

CrossMark  
click for updates

## Review

**Cite this article:** Platt ML, Seyfarth RM, Cheney DL. 2016 Adaptations for social cognition in the primate brain. *Phil. Trans. R. Soc. B* **371**: 20150096. <http://dx.doi.org/10.1098/rstb.2015.0096>

Accepted: 11 September 2015

One contribution of 18 to a theme issue 'The evolution of cooperation based on direct fitness benefits'.

**Subject Areas:**

behaviour, cognition, neuroscience

**Keywords:**

cooperation, neuroethology, non-human primates, social cognition, fitness

**Author for correspondence:**Dorothy L. Cheney  
e-mail: [cheney@sas.upenn.edu](mailto:cheney@sas.upenn.edu)

## Adaptations for social cognition in the primate brain

Michael L. Platt<sup>1</sup>, Robert M. Seyfarth<sup>2</sup> and Dorothy L. Cheney<sup>3</sup><sup>1</sup>Departments of Neuroscience, Psychology, and Marketing, <sup>2</sup>Department of Psychology, and <sup>3</sup>Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA

Studies of the factors affecting reproductive success in group-living monkeys have traditionally focused on competitive traits, like the acquisition of high dominance rank. Recent research, however, indicates that the ability to form cooperative social bonds has an equally strong effect on fitness. Two implications follow. First, strong social bonds make individuals' fitness interdependent and the 'free-rider' problem disappears. Second, individuals must make adaptive choices that balance competition and cooperation—often with the same partners. The proximate mechanisms underlying these behaviours are only just beginning to be understood. Recent results from cognitive and systems neuroscience provide us some evidence that many social and non-social decisions are mediated ultimately by abstract, domain-general neural mechanisms. However, other populations of neurons in the orbitofrontal cortex, striatum, amygdala and parietal cortex specifically encode the type, importance and value of social information. Whether these specialized populations of neurons arise by selection or through developmental plasticity in response to the challenges of social life remains unknown. Many brain areas are homologous and show similar patterns of activity in human and non-human primates. In both groups, cortical activity is modulated by hormones like oxytocin and by the action of certain genes that may affect individual differences in behaviour. Taken together, results suggest that differences in cooperation between the two groups are a matter of degree rather than constituting a fundamental, qualitative distinction.

## 1. Introduction

When cooperating and competing with one other, animals must make rapid, adaptive decisions based not only on the current behaviour of their social partners and opponents, but also on memory of previous interactions with those individuals and those individuals' allies [1]. This behavioural plasticity, or social competence [2,3], enables animals to respond optimally to rapidly changing social environments and should be under strong selective pressure. Indeed, analyses of the mechanisms involved in social decisions have indicated that the neural networks regulating both social behaviour and the evaluation of stimuli and rewards are evolutionarily ancient and highly conserved across a wide variety of vertebrates [4]. Because the same neural networks regulate a wide variety of behaviours—including aggression, parental behaviour and social bonding—selection appears to operate not on particular traits, but on general behavioural motifs that can be fine-tuned to specific physical and social contexts [5].

In order to survive and reproduce, group-living animals must both compete and cooperate with others—often with the same individuals simultaneously. Past examinations of the factors contributing to reproductive success in group-living animals were largely focused on competitive traits, such as the acquisition of dominance rank. It has become increasingly clear, however, that the ability to form cooperative social bonds has as strong an effect on an individual's fitness as its competitive ability, if not stronger [6,7]. These findings indicate that natural selection has favoured individuals that are equipped with the cognitive architecture to navigate a social world in which they must make rapid decisions about when to compete and when to cooperate and when and whether to involve themselves in a given social interaction. We are only beginning to understand the precise

neural and hormonal mechanisms that mediate adaptive decision-making in animals, and the degree to which such abilities vary among individuals remains largely unexplored [2,6,8–12]. We also still have little understanding about the extent to which such variation is heritable. To help guide future research, in this review, we discuss the links between competition, cooperation and fitness in non-human primates and describe some recent studies that use novel techniques to examine the neural, hormonal and genetic bases of social functions important for the expression of cooperative behaviour. We focus, in particular, on studies of Old World monkeys, because these species have been studied the most extensively.

