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The neuroethology of friendship

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Friendship pervades the human social landscape. These bonds are so important that disrupting them leads to health problems, and difficulties forming or maintaining friendships attend neuropsychiatric disorders like autism and depression. Other animals also have friends, suggesting that friendship is not solely a human invention but is instead an evolved trait. A neuroethological approach applies behavioral, neurobiological, and molecular techniques to explain friendship with reference to its underlying mechanisms, development, evolutionary origins, and biological function. Recent studies implicate a shared suite of neural circuits and neuromodulatory pathways in the formation, maintenance, and manipulation of friendships across humans and other animals. Health consequences and reproductive advantages in mammals additionally suggest that friendship has adaptive benefits. We argue that understanding the neuroethology of friendship in humans and other animals brings us closer to knowing fully what it means to be human.

Keywords: friendship; cognition; ethology; social networks; evolution

Introduction

Friendship is a hallmark of human behavior. Friends may promote our financial success,[1] health,[2] and even survival.[3,4] Social exclusion and the loss of social partners result in feelings akin to physical pain,[5] and deficits in the ability or motivation to form and maintain friendly relationships are a symptom of pathologies like autism and depression.[6] Yet despite its importance, the formalized scientific study of friendship is relatively new. This may be because friendship has been deemed a human construct outside the realm of biology[7] or as merely an epiphenomenon of pair bonds and parental care.[8] However, the last two decades have seen major shifts in thinking, with fields as diverse as psychology, anthropology, neurobiology, and economics converging to study friendship from a scientific perspective. Work in nonhuman animals has perhaps done the most in relation to ushering in this new trend; ground-breaking results have linked social bonds with reproductive success in mammals[9,10] and have shown that common neural and physiological mechanisms underlie social interactions in humans and other animals.[11,12] These findings undermine the idea that we are unique in our ability to make friends and invite the hypothesis that friendship is a product of natural selection that serves an adaptive function in social animals.

Here we discuss in detail the findings of the most recent research on the neuroethology of friendship. We largely focus on humans and other primates because this is where most research has been concentrated to date, but include substantial nods to other animals. We organize these findings around Nikolaas Tinbergen's four questions in ethology.[13] This framework celebrates the 50th anniversary of Tinbergen's publication of "On the Aims and Methods of Ethology" and draws attention to the fact that there are few topics for which the union of ethology and cognitive neuroscience has been as informative. This framework allows us to integrate research that probes friendship's evolutionary roots (question: evolutionary history) with studies that examine its neural, molecular, and developmental bases (questions: causation, ontogeny), as well as

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its ultimate function (question: function). A review of friendship would not be complete without addressing the puzzle posed by the evolution of cooperation and we also examine this complex issue. Therefore we aim to highlight some of the most pressing questions that remain unanswered in this burgeoning and important field.

Defining friendship based on the quality and patterning of interactions

We must begin by defining what we mean by *friendship*, which we use interchangeably with the term *social bond* throughout. The former is more commonly used in studies on humans and the latter in studies of other animals, yet both refer to the same concept.[7,14,15] People may have an explicit sense of what it means to call someone a friend, but definitions of friendship are often vague and qualitative.[15,16] We follow Hinde[17] and propose that, like all relationships, friendship should be defined on the basis of the quality and patterning of interactions between individuals. Accordingly, we define friends as pairs of individuals that engage in bidirectional affiliative (nonaggressive, nonreproductive) interactions with such frequency and consistency so as to differentiate them from nonfriends. That is, compared to nonfriends, friends engage in affiliative interactions considerably more often and over greater periods of time.[18] Affiliation can include spending time together, conversing, vocalizing, grooming, huddling, cooperatively foraging, and sharing food, as well as forming alliances against others (Fig. 1). We specify that friendly interactions are nonreproductive so as to include sex that occurs in a nonreproductive context, as in bonobos,[19] although we acknowledge that reproductive and nonreproductive sex between heterosexual partners can be difficult to differentiate in practice. Interactions should also be consistent over time; males and females that interact when the female is sexually receptive but not otherwise are not friends. But sexual partners that consistently engage in affiliative interactions over time are friends (by this definition, married couples are often friends, which fits with folk wisdom that spouses should be best friends[20]).

Our definition of friendship is thus one that focuses on the phenotype. Although tempting, we believe it best to steer clear of definitions that assume the involvement of specific proximate mechanisms (e.g., reciprocity). Friendship can be based on different evolutionary strategies depending on the types of interactions involved or the identities of the social partners. Kin selection is an obvious potential explanation for affiliative interactions between relatives[7,15,21] but cannot explain interactions between nonrelatives. This does not mean we should exclude affiliative relationships between kin from being defined as friends. Indeed, as we shall discuss, determining the mechanism(s) upon which cooperation between friends operates is a major line of inquiry open to much debate. We also wish to avoid definitions based on emotional engagement (e.g., love, attachment)[16,22] since this is also a proximate, neurobiological mechanism that serves to promote, modify, and maintain social bonds and does not directly represent the evolved function of the bond itself.

We suspect some may disagree with our definition and we welcome this debate. Yet we suggest that disputes over definitions are somewhat moot. The scientific study of friendship is in its infancy, thus limiting this review to strict definitions would be unhelpful and we have not done so. In addition, research need not be focused explicitly on friendship (and thus reliant on a specific definition) in order to contribute to our understanding of it. Studies that improve our understanding of affiliative interactions in general, including the biological mechanisms upon which those interactions are based, are necessary components of the study of friendship.

