. https://doi.org/10.12966/abc.04.08.2016.

Proctor, H., Carder, G., 2016. Can changes in nasal temperature be used as an indicator of emotional state in cows? Appl. Anim. Behav. Sci. 184, 1–6. https://doi.org/10.1016/J.APPLANIM.2016.07.013.

Puga-Gonzalez, I., Hoscheid, A., Hemelrijk, C.K., 2015. Friendships, reciprocation and interchange in an individual-based model. Behav. Ecol. Sociobiol. 69, 383–394.

Radford, A.N., Ridley, A.R., 2006. Recruitment calling: a novel form of extended parental care in an altricial species. Curr. Biol. 16, 1700–1704.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T., Dingemanse, N.J., 2007. Integrating animal temperament within ecology and evolution. Biol. Rev. 82, 291–318.

Reefmann, N., Bütikofer Kaszàs, F., Wechsler, B., Gygax, L., 2009. Physiological expression of emotional reactions in sheep. Physiol. Behav. 98 (1–2), 235–241. https://doi.org/10.1016/J.PHYSBEH.2009.05.017.

Reimers, L., Diekhof, E.K., 2015. Testosterone is associated with cooperation during intergroup competition by enhancing parochial altruism. Front. Neurosci. 9, 183. https://doi.org/10.3389/fnins.2015.00183.

Riedl, K., Jensen, K., Call, J., Tomasello, M., 2015. Restorative justice in children. Curr. Biol. 25 (13), 1731–1735. https://doi.org/10.1016/j.cub.2015.05.014.

Rilling, J.K., DeMarco, A.C., Hackett, P.D., Thompson, R., Ditzen, B., Patel, R., Pagnoni, G., 2012. Effects of intranasal oxytocin and vasopressin on cooperative behavior and associated brain activity in men. Psychoneuroendocrinology 37 (4), 447–461. https://doi.org/10.1016/J.PSYNEUEN.2011.07.013.

Roberts, P., Stewart, B.A., 2018. Defining the 'generalist specialist' niche for Pleistocene Homo sapiens. Nat. Hum. Behav. 2 (8), 542–550. https://doi.org/10.1038/s41562-018-0394-4.

Robins, R.W., Caspi, A., Moffitt, T.E., 2002. It's not just who you're with, it's who you are: personality and relationship experiences across multiple relationships. J. Pers. 70 (6), 925–964. https://doi.org/10.1111/1467-6494.05028.

Ross, H.S., Lollis, S.P., 1987. Communication within infant social games. Dev. Psychol. 23 (2), 241–248.

Ryan, A.M., Freeman, S.M., Murai, T., Lau, A.R., Palumbo, M.C., Hogrefe, C.E., Bales, K.L., Bauman, M.D., 2019. Non-invasive eye tracking methods for New World and Old World monkeys. Front. Behav. Neurosci. 13, 39.

Samuni, L., Preis, A., Deschner, T., Crockford, C., Wittig, R.M., 2018a. Reward of labor coordination and hunting success in wild chimpanzees. Commun. Biol. 1, 138.

Samuni, L., Preis, A., Deschner, T., Wittig, R.M., Crockford, C., 2019. Cortisol and oxytocin show independent activity during chimpanzee intergroup conflict. Psychoneuroendocrinology. https://doi.org/10.1016/j.psyneuen.2019.02.007.

Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R.M., Crockford, C., 2018b. Social bonds facilitate cooperative resource sharing in wild chimpanzees. Proc. R. Soc. B 285 (1888), 20181643. https://doi.org/10.1098/rspb.2018.1643.

Samuni, L., Preis, A., Mundry, R., Deschner, T., Crockford, C., Wittig, R.M., 2017. Oxytocin reactivity during intergroup conflict in wild chimpanzees. Proc. Natl. Acad. Sci. 114 (2), 268–273. https://doi.org/10.1073/pnas.1616812114.

Sánchez-Amaro, A., Duguid, S., Call, J., Tomasello, M., 2016. Chimpanzees coordinate in a snowdrift game. Anim. Behav. 116, 61–74. https://doi.org/10.1016/j.anbehav.2016.03.030.

Scharlemann, J., Eckel, C., Kacelnik, A., Wilson, R., 2001. The value of a smile: game theory with a human face. J. Econ. Psychol. 22 (5), 617–640.