## 2. The adaptive value of social bonds

Females in many species of Old World monkeys, including baboons and macaques, remain in their natal social groups throughout their lives, where they form stable, differentiated relationships with particular other females [1,13,14]. Close social bonds are manifested through a variety of different behaviours, including grooming, the maintenance of proximity and coalitionary support. By many measures, therefore, these are cooperative relationships: grooming and other affiliative behaviours occur at high rates, reproductive skew is typically low and all females are able to breed.

Nonetheless, the same individuals are also competitors: females form stable, linear matrilineal dominance hierarchies in which high-ranking individuals enjoy priority of access to food, mates and in some species, paternal care [15–17]. Female dominance rank appears to depend in large part on the presence of allies, who are usually close kin, and females without such allies typically fall in rank to larger matrilines [18–20].

Because the presence of allies often appears to be essential for establishing and maintaining dominance rank, it was long thought that cooperative social bonds functioned primarily to enhance individuals' competitive abilities, which, in turn, improved fitness [21]. In recent years, however, it has become evident that cooperation itself, even in the absence of any competitive advantages it may confer, may also enhance fitness. In two long-term studies of baboons (*Papio* spp.), for example, dominance rank was not the best predictor of two measures of female reproductive success: offspring survival and longevity. Instead, females with the highest fitness were those with the strongest and most persistent bonds with other females [22–25]. Similar correlations between cooperative social bonds and components of fitness have been observed in a variety of other social mammals, including in particular humans [6].

Most recent research on the adaptive value of social bonds has focused on group-living females, where rank-related reproductive skew is low. Less attention has been paid to correlates of cooperation and fitness among primate males, for whom reproductive success is often more strongly correlated with dominance rank, which in turn is related to condition and fighting ability [26]. In recent years, however, it has become evident that the presence of allies can, in some instances, also influence the dominance ranks, tenure and reproductive success of primate males (Assamese macaques, *Macaca assamensis* [27]; Barbary macaques, *Macaca sylvana* [28]; geladas, *Theropithecus gelada* [29]). This observation also holds true for chimpanzees (*Pan troglodytes* [30,31]), whose male-bonded, fission–fusion society is very different from that of most Old World monkeys. Thus,

mechanisms that favour cooperation should be evident in males as well as females.

In addition to alliance support, a number of other factors may contribute to the relationship between social bonds and fitness. For example, female baboons with stronger and more stable bonds may be less spatially peripheral in sleeping trees and while feeding, and they and their offspring may be less vulnerable to predators. Strong, enduring social bonds may also alleviate stress. Female baboons appear to rely on their social bonds as a coping mechanism when a potentially infanticidal male immigrates into their group. During such events, females' grooming networks become less diverse, and females whose grooming had already focused on a few predictable partners show a less dramatic rise in levels of faecal glucocorticoids (fGCs), a hormone metabolite associated with stress [32]. Similarly, lactating females who establish 'friendships' with a resident adult male exhibit a smaller increase in glucocorticoid levels when compared with females who do not form such friendships [19,33]. Comparable correlations between fGC levels and focused female–female bonds have been observed in rhesus macaques (*Macaca mulatta*) [34] and Assamese macaques [35].

Female baboons also experience elevated fGC levels following the death of a close relative. Individuals who increase their number of grooming partners in subsequent months experience a more rapid decrease in fGC levels than females that fail to do so, perhaps because increased grooming allows 'bereaved' females to repair the damage to their grooming network [36]. The link between stress and social attachment may occur, in part, because stress prompts the release of the peptide oxytocin (OT), a hormone that motivates attachment, trust and pair-bonding behaviour (see below) [37–39] and suppresses social wariness [40].

The advantages of a close social network may also extend to females' offspring. Data from a variety of species have indicated that maternal exposure to environmental and social stressors can have detrimental impacts on their offspring's health and behaviour [41–47].