The evolutionary history of friendship

The evolution of social groups

For friendships to form, individuals must first have access to others. In primates, the ancestral state is one of solitary living. In a landmark paper, Shultz *et al.*[23] modeled the trajectory of primate social systems and found that stable groups composed of multiple adult males and females arose from solitary life, with harems and pair-bonded groups arising afterward. Primates are unusual in their rarity of pair bonds, which are more common in other animals, particularly birds.[16,23,24] Differences in the trajectories toward social life across taxa hint at the fact that the selective pressures driving the formation of stable social groups have differed. Group living in primates is believed to have followed the shift from nocturnal to diurnal living as a means to defend against predators in a more visual world,[23,25] whereas other factors, such as cooperative hunting

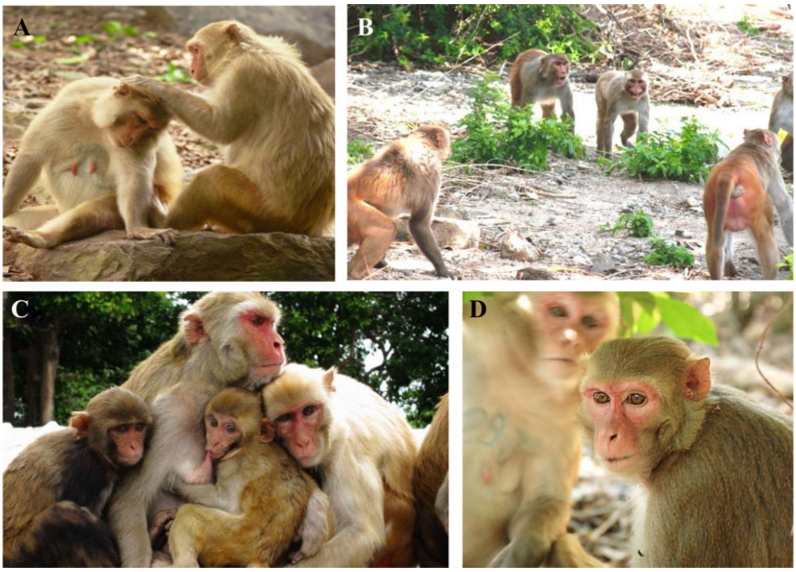

Figure 1. In highly social animals like rhesus macaques (*Macaca mulatta*), (A) friends groom each other and (B) provide each other with support in agonistic encounters against other group mates. (C) Affiliative behaviors positively predict reproductive output in this species, suggesting that social bonds are adaptive.[28] These bonds may function to mediate the costs of competition that arise from living in stable social groups. Friendship is underpinned by numerous neural and physiological mechanisms, and may require specific cognitive abilities, such as (D) gaze following, that allow individuals to successfully coordinate their actions with others and navigate a complex social world. Photo credits: Lauren J.N. Brent

(in carnivores) and cooperative breeding (in birds), are thought to be the selective pressures driving group living in other taxa.[16] Following the formation of stable social groups, regular interactions between conspecifics became possible. Affiliative tendencies have a heritable basis in humans,[26] marmots (*Marmota flaviventris*),[27] and rhesus macaques (*Macaca mulatta*)[28] (Fig. 2), confirming that sociality is under genetic control and is thus a trait upon which selection may act. The relationship between genes and social behavior is, of course, mediated by the nervous system. The social brain hypothesis posits that group living created selective pressures for larger and more complex brains.[29,30] The last decade has been replete with evidence that brain size scales with social complexity across species,[8,24,31] drawing ties between neural complexity and increased cognitive demands of social life.

Friendship in primates and other animals

In a recent review, Seyfarth and Cheney[14] describe the marked increase in the diversity of taxa in which friendships have been reported in the last decade. As we summarize in Table 1, social bonds exist in birds, ungulates, cetaceans, and primates. Many of these relationships are between closely related individuals. Mother–daughter pairs are the most common, followed by siblings.[14] Female giraffes (*Giraffa camelopardalis thornicroftii*) are more likely to associate with their mothers,[32] a pattern common in other herd-living mammals, including red deer (*Cervus elaphus*),[33] bison (*Bison bison*),[34] and elephants (*Loxodonta africana*).[35] In many primates, females remain in their natal groups, while males disperse. In these primates, kin-biased affiliative interactions, often measured using grooming and proximity, are common.[36] These include interactions between close maternal relatives (mother–daughters, maternal–siblings)[37–42] and, to a lesser extent, paternal relatives[38–41] (Fig. 2). Even when animals disperse from their natal groups, and are thus less likely to encounter close relatives in their lifetimes, relatives are more likely to form social bonds than nonrelatives (chimpanzees, *Pan troglodytes*,[43] but see Ref. 44; bonobos, *Pan paniscus*;[45] dolphins, *Tursiops sp.*[46]). Animals that are close in age are also frequent social partners. In many species, the highest ranking male(s) sires the majority of offspring in a given year, and individuals that are close in age are often paternal siblings.[47]