Scheid, C., Noë, R., 2010. The performance of rooks in a cooperative task depends on their temperament. Anim. Cogn. 13 (3), 545–553. https://doi.org/10.1007/s10071-009-0305-1.

Schel, A.M., Machanda, Z., Townsend, S.W., Zuberbühler, K., Slocombe, K.E., 2013. Chimpanzee food-calls are directed at specific individuals. Anim. Behav. 86, 955–965.

Schino, G., Aureli, F., 2008. Grooming reciprocation among female primates: a meta-analysis. Biol. Lett. 4 (1), 9–11. https://doi.org/10.1098/rsbl.2007.0506.

Schino, G., 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. Behav. Ecol. 18 (1), 115–120. https://doi.org/10.1093/beheco/arl045.

Schino, G., Aureli, F., 2009. Chapter 2 reciprocal altruism in primates. Advances in the Study of Behavior Vol. 39. pp. 45–69. https://doi.org/10.1016/S0065-3454(09)39002-6.

Schino, G., di Sorrentino, E.P., Tiddi, B., 2007. Grooming and coalitions in Japanese macaques (Macaca fuscata): partner choice and the time frame reciprocation. J. Comp. Psychol. 121 (2), 181–188. https://doi.org/10.1037/0735-7036.121.2.181.

Schino, G., Massimei, R., Pinzaglia, M., Addessi, E., 2016. Grooming, social rank and 'optimism' in tufted capuchin monkeys: a study of judgement bias. Anim. Behav. 119, 11–16.

Schmelz, M., Duguid, S., Bohn, M., Völter, C.J., 2017. Cooperative problem solving in giant otters (Pteronura brasiliensis) and Asian small-clawed otters (Aonyx cinerea). Anim. Cogn. 20 (6), 1107–1114. https://doi.org/10.1007/s10071-017-1126-2.

Schroeder, K.B., Nettle, D., McElreath, R., 2015. Interactions between personality and institutions in cooperative behaviour in humans. Philos. Trans. Biol. Sci. 370 (1683), 20150011. https://doi.org/10.1098/rstb.2015.0011.

Schweinfurth, M.K., Taborsky, M., 2018a. Reciprocal trading of different commodities in Norway rats. Curr. Biol. 28 (4), 594–599. https://doi.org/10.1016/j.cub.2017.12.058. e3.

Schweinfurth, M.K., Taborsky, M., 2018b. Relatedness decreases and reciprocity increases cooperation in Norway rats. Proc. R. Soc. B 285 (1874), 20180035. https://doi.org/10.1098/rspb.2018.0035.

Schweinfurth, M.K., Taborsky, M., 2018c. Noway rats (*Rattus norvegicus*) communicate need, which elicits donations of food. J. Comp. Psychol. 132, 119–129.

Schwing, R., Jocteur, E., Wein, A., Noë, R., Massen, J.J.M., 2016. Kea cooperate better with sharing affiliates. Anim. Cogn. 19 (6), 1093–1102. https://doi.org/10.1007/s10071-016-1017-y.

Seed, A.M., Clayton, N.S., Emery, N.J., 2008. Cooperative problem solving in rooks (Corvus frugilegus). Proc. R. Soc. B: Biol. Sci. 275 (1641), 1421–1429. https://doi.org/10.1098/rspb.2008.0111.

Seip, E.C., Van Dijk, W.W., Rotteveel, M., 2014a. Anger motivates costly punishment of unfair behavior. Motiv. Emot. https://doi.org/10.1007/s11031-014-9395-4.

Seip, E.C., Van Dijk, W.W., Rotteveel, M., 2014b. Anger motivates costly punishment of unfair behavior. Motiv. Emot. 38 (4), 578–588. https://doi.org/10.1007/s11031-014-9395-4.

Shamay-Tsoory, S.G., Fischer, M., Dvash, J., Harari, H., Perach-Bloom, N., Levkovitz, Y., 2009. Intranasal administration of oxytocin increases envy and schadenfreude (gloating). Biol. Psychiatry 66 (9), 864–870.

Shamay-Tsoory, S.G., Abu-Akel, A., 2016. The social salience hypothesis of oxytocin. Biol. Psychiatry 79 (3), 194–202.