From a functional perspective, then, cooperation—even independent of any benefit associated with enhanced competitive ability—is linked to fitness and health, especially for females. Given this relation, the dilemma posed by free-riding—which has vexed so many theoretical debates about the evolution of cooperation—may largely disappear. Because free-riding occurs within the constraints of a system that favours cooperation, an individual can 'cheat' only so much before its partner defects to a more cooperative partner. Individuals rely on each other to form close social bonds, and the fitness of partners therefore becomes interdependent [48]. Indeed, among non-human primates, the affiliative interactions of individuals who share a close social bond tend to become highly reciprocal over time (female baboons [14]; male chimpanzees [49,50]). Such reciprocity is evident even among kin, where the opportunity for indirect as well as direct benefits should be expected to result in high skew.

## 3. Mechanisms mediating the evaluation of social partners' value and status

If natural selection has favoured individuals who are successfully able both to compete and to cooperate with others, then it should also promote the cognitive architecture to support

these abilities. Non-human primates—indeed, many social animals—are skilled voyeurs of other individuals' behaviour. They not only recognize other individuals' relative dominance ranks and social relationships, but also the nature and quality of recent interactions, the value of particular partners and perhaps even other individuals' intentions [1,51]. Moreover, many of their social interactions are contingency-based, and vary with the nature and quality of recent social interactions.

Monkey groups are noisy, tumultuous societies and an individual could not manage her social interactions if she interpreted every vocalization and behavioural gesture she heard or observed as directed at her. Inferences about the directedness of vocalizations are probably often mediated by gaze direction and relatively simple contingencies. Even in the absence of visual signals, however, monkeys are able to make inferences about the intended recipient of a call based on their knowledge of a signaller's identity and the nature of recent interactions. For example, in playback experiments in which female baboons were played the 'reconciliatory' grunt of their aggressor within minutes after being threatened, they behaved as if they assumed the call was directed at themselves, as a signal of benign intent. As a result, they were more likely to approach their former opponent and to tolerate their opponent's approaches than after hearing either no grunt or the grunt of another dominant female unrelated to their opponent [52]. Call type was also important, because subjects avoided their recent opponent if they heard her threat-grunt rather than her reconciliatory grunt [53]. By contrast, if subjects heard a female's threat-grunt shortly after grooming with her, they ignored the call and acted as if they assumed that the female was threatening another individual. Thus, baboons use their memory of recent interactions to make inferences about the caller's intention to communicate with them. Experiments on free-ranging chimpanzees similarly suggest that individuals rely on memory of the nature and quality of recent interactions when deciding whether or not to respond to a group-mate's calls [54].

The neural mechanisms underlying the complex decisions that monkeys and other animals must make when managing their interactions remain largely unexplored. Considerably more progress has been made, however, in studies that focus on simpler forms of social behaviour, including social attention, which mediates the initial acquisition and prioritization of information about the identity, status and attentive states of others, and social motivation, which drives individuals to interact with others. The fundamental importance of these basic social functions for individuals to survive and thrive is made plain in human disorders, such as autism, schizophrenia and social anxiety, in which these mechanisms are disrupted.

In order to make adaptive decisions about how to respond to others, animals must be motivated to attend to social stimuli. In fact, both humans and non-human primates find social stimuli intrinsically rewarding, and some social stimuli are more interesting and valuable than others. Captive male rhesus macaques, for example, will give up juice rewards in order to view the faces of dominant males or female hindquarters, but have to be paid extra juice to view images of the faces of females and subordinate males [55,56]. Subsequent work has shown that female rhesus macaques value the same classes of social information, particularly male signals related to testosterone [57]. These

findings endorse the idea that the primate brain prioritizes the acquisition and evaluation of social information, including the reproductive quality of potential mates and the status of potential social partners.