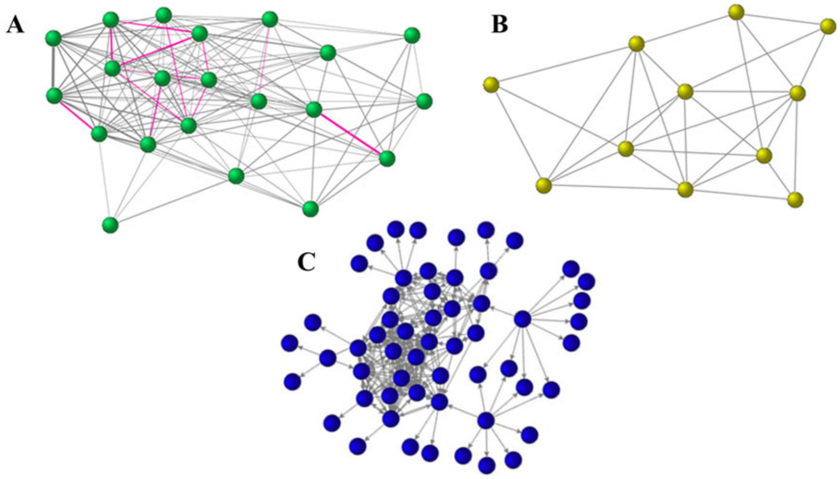

Figure 2. Social networks in three primate species. Networks are based on (A) spatial proximity in female rhesus macaques ($n = 21$), (B) coalitionary support in male chimpanzees ($n = 10$), and (C) named friendships in humans ($n = 57$). Nodes represent individuals; lines represent interactions between pairs of individuals. The thickness of the lines in A increase with the frequency of interaction. Arrows in C indicate whether named friendships were reciprocal. Individuals toward the center are more embedded in their social networks than those toward the periphery. Ties between closely related female rhesus macaques are highlighted in pink and demonstrate maternal kin bias (A). Social network position is heritable in humans[26] and rhesus macaques,[28] and has been associated with reproductive success in rhesus macaques[28] and chimpanzees.[167] Figure A was generated from the authors' unpublished data; Figures B and C were reproduced with permission from Refs. 167 and 26, respectively.

But friends are not always related. Horses (*Equus caballus*) live in groups composed of a single stallion and several unrelated females. Yet, pairs of unrelated females form differentiated affiliative relationships.[9] Unrelated spotted hyenas (*Crocuta crocuta*), and unrelated members of many primate species also form close and enduring bonds. People may be unique in the extent to which friends are unrelated.[21,48,49] This pattern could be driven by a lack of available kin, since nonkin make up the majority of hunter–gatherer groups.[50]

In summary, many animals form friendships with conspecifics. Social bonds are often between related individuals, but bonds between nonrelatives are not uncommon. Further research in a wider variety of taxa is required to determine whether friendship is a feature of all species that form stable social groups. Questions also remain about the impact of group composition. Apart from some exceptions, are individuals only friends with nonrelatives when kin are unavailable? To answer this question, we need comprehensive data on within-group relatedness across many taxa.

Causation: the cognitive, neural, and biochemical basis of friendship

To form friendships, animals must recognize the other members of their social group as unique individuals.[51] They must track those individuals through space and time in order to coordinate their actions,[16,52] and must make decisions about when to interact with others and what form those interactions should take. Social animals must also keep track of the quality of their relationships with others; that is, are they friends or foes?[17,51,53] Recognizing the quality of relationships between pairs of other individuals (i.e., friends of friends, friends of foes) may also be crucial to successful navigation of the social world.[53,54]

Of Tinbergen's four questions, the causation of social bonds, which encompasses their cognitive, neural, and biochemical bases, has perhaps received the greatest attention. From this research it has become apparent that the same or homologous mechanisms underlie social behaviors in a range of taxa,[11,12,55] which speaks to sociality's deep roots in our evolutionary history.