Shettleworth, S.J., 2012. Modularity, comparative cognition and human uniqueness.

Philos. Trans. R. Soc. Lond. B. Biol. Sci. 367, 2794–2802.

Sierro, J., Loretto, M.C., Szipl, G., Massen, J.J.M., Bugnyar, T., 2019. Food calling in ravens (Corvus corax) revisited: who is addressed? (in review). Ethology.

Silk, J.B., 2007. Empathy, sympathy, and prosocial preferences in primates. In: Dunbar, R.I.M., Barrett, L. (Eds.), The Oxford Handbook of Evolutionary Psychology. Oxford University Press., Oxford, Uk, pp. 115–126.

Silk, J.B., House, B.R., 2016. The evolution of altruistic social preferences in human groups. Philos. Trans. Biol. Sci. 371 (1687), 20150097. https://doi.org/10.1098/rstb.2015.0097.

Smith, M.F., Leverett, K.L., Wilson, B.J., Brosnan, S.F., 2019. Capuchin monkeys (*Cebus [Sapajus] apella*) play Nash equilibria, but their decisions are not influenced by oxytocin. Am. J. Primatol. 81, e22973.

Smith, M.F., Watzek, J., Brosnan, S.F., 2018. The importance of a truly comparative methodology for comparative psychology. Int. J. Comp. Psychol. 31 (0).

Soares, M.C., Bshary, R., Fusani, L., Goymann, W., Hau, M., Hirschenhauser, K., Oliveira, R.F., 2010. Hormonal mechanisms of cooperative behaviour. Philos. Trans. R. Soc. Lond. B Biol. Sci. 365 (1553), 2737–2750. https://doi.org/10.1098/rstb.2010.0151.

Soares, M.C., Cardoso, S.C., Grutter, A.S., Oliveira, R.F., Bshary, R., 2014. Cortisol mediates cleaner wrasse switch from cooperation to cheating and tactical deception. Horm. Behav. 66 (2), 346–350. https://doi.org/10.1016/j.yhbeh.2014.06.010.

Staes, N., Koski, S.E., Helsen, P., Fransen, E., Eens, M., Stevens, J.M.G., 2015. Chimpanzee sociability is associated with vasopressin (Avpr1a) but not oxytocin receptor gene (OXTR) variation. Horm. Behav. 75, 84–90. https://doi.org/10.1016/j.yhbeh.2015.08.006.

Stephens, D.W., McLinn, C.M., Stevens, J.R., 2002. Discounting and reciprocity in an iterated prisoner's dilemma. Science 298 (5601), 2216–2218. https://doi.org/10.1126/science.1078498.

Stevens, J.R., Hauser, M.D., 2004. Why be nice? Psychological constraints on the evolution of cooperation. Trends Cogn. Sci. 8 (2), 60–65. https://doi.org/10.1016/j.tics.2003.12.003.

Stocker, M., Loretto, M.-C., Sterck, E.H.M., Bugnyar, T., Massen, J.J.M., 2019. Cooperation with closely bonded individuals reduces cortisol levels in long-tailed macaques (in review). Proc. R. Soc. Lond. B.

Stouten, J., de Cremer, D., 2010. Seeing is believing": the effects of facial expressions of emotion and verbal communication in social dilemmas. J. Behav. Decis. Mak. 23 (3), 271–287.

Suchak, M., Eppley, T.M., Campbell, M.W., de Waal, F.B.M., 2014. Ape duos and trios: spontaneous cooperation with free partner choice in chimpanzees. PeerJ 2, e417. https://doi.org/10.7717/peerj.417.

Suchak, M., Eppley, T.M., Campbell, M.W., Feldman, R.A., Quarles, L.F., de Waal, F.B.M., 2016. How chimpanzees cooperate in a competitive world. Proc. Natl. Acad. Sci. 113 (36), 10215–10220. https://doi.org/10.1073/pnas.1611826113.

Suchak, M., Watzek, J., Quarles, L.F., de Waal, F.B.M., 2018. Novice chimpanzees cooperate successfully in the presence of experts, but may have limited understanding of the task. Anim. Cogn. 21 (1), 87–98. https://doi.org/10.1007/s10071-017-1142-2.