Recent evidence from cognitive and systems neuroscience strongly suggests that specific neural circuits mediate perceptual and cognitive functions necessary for strategic social behaviour. For example, using structural magnetic resonance imaging (MRI), Bickart *et al.* [58] showed that the size of the amygdala—a brain nucleus important for emotion, vigilance and rapid behavioural responses—is correlated with social network size in humans. Subsequent studies showed similar relationships for other brain regions implicated in social function, including the orbitofrontal cortex (OFC) [59] and ventromedial prefrontal cortex (vmPFC) [60]. One study even found an association between grey matter density in the superior temporal sulcus (STS) and temporal gyrus and an individual's number of Facebook friends [61].

Collectively, these studies suggest that the number, and possibly the complexity, of relationships one maintains varies with the structural organization of a specific network of brain regions that are recruited when humans and non-human primates perform tests of social cognition such as recognizing faces or inferring others' mental states [62,63]. Such results, however, do not reveal whether social complexity actively changes these brain areas through plasticity, or whether individual differences in the structure of these networks ultimately determine social abilities.

To address this question, Sallet *et al.* [8] experimentally assigned male rhesus macaques to social groups of different sizes and later scanned their brains with MRI. There were significant positive associations between social network size and grey matter thickness in mid-STS, rostral STS, inferior temporal (IT) gyrus, rostral prefrontal cortex (rPFC), temporal pole and amygdala. There was also a region in rPFC in which grey matter thickness scaled positively with social rank; as grey matter in this region increased, so did the monkey's rank in the hierarchy. As in the human studies described previously, many of these regions have been implicated in various aspects of social cognition and perception [64]. These findings support the ideas that homologous neural mechanisms underlie social cognition in human and non-human primates, and that neural plasticity in specifically social brain areas actively responds to the demands of the social environment.

Probing beyond structural variation, Sallet *et al.* [8] also examined spontaneous coactivation among these regions using functional MRI (fMRI). Measures of coactivation are thought to reflect coupling and potential interaction of information flow between regions. Coactivation between STS and rPFC increased with social network size, whereas coactivation between IT and rPFC increased with social rank. These findings show not only that structural changes occur in these regions to meet the demands of the social environment, but also that these structural changes are associated with changes in function.

Although variation in the structure and intrinsic connectivity of these and other brain areas provide a substrate for social information processing, these findings tell us little about the underlying neural code for social information. Early studies in the 1970s identified neurons in the temporal lobe of macaques that responded specifically to faces [65,66], and subsequent brain imaging studies showed that portions

of the temporal lobe and fusiform gyrus also respond in humans viewing faces [67,68]. More recently, Tsao *et al.* [69] used a combination of fMRI and direct electrophysiological recordings in macaques to demonstrate that hemodynamic activation of these brain areas indexes the spiking of local patches of neurons that respond uniquely to faces. Disruption of signalling by these neurons, as occurs in disorders like congenital prosopagnosia or following lesions, severely impairs social identification and recognition behaviour [70–72]. Collectively, these studies suggest that initial identification and recognition of the immediate social context are mediated by highly specialized neurons that may be dedicated to this purpose.

New functional imaging and neuronal recording studies have begun to reveal how subsequent social motivation and attention are encoded in the primate brain. For example, Smith *et al.* ([73]; see also [74]) demonstrated that humans viewing pictures of attractive and unattractive faces activated regions of the ventral striatum, vmPFC and OFC—brain areas typically associated with reward and decision-making—that were also involved in processing monetary gains and losses. This finding endorses the idea that social and non-social decisions are mediated ultimately by an abstract, domain-general mechanism [75]. Two follow-up studies using direct electrical recordings from neurons in male rhesus macaques found that some neurons in these same brain areas respond strongly when monkeys select either a preferred social image (e.g. female perineum, high status male face) or a large juice reward, but respond less when the same monkeys choose unrewarded social images (e.g. low status faces) or small juice rewards [76–78], consistent with an abstract code for value.