Table 1. Affiliative relationships in primates and other animals

Order	Common name	Species	Social structure	Dispersal	Affiliative relationships†	Kin biases	Interaction type(s)	Nonkin bonds	3rd party recognition	Fitness benefits	Refs.
Anseriformes	Greylag geese	*Anser anser*	MM–MF‡	F	F–F	Mat, Full Sib	proximity				179
Artiodactyla	Bison	*Bison bison*	MF	M	F–F	Mat	proximity				33
Artiodactyla	Red deer	*Cervus elphanus*	MM–MF	M	F–F	Mat	proximity				32
Artiodactyla	Giraffe	*Giraffa camelopardalis thornicroftii*	MF	M	F–F	Mat	proximity				31
Carnivores	Spotted hyena	*Crocuta crocuta*	MM–MF	M	M–M, F–F	Full Sib, Mat, Pat	grooming, proximity, cooperative hunting	Yes	Yes		180, 181, 182
Cetacea	Bottlenose dolphin	*Tursiops spp.*	MM–MF	M & F	M–M		mate-guarding alliances		Yes	Yes	45, 163
Cyprinodontiformes	Guppy	*Poecilia reticulata*	MM–MF	M & F	F–F	F	proximity, predator inspection				183
Passeriformes	Raven	*Corvus corax*	MM–MF‡	M & F	M–F, M–M, F–F	Yes	contact sitting, allopreening, play, pair displays, coalitionary support	Yes		Yes	69, 70, 93
Passeriformes	Rook	*Corvus frugilegus*	MM–MF‡	M & F	M–M, M–F, F–F		food sharing, agonistic support, allopreening, bill twinning, dual food caching	Yes	Yes	Yes	23
Perissodactyla	Donkey	*Equus asinus*	No data	no data	M–M, M–F, F–F		spatial proximity, nonsexual mounting	Yes			184
Perissodactyla	Horse	*Equus caballus*	UM–MF or MM–MF	M & F	F–F	No	grooming, proximity	Yes		Yes	9
Primates	Spider monkey	*Ateles belzebuth*	MM–MF	M	M–F		vocalizations				185
Primates	White-faced capuchin	*Cebus capuchinus*	MM–MF	M	F–F	Mat, Pat	grooming, proximity, coalitionary support		Yes		41, 86
Primates	Sooty mangabey	*Cercocebus torquatus*	MM–MF	M			coalitionary support		Yes		87
Primates	Blue monkey	*Cercopithecus mitis*	MM–MF	M	F–F	No	grooming	Yes			186
Primates	Vervet monkey	*Chlorocebus aethiops*	MM–MF	M	F–F		grooming, coalitionary support		Yes		90, 187
Primates	Crown lemur	*Eulemur coronatus*	MM–MF	M	M–F, M–M		grooming				188
Primates	Brown lemur	*Eulemur fulvus*	MM–MF	M	M–F	No	grooming				188
Primates	Human	*Homo sapiens*	MM–MF	M & F	M–M, M–F, F–F	Mat, Pat	grooming, food sharing, coalitionary support, spatial proximity	Yes	Yes	Yes	4, 49, 145
Primates	Ring-tailed lemur	*Lemur catta*	MM–MF	M	M–F	No?	grooming				188
Primates	Assamese macaque	*Macaca assamensis*	MM–MF	M	M–M, F–F		grooming, coalitionary support			Yes	160, 189
Primates	Japanese macaque	*Macaca fuscata*	MM–MF	M	F–F	Mat	grooming		Yes		36
Primates	Rhesus macaque	*Macaca mulatta*	MM–MF	M	F–F	Mat, Pat	grooming, proximity, coalitionary support			Yes	27, 37, 38, 141, 142, 190
Primates	Bonnet macaque	*Macaca radiata*	MM–MF	M	M–M		grooming, proximity, coalitionary support, huddle, greet		Yes		191, 192
Primates	Barbary macaque	*Macaca sylvanus*	MM–MF	M	M–M		grooming, proximity, coalitonary support, triadic interactions, body contact	Yes			193
Primates	Bonobo	*Pan paniscus*	MM–MF	F	M–F, M–M, F–F	Mat	grooming, proximity, coalitionary support	Yes			44
Primates	Chimpanzee	*Pan troglodytes*	MM–MF	F	M–M, M–F, F–F	Mat, not Pat	grooming, coalitionary support, others	Yes		Yes	42, 167, 194–196
Primates	Hamadryas baboon	*Papio hamadryas*	multi-level	M	M–F, F–F	Mat	grooming, proximity				197
Primates	Baboon	*Papio spp.*	MM–MF	M	F–F, M–F	Mat, Pat	grooming, proximity, coalitionary support, greet	Yes	Yes	Yes	10, 39, 40, 52, 67, 89, 155, 162
Primates	Gelada monkey	*Theropithecus geleda*	multi-level	M	F–F	Yes	grooming, proximity, vocalizations(?)				16, 169
Proboscidea	Elephant	*Loxodonta africana*	MF	M	F–F	Mat	proximity				34
Rodentia	Degu	*Octodon degus*	MM–MF	M & F	F–F		proximity			Yes	198

NOTE: Although we intend this table to be comprehensive, species for which social relationships have been documented but little studied may be absent. Additionally, we expect many species closely related to those represented also exhibit social relationships (e.g., other species of macaque), but to our knowledge no explicit study has been published for these species to date. † differentiated affiliative relationships documented to date, not necessarily adhering to a strict definition of social bonds but may simply indicate an interactional bias. MM = multi-male, MF = multi-female, UM = uni-male, ‡ = nonbreeding flocks, M = male, F = female, Mat = bonds biased toward maternal kin (e.g., mother–offspring pairs, maternal half-siblings), Pat = bonds biased toward paternal kin (e.g., father–offspring pairs, paternal half-siblings), Full Sib = bonds biased toward full siblings. Blank cells = no available data or unknown.

Recognizing others

In order to distinguish each other as unique individuals, animals must learn the unique recognition cues of others and use those cues to identify those individuals in the future.[51] Recognition cues can include olfactory, vocal, and visual cues, which can be integrated in a multimodal fashion.[11,51] Individual recognition has been documented in both vertebrates and invertebrates.[51] Hermit crabs (*Pagurus longicarpus*) and lobsters (*Homarus americanus*) recognize competitors, probably via scent.[56,57] Faces are important for individual recognition in sheep (*Ovis aries*),[58] paper wasps (*Polistes fuscatus*),[59] and primates, including rhesus macaques,[60] chimpanzees,[60] and humans.[61] Similar regions of the brain seem to be involved in face recognition in humans and macaques,[62] where highly modular and hierarchically organized neural networks in the inferior temporal cortex known as face patches process visual information about faces, but not other objects.[63,64] The presence of neural face patches in humans and monkeys strongly argues for the importance of individual recognition in the evolution of primate sociality.

Animals not only recognize their conspecifics, but they also remember them. Hooded warblers (*Wilsonia citrina*) remember their neighbors from the previous breeding season,[65] sheep differentiate former group mates after 2 years of separation,[58] and dolphins remember each other's signature whistles for up to 20 years.[66] Some animals even recall the quality of past interactions. Female vervet monkeys (*Chlorocebus aethiops*) and chacma baboons (*Papio hamadryas ursinus*) discriminate the alarm calls of group mates that recently groomed them compared to those that did not.[67,68] Ravens (*Corvus corax*) form differentiated affiliative relationships in nonbreeder flocks.[69] In an experiment with captive ravens, the birds responded differently to the playback calls of former flock members compared to unfamiliar individuals.[70] Fascinatingly, these corvids also differentiated among former group mates with whom they had an affiliative relationship compared to nonaffiliates, even in cases where social partners had been separated for as long as 3 years.[70]

Humans remember and also maintain friendships despite long periods of separation; young adults living long distances apart remain friends for 8 years or more.[71] People also tend to be over-inclusive when differentiating kin from nonkin. These false-positive kin-recognition errors (i.e., treating nonkin as kin) appear to be more prominent in women than men, the latter of which may suffer higher costs from forming alliances with nonrelatives.[21] Unrelated individuals may nonetheless be genetically similar and friends may be a kind of "functional kin."[49] This, as we will discuss, could have immense implications to our understanding of the evolution of cooperation between friends.