Taborsky, M., Frommen, J.G., Riehl, C., 2016a. Correlated pay-offs are key to cooperation. Philos. Trans. R. Soc. B: Biol. Sci. 371, 20150084.

Taborsky, M., Frommen, J.G., Riehl, C., 2016b. The evolution of cooperation based on direct fitness benefits. Philos. Trans. R. Soc. B: Biol. Sci. 371 (1687), 20150472. https://doi.org/10.1098/rstb.2015.0472.

Talbot, C.F., Price, S.A., Brosnan, S.F., 2015. Inequity responses in nonhuman animals. In: Sabbagh, C., Schmitt, M. (Eds.), Handbook of Social Justice Theory and Research. Springer, New York, NY, pp. 387–403.

Tassin de Montaigu, C., Durdevic, K., Brucks, D., Krasheninnikova, A., von Bayern, A., 2019. Blue-throated macaws (*Ara glaucogularis*) succeed in a cooperative task without coordinating their actions (in press). Ethology.

Tebbich, S., Taborsky, M., Winkler, H., 1996. Social manipulation causes cooperation in keas. Anim. Behav. 52 (1), 1–10. https://doi.org/10.1006/anbe.1996.0147.

Tennie, C., Jensen, K., Call, J., 2016. The nature of prosociality in chimpanzees. Nat. Commun. 7, 13915. https://doi.org/10.1038/ncomms13915.

Tinbergen, N., 1963. On aims and methods of ethology. Zeitschrift für Tierpsychologie 20, 410–433.

Travain, T., Colombo, E.S., Grandi, L.C., Heinzl, E., Pelosi, A., Prato Previde, E., Valsecchi, P., 2016. How good is this food? A study on dogs' emotional responses to a potentially pleasant event using infrared thermography. Physiol. Behav. 159, 80–87. https://doi.org/10.1016/J.PHYSBEH.2016.03.019.

Trivers, R.L., 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 46 (1), 35–57.

Troisi, A., 2002. Displacement activities as a behavioral measure of stress in nonhuman primates and human subjects. Stress. Int. J. Biol. Stress. 5 (1), 47e54.

Trumble, B.C., Jaeggi, A.V., Gurven, M., 2015. Evolving the neuroendocrine physiology of human and primate cooperation and collective action. Philos. Trans. R. Soc. Lond. B Biol. Sci. 370. https://doi.org/10.1098/rstb.2015.0014.

Vail, A.L., Manica, A., Bshary, R., 2013. Referential gestures in fish collaborative hunting. Nat. Commun. 4, 1765. https://doi.org/10.1038/ncomms2781.

Vail, A.L., Manica, A., Bshary, R., 2014. Fish choose appropriately when and with whom to collaborate. Curr. Biol. 24 (17), R791–R793. https://doi.org/10.1016/j.cub.2014.07.033.

Vaish, A., Carpenter, M., Tomasello, M., 2009. Sympathy through affective perspective taking and its relation to prosocial behavior in toddlers. Dev. Psychol. 45 (2), 534–543. https://doi.org/10.1037/a0014322.

Vale, G.L., Williams, L.E., Schapiro, S.J., Lambeth, S.P., Brosnan, S.F., 2019. Responses to economic games of cooperation and conflict in squirrel monkeys (Saimiri boliviensis). Anim. Behav. Cogn. 6 (1), 32–47. https://doi.org/10.26451/abc.06.01.03.2019.

van Hooff, J.A.R.A.M., 1971. Aspecten Van Het Sociale Gedrag En De Communicatie Bij Humane En Hogere Niet-humane Primate. PhD-thesis. Utrecht University.

van Hooff, J.A.R.A.M., 1976. The comparison of facial expression in man and higher primates. In: vo Cranach, M. (Ed.), Methods of Inference from Animal to Human Behaviour. Mouton, Den Haag, Aldine, Chicago, pp. 165–196.

van Hooff, J.A.R.A.M., Wensing, J.A.B., 1987. Dominance and its behavioral measures in a captive wolf pack. In: Frank, H. (Ed.), Perspectives in Vertebrate Science, Vol. 4. Man and Wolf: Advances, Issues, and Problems in Captive Wolf Research. Dr W Junk Publishers, Dordrecht, Netherlands, pp. 219–252.