Nevertheless, the same studies also identified populations of neurons in OFC and striatum that encoded the type and importance of social information, in addition to its value [77,78]. Even more notably, neurons signalling social information were distinct from those signalling gustatory information. These findings suggest that parallel-processing streams devoted to gustatory and social information may have arisen by duplicating a primitive neural network that originally evolved to support foraging for food and water and repurposing it to processing social information [79]. Duplication and specialization of such a network for the purpose of social information processing seems likely to have emerged within the primate lineage in concert with the evolution of large, complex, dynamic social groups and the demands they impose on the acquisition and evaluation of social information [79–81].

By contrast, neurons in brain areas that mediate attention and visual orienting behaviour, such as the parietal cortex, signal the abstract value of a particular location or object, derived from both its social and non-social value to the animal [76]. Convergence of social and non-social value signals in these neurons indicates that target selection and oculomotor planning represent a final common pathway in which information initially processed in segregated channels must be integrated to support the coherent guidance of behaviour [5]. These findings resonate with embodied cognition models that situate information processing and decision-making in circuits that control action and behaviour [82–84].

As noted above, social hierarchy is a predominant feature of behaviour in most primate societies, and thus social rank appears to be a key factor shaping attention and motivation [55,85], as well as more complex behaviours like grooming and alliance formation [1,13,21]. Despite the importance of

social rank, however, there remain gaps in our understanding of how neural circuits mediate status-related behaviours. Although regions in the amygdala, brainstem and hypothalamus vary structurally and functionally with social rank, it remains unknown precisely how they contribute to or respond to social status. For example, though amygdala function and structure correlate with social status in both humans and non-human primates [12,86,87], it remains unknown which aspects of dominance this set of nuclei contributes to or underlies. One model suggests that the amygdala contributes to learning or representing one's own status within a social hierarchy [87,88]. Alternatively, the amygdala could contribute to behaviours that support social hierarchy, including gaze-following [88] and theory of mind (ToM) [89] (see below). The amygdala could also contribute to social rank via interpersonal behaviours or personality traits, such as aggression [90], grooming [90] or fear responses [91,92]. Finally, scaling of the activity of neurons in parietal cortex, and possibly other areas, by the rank of other individuals in the visible scene [76] likely mediates the selective allocation of attention to dominant individuals over subordinates in many primate groups [1,13,93].

Together, these studies, and others like them, suggest the following back-of-the-envelope framework for the organization of basic social processes in the primate brain. Specifically, patches of neurons in the temporal lobe (in non-human primates) and fusiform gyrus (in humans) mediate the initial decoding of the current social environment. Next, processing by specialized neurons in OFC, vmPFC and striatum computes the nature, importance and value of social agents for guiding subsequent behaviour. Neurons in amygdala and brainstem areas may contribute to processing the relative ranks of self and others in order to regulate attention, as well as approach and retreat. Finally, neurons in parietal cortex, and possibly other areas involved in attention, signal the abstract value or importance of objects and individuals in the local environment, in order to shape the adaptive allocation of attention to others. Notably, current evidence suggests that social and non-social information remains segregated from perception through evaluation and may only be integrated during the process of making decisions and planning action ([75]; but see [94]). These circuits provide the foundation upon which more complex social behaviours, like cooperation and alliance formation, are developed and elaborated.

#### 4. Cognitive and neural boundaries of cooperation

Despite the complexity of their social behaviour, non-human primates fail to achieve the high levels of prosociality so evident in human interactions. These failures have been attributed to both cognitive and emotional constraints [51]. Because non-human primates appear to lack the ability to attribute to others mental states that are different from their own, they may be unable to empathize with others, to recognize the need for help in the absence of a request, and to recognize attempts by others to cheat or free-load [51,95–98].