Obtaining social information and making social decisions

To select, acquire, and maintain friends requires information about others. But what motivates animals to obtain social information, and how do they do it? Many animals attribute reward value to social information. Both humans and other primates find social stimuli intrinsically rewarding, and certain types of social stimuli are more interesting and reinforcing than others.[72–75] For instance, human infants look longer at faces than at nonface stimuli,[76] while monkeys direct their gaze more often toward higher-ranking than lower-ranking animals.[77,78]

Consistent with these observations are findings that social information activates reward-related areas of the brain, including the anterior cingulate cortex (ACC), the orbitofrontal cortex (OFC), the nucleus accumbens, and the caudate nucleus.[79–82] While some of these areas respond to social and nonsocial rewards in a similar fashion, some areas appear to be partly specialized for social information processing. For instance, when rhesus macaques were asked to choose between juice rewards and information about others, a small proportion of neurons in the OFC responded to juice rewards, while another, greater (and nonoverlapping) proportion responded to social information.[82] This finding, along with the observed relationship between OFC size and social network size in humans[83] and group size across primates,[30] suggests that OFC is part of a specialized neural circuit involved in social behavior.

Outside the laboratory, animals are not conveniently presented with social information, but must go out and get it. Just like an animal foraging for food among sparsely distributed patches,[84] an animal searching for social information must weigh the benefits of obtaining such information against the costs, which include missed opportunities to eat, drink, or sleep.[12] In the wild, animals often interrupt their current activity to scan their surroundings. Whether this behavior requires the systematic tradeoff between one type of reinforcement and another is nearly impossible for researchers to discern without knowing precisely what the animal is looking at. Yet there is evidence from the laboratory that animals take this information into account; male rhesus macaques will forgo a small amount of juice reward in order to see a picture of another monkey. Crucially, the amount of juice they forgo depends on the type of social information on offer, with pictures of female perinea garnering the highest payments, and images of low-status males garnering negative payments (i.e., they must be paid juice to look at them).[72,82] This suggests that monkeys weigh the costs and benefits of their social decisions.

One type of social information that is likely to be of particular value is information about the relationships between others.[85] Evidence that animals have some understanding of these third-party relationships come from studies showing, for example, that rooks redirect aggression to the social partners of their aggressors,[23] and that many primates solicit help from individuals that are higher ranking than their aggressors.[86–88] In an experimental setting, baboons and vervets looked longer in the direction of playback speakers when played a sequence of calls that represented monkey A winning an agonistic encounter against monkey B in cases where A was subordinate to B, compared to cases where A was dominant to B.[89,90] That is, these monkeys seemed to recognize the dominance relationship between A and B and to be surprised when they heard calls that suggested it had been overturned.

In addition to recognizing the relationships between others, the ability and drive to understand the motives, intentions, and mental states of others (so-called theory of mind, or ToM) may help animals predict social challenges.[85] ToM, however, is assumed to be cognitively complex and may be an ability at which animals other than humans are not very skilled. Nevertheless, some nonhuman animals express some ToM-related abilities. For instance, the ability to understand the visual perspectives of others has been demonstrated in goats,[91] birds,[92,93] and primates[94] (Fig. 1). In one experiment, rhesus macaques showed a bias toward stealing food from experimenters whose backs were turned rather than from experimenters who could see that the food was being stolen.[95] Identifying where others are looking appears to be accomplished by neurons along the superior temporal sulcus (STS),[96,97] in the lateral intraparietal area,[98] and in the amygdala.[99] Unilateral inactivation of the STS impairs spontaneous gaze following in rhesus macaques, consistent with a role in identifying the locus of other animals' attention.[97]

Understanding the relationships and intentions of others requires the brain to keep track of information that is relative not only to oneself but also to others.[100] This process may be similar to the computations required to convert sensory information into a frame of reference appropriate for guiding movement.[80,101,102] Consistent with this idea, a recent study found remarkable specializations in the way neurons encoded reward outcomes while rhesus macaques chose to deliver juice rewards to themselves (the subject), to a recipient monkey, or to no one. OFC neurons predominantly signaled rewards received by the actor, anterior cingulate sulcus (ACCs) neurons predominantly signaled foregone rewards, and the majority of anterior cingulate gyrus (ACCg) neurons signaled rewards delivered to the recipient or mirrored rewards delivered to either the subject or the recipient.[80] Thus, ACCg neurons incorporate the experiences of others into their reward-related signals. These findings resonate with work showing that lesions in the ACCg lead to social deficits,[103] and that portions of the ACC are activated when people observe events happening to others or think about others' states of mind.[104,105] These observations also suggest that differences in the structure and function of the ACCg, along with other areas associated with awareness and empathy (e.g., the anterior insular cortex[106,107]), may underlie differences in socio-cognitive abilities between humans and other animals, as well as differences between individuals within a species.