Van Lange, P.A.M., Finkenauer, C., Popma, A., van Vugt, M., 2011. Electrodes as social glue: measuring heart rate promotes giving in the trust game. Int. J. Psychophysiol. 80 (3), 246–250. https://doi.org/10.1016/J.IJPSYCHO.2011.03.007.

van't Wout, M., Kahn, R.S., Sanfey, A.G., Aleman, A., 2006. Affective state and decision-making in the Ultimatum Game. Exp. Brain Res. 169 (4), 564–568. https://doi.org/10.1007/s00221-006-0346-5.

von Borell, E., Langbein, J., Després, G., Hansen, S., Leterrier, C., Marchant-Forde, J., et al., 2007. Heart rate variability as a measure of autonomic regulation of cardiac activity for assessing stress and welfare in farm animals — a review. Physiol. Behav. 92 (3), 293–316. https://doi.org/10.1016/J.PHYSBEH.2007.01.007.

Vygotsky, L.S., 1978. Mind in Society: the Development of Higher Psychological Processes. Harvard University Press, Cambridge, MA.

Waller, B.M., Cherry, L., 2012. Facilitating play through communication: significance of teeth exposure in the gorilla play face. Am. J. Primatol. 74, 157–164.

Waller, B., Julle-Daniere, E., Micheletta, J., 2019. Measuring the evolution of facial expression using multi-species FACS (this issue). Neurosci. Biobehav. Rev.

Warneken, F., Chen, F., Tomasello, M., 2006. Cooperative activities in young children and chimpanzees. Child Dev. 77 (3), 640–663. https://doi.org/10.1111/j.1467-8624.2006.00895.x.

Wascher, C.A.F., Bugnyar, T., 2013. Behavioral responses to inequity in reward distribution and working effort in crows and ravens. PLoS One 8 (2).

Werdenich, D., Huber, L., 2002. Social factors determine cooperation in marmosets. Anim. Behav. 64, 771–781. https://doi.org/10.1006/anbe.2002.2001.

West, S.A., El Mouden, C., Gardner, A., 2011a. Sixteen common misconceptions about the evolution of cooperation in humans. Evol. Hum. Behav. 32 (4), 231–262. https://doi.org/10.1016/j.evolhumbehav.2010.08.001.

West, S.A., Griffin, A.S., Gardner, A., 2007. Evolutionary explanations for cooperation. Curr. Biol. 17 (16), R661–R672. https://doi.org/10.1016/j.cub.2007.06.004.

West, S.A., El Mouden, C., Gardner, A., 2011b. 16 common misconceptions about the evolution of cooperation in humans. Evol. Hum. Behav. 32, 231–262.

Whitehouse, J., Micheletta, J., Kaminski, J., Waller, B.M., 2016. Macaques attend to scratching in others. Anim. Behav. 122, 169–175.

Wichman, H., 1970. Effects of isolation and communication on cooperation in a two-person game. J. Pers. Soc. Psychol. 16, 114–120.

Williams, L.A., 2019. Anthropomorphism in Comparative Affective Science: Advocating a Mindful Approach. Neurosci. Biobehav. Rev.

Wittig, R.M., Crockford, C., Deschner, T., Langergraber, K.E., Ziegler, T.E., Zuberbuhler, K., 2014. Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. Proc. R. Soc. B: Biol. Sci. 281 (1778), 20133096. https://doi.org/10.1098/rspb.2013.3096.

Wood, R.I., Kim, J.Y., Li, G.R., 2016. Cooperation in rats playing the iterated Prisoner's Dilemma game. Anim. Behav. 114, 27–35.

Youyou, W., Stillwell, D., Schwartz, H.A., Kosinski, M., 2017. Birds of a feather do flock together: behavior-based personality-assessment method reveals personality similarity among couples and friends. Psychol. Sci. 28 (3), 276–284. https://doi.org/10.1177/0956797616678187.

Zhang, H., Gross, J., De Dreu, C., Ma, Y., 2019. Oxytocin promotes coordinated out-group attack during intergroup conflict in humans. ELife 8, e40698. https://doi.org/10.7554/eLife.40698.

Ziegler, T.E., Crockford, C., 2017. Neuroendocrine control in social relationships in nonhuman primates: Field based evidence. Horm. Behav. 91, 107–121. https://doi.org/10.1016/j.yhbeh.2017.03.004.