Nonetheless, this distinction between human and non-human primates is not as clear-cut as it might seem. Although non-human primates obviously do not possess adult humans' full-blown, reflective ToM, they do share with humans many of ToM's more fundamental attributes, including sensitivity to



gaze, intentions and emotional empathy [11]. For instance, non-human primates are acutely sensitive to others' gaze and attention. Gaze-following—orienting attention in the same direction as another individual—is a component of joint attention and may be foundational for ToM. Recent fMRI studies and lesion studies in humans implicate the temporoparietal junction (TPJ) in gaze perception and ToM [99]. One neuroimaging study suggested human TPJ may be homologous with the posterior STS in monkeys, based on patterns of resting-state connectivity measured using fMRI. Identifying where others are looking appears to be accomplished by neurons along the STS [100] and in the amygdala [101] that respond to the sight of another individual looking in a particular direction. Inactivation of neurons in the STS using a drug to block neuronal spiking impairs gaze-following in rhesus macaques, consistent with a role in identifying the locus of other animals' attention [102]. Shifting attention in response to the direction in which another individual is looking appears to be mediated by 'mirror' neurons in the lateral intraparietal area (LIP) that respond both when monkeys look in a particular direction and when they observe another monkey look in the same direction [103], another example of embodied cognition. Together, these findings suggest that a circuit connecting STS, amygdala and LIP subserves rapid, reflexive gaze-following in non-human primates. Moreover, this circuit appears to have become further elaborated during human evolution to support joint attention and ToM [104].

Gaze-following and joint attention appear to be critical for the coordinated behaviour required by both cooperation and competition, but social interactions also require that the brain keep track of information regarding the experiences and expectations of others. Human brain imaging studies have identified a number of areas that respond when people make decisions with regard to others, including OFC, dorsal anterior cingulate cortex (ACCs), anterior cingulate gyrus (ACCg), ventral striatum, dorsolateral prefrontal cortex and TPJ. TPJ and ACCg in particular appear to contribute uniquely to social decisions and may mediate complex social functions like empathy and ToM.

A recent study assessed how social information is encoded by neurons in OFC, ACCs and ACCg in male rhesus macaques that were making simple decisions to reward or withhold a reward from another monkey [80]. In this task, subjects were given the choice between either withholding or providing juice to another monkey in the absence of any reward to themselves. Subjects were significantly more likely to choose the reward than the withhold option, and this prosocial tendency was enhanced by familiarity [105]. By contrast, subjects were selfish when choosing between rewarding themselves alone or rewarding both themselves and another monkey. Thus, the monkeys' responses were both competitive and cooperative, and their decisions exhibited considerable flexibility.

Neurophysiological recordings found that OFC neurons responded when monkeys chose to reward themselves. By contrast, ACCs neurons responded whenever monkeys chose to give up rewards. Most importantly for cooperation, ACCg neurons selectively encoded the rewarding experiences of the recipient monkey, either responding only when monkeys chose to reward the recipient or responding equivalently to giving and receiving reward. Increased frequency of prosocial decisions was associated with enhanced signal-to-noise in the responses of ACCg neurons, suggesting that signal fidelity or integrity in this area contributes to variation in prosocial behaviour.

These data confirm the critical role of ACCg for complex social functions, including social reward and empathy-like processes, and resonate with prior work showing activation of ACCg and medial PFC in humans associated with empathy and ToM. Such observations suggest that ACCg is a key nexus for computing shared experience and may be specialized to support complex social decisions, such as whether or not to cooperate, in primates. Results also suggest that differences in the structure and function of ACCg, along with other areas associated with awareness and empathy (e.g. anterior insular cortex [106,107]), may underlie differences in cooperative abilities between humans and other primates, as well as differences between individuals within a species.

## 5. Neuromodulatory sources of variation in cooperative potential

There is strong evidence that variation in cooperative tendencies, both between species and individuals within species, arises through the interaction of genetic influences on the development of neural circuits and experience-dependent plasticity during development and even into adulthood. One relatively basic source of variation in cooperative potential is via neuromodulatory effects on neural circuits mediating social bonding [40,108]. For example, OT plays a crucial role in mammalian social behaviour. OT is necessary for mother–infant and pair-bonding in many mammals [109,110]. Joint attention, joint action and physical contact activate areas of the brain associated with the processing of reward, and these behaviours are facilitated by the release of OT. Importantly, what seems to be rewarding to animals is not physical contact *per se* but the specific identity of the social partner. For example, in socially monogamous tamarins (*Saguinus oedipus*), strongly bonded pairs exhibit higher OT levels than more weakly bonded pairs [111]. Among wild chimpanzees, urinary concentrations of OT are higher after individuals groom with a closely bonded partner (both kin and non-kin) than with a less closely bonded partner [112]. Evidently, grooming with a close friend or relative is more emotionally rewarding than engaging in the same behaviour with a less preferred partner. Chimpanzees also exhibit elevated OT levels after sharing food [113].