Biochemical regulation of friendship

The hormonal and peptidergic mechanisms that modulate affiliative interactions in mammals have received extensive attention, the results of which have been summarized in a number of comprehensive reviews.[5,11,55,108,109] We aim not to cover this information in detail but instead to highlight the most current findings and recent debates regarding some of the major biochemical systems that regulate friendship, namely those involving oxytocin (OT), endorphins, dopamine, serotonin, and the hypothalamic–pituitary–adrenal (HPA) axis.

Social behavior is largely reinforcement driven. OT is a neuropeptide that stimulates lactation in mammals and is involved in bonding between mothers and infants, as well as between pair-bonded reproductive partners.[110,111] OT has also been associated with social relationships outside of pair and maternal bonds. For example, OT is involved in individual recognition and social memory.[112,113] Exogenous application of OT increases prosocial decisions and attention to others,[114] increases feelings of trust,[115] and encourages generosity.[116]

In addition to OT, the opioid β-endorphin is also involved in reward processes and has been associated with social behavior, especially in primates.[55,117] Some researchers have proposed that while OT facilitates social interaction, it is β-endorphin that is crucial to the formation and maintenance of social bonds.[55,109,118] The idea that OT facilitates social interaction, but not bonding, stems from the fact that the effects of OT are relatively short-lived[119,120] and that OT reduces social vigilance,[78] which may be a prerequisite for social interaction. Although not much is known about the relationship between endorphins and social interactions,[118] the results of one new study support the association between endorphins and social bonds; individuals release more endorphins when rowing a boat in a social context—a prime example of behavioral synchrony, which is a key component of friendship[51]—compared to when rowing alone, despite exerting the same amount of physical effort in both cases.[121]

Regardless of the role of endorphins, new findings contradict the idea that OT merely facilitates interactions and is not also involved in bonding itself. In one study, urinary OT levels in wild male chimpanzees were elevated following social grooming.[122] Crucially, increases in urinary OT were only observed in males that had groomed a chimpanzee with whom they already possessed a bond (bonded males were kin or unrelated). What mattered with reference to OT release, therefore, was not grooming in general, but grooming with a friend.[122] This observation resonates with other recent findings that the positive effects of exogenously administered OT on trust-related feelings or behaviors only occur when subjects interact with people they know or with members of their in-group.[123,124] Together, the results of these studies suggest that both OT and endorphins contribute to the formation and maintenance of social bonds.

Serotonin and dopamine are also ancient and potent neuromodulators. The contribution of dopamine to the formation of social memories and social preference as part of the ventral tegmental area–dopamine projection system has been well described.[109,125] Much of the work on serotonin, on the other hand, has been at the phenotypic level, exploring the association between serotonin and social behaviors. For instance, administration of selective serotonin reuptake inhibitors (SSRIs) alters the rate of affiliative and aggressive interactions.[126,127] Serotonin transporter binding in the midline cortex is associated with aggressive and friendly traits in rhesus macaques,[128] and genetic polymorphisms in the serotonergic pathway are associated with social integration.[28] The majority of research on the correlates of serotonin points to links between this neuromodulator and sensory inputs, including social stimuli.[129] This has led to the proposition that serotonin modulates how individuals perceive and respond to social information.[109,129] Nevertheless, the molecular processes underlying the association between serotonin and sociality are little understood and will require concerted future research efforts to disentangle.

The stress response, produced via activation of the HPA axis, warns animals that homeostasis has been disrupted and mobilizes energy to restore a homeostatic state.[130] In animals for whom social relationships are crucial to success and survival,[10,27] the stress response is part of the motivational system that underpins social interaction. Many animals, including humans, exhibit smaller increases in stress hormone (cortisol) levels during exposure to averse stimuli when a friend is present compared to when alone.[131] In primates, social grooming reduces heart rate,[132] and individuals with more tightly-knit social networks have lower baseline levels of cortisol metabolites in their feces.[133,134] For animals with tightly-knit and predictable social networks, low baseline cortisol levels may be a result of these individuals being able to cope effectively with social challenges. The acute reduction of heart rate in response to social grooming can be interpreted as a response to the fulfillment of a social need (negative feedback between endorphins, OT, and the HPA axis is also likely to play a part).

Chronic activation of the stress response has well-known negative consequences for health[135] and reproduction,[136] both of which may negatively affect evolutionary fitness. This has led to the suggestion that stress reduction is a selective pressure in the evolution of social bonds and is, therefore, one of the ultimate functions of social bonding.[7,9,14] However, it is important to remember that an association between the stress response and social behavior reflects the role of the stress response as a proximate mechanism underlying social interactions.[133] To propose that stress reduction is the ultimate reason individuals make friends is akin to suggesting that thirst is the ultimate reason we drink. Clarifying the type of biological mechanism the stress response represents (proximate, not ultimate) will positively influence how research linking the HPA axis to social behavior is interpreted and, as such, will improve our understanding of the evolution of friendship.

The ontogeny of friendship

Little is known from an empirical standpoint about how friendships are initially formed. Yet systematic biases in the identities of social partners may hold clues to the establishment of friendships. Many animals prefer to be friends with close kin.[36] Friends are also often characterized by homophily, the tendency to share similar characteristics,[48] including age,[39] and social status.[137] Biases toward individuals of similar status have been proposed to result from competition for partners of the highest quality.[137] Under this principle, high-ranking individuals prefer to be friends with each other to the exclusion of lower-ranking animals. This tendency results in everyone being friends with the highest ranking individual available to them—low-ranking individuals are friends with other low-ranking individuals and high-ranking individuals are friends with other high-ranking individuals.

Homophily between friends may also be a result of attraction to individuals of similar personalities or skills.[48] Humans are especially predisposed toward homophily,[138] with recent evidence suggesting this even extends to the genetic level; people are more likely to be friends if they have similar genotypes.[139,140] Taken together, these findings advocate the need to consider not only an individual's genome, but also their metagenome, when asking questions about the causes of friendship biases.[139]

There are also clear differences in the friendships formed by males and females in some species. In rhesus macaques, where males disperse from the group where they were born, while females remain, males spend significantly less time grooming and are less socially connected compared to females.[28,141] In chimpanzees, on the other hand, where females disperse instead of males, there is some evidence that females are comparatively aloof.[43] This patterning can be explained by attraction toward kin, as well as by maternal influence. Berman *et al.* have shown that young rhesus macaques tend to interact with the offspring of their mothers' friends.[141,142] That is, mothers seem to introduce their infants to potential social partners. Human children, too, inherit friends from their parents.[138] If parental introductions are an important step to becoming friends, it is unsurprising that individuals that disperse away from their mothers are less socially integrated.

Some human studies suggest that men have a larger number of friends than women but sacrifice quality for quantity since men tend to spend less time with each friend and rate their friendships as less important than do women.[6,143] Men also tend to treat friends to whom they are unrelated in a similar fashion to how they treat strangers, whereas women treat unrelated friends as though they were kin.[21] Differences have also been noted in the cognitive domain, where women are often better at empathizing and inferring the thoughts and intentions of others.[144] If humans follow the typical primate pattern of male dispersal, these findings make sense; dispersing men are relatively asocial compared to women. Yet, humans have been characterized by either female dispersal[145] or dispersal of both sexes.[50] Friendship, it seems, is about more than dispersal, and differences in friendship between men and women require another explanation. On the other hand, it might be that gender-based differences in human friendship have been exaggerated. Meta-analyses have revealed that men and women cultivate and define friends in very similar ways, and that sex is not a very strong predictor of how much personal information people share with their friends.[138] A comparative approach, whereby the causes and consequences of differences in friendship between the sexes in a range of species, cultures, and social systems are catalogued and explored, would address some of these issues.

While little is known about how friendships are initiated and solidified, research has begun to reveal the ontogenetic basis of socio-cognitive abilities. The ability to understand false beliefs, to cast moral judgments, and ToM are present in children as young as 4 years in some cases, but improve into adulthood.[146–149] On the other hand, similar levels of prosociality are expressed throughout childhood (3–8 years old),[150] suggesting human prosocial tendencies arise early in life. The development of socio-cognitive skills can be influenced by the environment. For instance, children that have had negative interactions with peers are less likely to perform well in ToM experimental tasks later in life.[151] Similarly, social isolation in monkeys results in abnormal behaviors in both social and nonsocial domains.[152] Autistic children that have an older sibling (i.e., that have consistent access to social partners) score higher in ToM tests than those without older siblings.[153] These findings are consistent with a recent study that demonstrated the impact of social environment on brain anatomy; monkeys experimentally introduced to larger social groups showed an increase in grey matter volume in two brain areas implicated in social cognition, the mid-superior temporal sulcus and the rostral prefrontal cortex.[154] Together, these studies demonstrate that socio-cognitive skills are present in early life but can be tuned by social interactions.

Getting by with a little help: the function of friendship

If social bonds serve a useful function and have been favored by selection, we expect them to be associated with increased survival and/or reproductive success, which are proxies of evolutionary fitness. In the first seminal paper to demonstrate such an association, Silk *et al.* showed female baboons that spend a greater amount of time grooming and associating with others have offspring that are more likely to survive to 1 year of age.[155] A similar association between affiliation and infant survival has since been found in both male and female rhesus macaques[27] (Fig. 2). This is also true outside the primate order; affiliative interactions are a significant predictor of the number of foals born to female horses,[9] and of lifetime reproductive success in marmots.[27]

In humans, research has focused on the ties between sociality and health.[156] Socially isolated people are at greater risk of cardiovascular disease,[157,158] infectious diseases,[6] and elevated blood pressure.[159] One recent meta-analysis found a 50% increased likelihood of survival for people with stronger social relationships, even after controlling for age, sex, health, and cause of death.[3] The link between affiliative tendencies and fitness seems to go beyond the mere frequency of social interactions to the formation of high-quality relationships. At least this is the case in female baboons, male Assamese macaques (*M. assamensis*), and dolphins, where individuals with the strongest, most enduring social bonds sire the most offspring[160] and have the highest offspring survival[161,162] and greatest longevity.[10] Together, these findings suggest that there are adaptive benefits to social bonds. But the question remains: What causes the association between friendship and fitness?

In female horses, social integration reduces harassment from males, which has direct reproductive costs.[9] Male dolphins help their alliance partners herd females away from their groups to mate.[163] Most primates live in relatively stable social groups, probably to reduce predation risk.[25] However, along with the benefits of group living come costs, including competition between group members for resources, such as food, space, and sex. One way to navigate a competitive world is to obtain tolerance and support from a subset of group mates. In other words, one way to cope is to make friends.

Some primates tolerate the presence at food sources of some group mates but not others, and provide those individuals with services they cannot obtain on their own, such as grooming.[164] Scholars' extensive interest in primate grooming has been fueled by the observation that many primates spend more time grooming than is likely to be necessary for hygienic purposes alone.[165] As a result, grooming has been proposed to function as a type of behavioral service, or relational currency, that can be exchanged for grooming itself, or for other services, such as coalitionary support.[68,137,164] Primate grooming partners are indeed more likely to support each other in fights.[166] The association between grooming and coalitionary support may explain the positive relationship between grooming and reproductive success.[14,155] Empirical evidence in support of this idea comes from a recent study of the social networks of wild male chimpanzees. Males that were more integrated in the coalition network were more likely to be higher ranking in the period of study that followed (a predictor of reproductive success in chimpanzees) and were also more likely to sire offspring[167] (Fig. 2). For male chimpanzees, at least, grooming may lead to coalitionary support, which may translate into reproductive success.

Questions still linger about whether friendship does in fact help individuals cope with competition. According to socio-ecological theory, within-group competition is relaxed in species with low-quality and abundant food sources.[168] Yet social bonds have been documented in ungulates and folivorous primates,[32,33,169] whose diets predict relaxed within-group competition. In addition to behavioral services, the ultimate benefit of friendship might come from what individuals learn from their friends (social learning[170]), or from the flow of behaviors, affective states, or attitudes between friends (social contagion[140]). Additional quantitative data on the connections between social learning, social contagion, and social bonds, as well as on the types of bonds found in species with relaxed intra-group competition, are necessary to begin to address these questions.

There are also questions about variation in social tendencies between individuals of the same species. Personalities differ between members of the same social group in seemingly every species studied to date, including differences in affiliative tendencies.[171] But how do we reconcile these differences with the idea that social bonds are adaptive? If friendship is the route to success, why isn't every individual hypersocial? What other behavioral strategies and selective pressures might explain what otherwise appears to be noise in the system? The study of personality in animals is relatively new and further research is required to begin to answer these questions. Finally, one of the most pervasive questions hanging over the heads of researchers attempting to understand the neuroethology of friendship concerns the evolution of cooperation.

You scratch my back, I'll scratch yours? Friendship and the puzzle of cooperation

If friendship is about helping one another, we need to ask how this helping behavior evolved. That is, in order to understand the patterning of interactions associated with friendship, we must understand how to frame those interactions in light of the evolution of cooperation. As cooperation is a seemingly selfless act, explaining its evolution is a classic problem. Biologists have struggled to answer how cooperation persists given the selfish nature of individuals and their genes. Kin selection and indirect fitness benefits can explain the exchange of services between close relatives.[172] Cooperation between nonrelatives is often explained by the reciprocal exchange of services.[173] Yet reciprocal investment has infrequently been demonstrated in naturalistic settings, leading some researchers to conclude that alternative explanations are required.[174,175]

Before we put reciprocity to the side, it is worth considering how the complexities of the problem might hamper our ability to uncover evidence of it. First, we must determine how best to frame cooperation between unrelated individuals in a natural setting. Let's take the example of grooming in primates. In a typical prisoner's dilemma game, strangers simultaneously exchange a discrete service on a one-shot basis, and cheating is clearly defined as failure to cooperate. In contrast, for grooming primates, unrelated groupmates of different social status that have past experience of each other exchange continuous (nondiscrete) goods many times over their lifetimes. These goods aren't necessarily the same (i.e., grooming might be exchanged for coalitionary support), making it difficult for researchers to know what constitutes a defective move.[174] Indeed, temporary imbalances are common in consistent social partners, suggesting that these imbalances do not constitute cheating, or are a level of cheating that is tolerated.[174] In addition, individuals often do not play simultaneously, but rather take turns in an alternating fashion where one individual grooms the other first. If primate grooming were expressed as a prisoner's dilemma game, it would therefore take the form of an iterated and continuous prisoner's dilemma with multiple players of varying degrees of social status that play in an alternating order. This is a complicated game to play with a difficult payoff matrix to solve. It may be no wonder that the cooperative mechanism underlying the exchange of grooming in primates has been hotly debated.

Positive reciprocity has been supported as an explanation underlying primate grooming in studies that have used experimental setups to demonstrate contingency, such that services rendered are dependent upon grooming received.[67,176] Unfortunately, contingent exchange is almost impossible to demonstrate using observational data alone, which may explain why most naturalistic studies have failed to do so. When alternative grooming partners are available, negative pseudoreciprocity, whereby contingency takes the form of sanctions and results in a subject switching to a new partner,[174] may also explain primate grooming. Future work should continue to explore the roles of these cooperative strategies despite previous (perhaps unsurprising) failings.

Another way to evaluate strategies underlying reciprocal exchange is to examine the cognitive machinery they require. Many have argued that calculated bookkeeping must be used to keep track of past interactions, and that this is beyond the abilities of most animals.[177,178] The typical response to this statement is that calculated bookkeeping is not the only solution to this problem. Animals may instead use something less cognitively demanding, termed *emotional bookkeeping*, whereby individuals base their interactions on their attitudes toward others.[164] Indeed, emotional bookkeeping resonates with evidence that social bonds are mediated by reinforcement and are associated with trust and relaxation (described in the section on the biochemical regulation of friendship).

Nevertheless, a recent study in humans may turn the discussion of exchange between nonrelatives on its head. Unrelated friends are more likely to be genetically similar, equivalent to the level of fourth cousins,[140] compared to unrelated strangers. Thus friends may gain indirect fitness benefits from each other, and cooperation between friends may be explained by (a green-beard form of) kin selection. Regardless of the mechanism, the study of the neuroethology of friendship is inexorably entwined with the study of the evolution of cooperation. Advances in both areas will considerably improve our understanding of the foundations of sociality.

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Conflicts of interest

The authors declare no conflicts of interest.

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