In healthy humans, inhaling OT, which translocates the peptide into the brain, increases trust and prosocial behaviour [114,115]. Children with autism spectrum disorder (ASD), which is associated with disruptions in social behaviour and communication, show significantly lower plasma OT compared with typically developing children [116], and a mutation in the OT receptor gene has been linked to ASD [117,118]. OT inhalation improves social skills and reduces stereotypy in people with ASD [119].

Inhalation of OT also influences social attention and prosocial behaviour in rhesus macaques. In one study, inhaling OT increased attention to faces and eyes during free viewing, as in humans [40]. By contrast, it reduced species-typical vigilance for unfamiliar, dominant and emotional faces in two additional tasks. Relaxed vigilance induced by OT inhalation also promotes attention to others in live, dyadic interactions [120]. These findings suggest that OT promotes attention to others, in part, by relaxing vigilance and possibly by enhancing social reward. Endorsing this hypothesis, inhaling OT significantly increased the frequency of prosocial decisions made by rhesus macaques when choosing whether or not

to reward another monkey [120], a result that is consistent with an increase in empathy or vicarious social reward. Importantly, the effects of exogenous OT on social behaviour depend on context. For example, inhaling OT enhances pro-social behaviour towards in-group individuals, but increases selfish behaviour towards out-group individuals [121]. Together, these findings strongly implicate OT in the regulation of social behaviour and cognition by both social context and internal state.

Precisely how OT regulates the structure and function of neural circuits mediating social behaviour remains only partially understood. Endogenous OT levels vary both across species [122,123] and across individuals within a species [124], thus potentially contributing to species' and individuals' differences in social behaviour [125]. Variation in the distribution and abundance of OT receptors also appears to contribute to OT regulation of social behaviour [126]. For example, pair-bonding in the monogamous prairie vole (*Microtus ochrogaster*) is mediated, in part, by activation of OT receptors localized to circuits associated with reward. Lack of OT receptors in these classic reward circuits may underlie lack of pair-bond formation in polygynous meadow voles (*Microtus pennsylvanicus*) and montane voles (*Microtus montanus*) [122]. Recent studies have demonstrated that OT receptors in both monogamous titi monkeys (*Callicebus cupreus*) and rhesus macaques [127,128] appear to be limited to areas of the hypothalamus and brainstem implicated in arousal and visual orienting behaviour. Notably, vasopressin receptors are much more widespread in cortex and basal ganglia, and OT may bind to these receptors when released at higher volumes or delivered exogenously.

Once OT binds to a receptor, it may influence neuronal signalling in a variety of ways that may ultimately impact social behaviour. For example, OT applied to hippocampus in rats enhances signal-to-noise ratio of neurons by increasing spike probability while simultaneously decreasing spontaneous background activity [129], potentially providing a foundation for enhanced learning and memory. OT receptor binding leads to a cascade of intracellular events via G proteins, with downstream effects on neuronal activity that can vary across regions depending on receptor subtype or cell-specific receptor coupling mechanisms [130]. OT signalling is also influenced by other signalling molecules. In prairie voles, for example, OT receptors in the ventral striatum must be coactivated with dopamine D2 receptors in the same area in order for pair-bonding to occur [131]. In rats, OT receptor expression is modulated by female sex hormones, as is the localization of OT receptors to dendrites or axons [130].

Thus, OT may exert complex effects on social behaviour via activation of both OT and vasopressin receptors localized in different neural circuits, depending on current context, internal state, and genetic factors that shape OT release and the expression of both OT and vasopressin receptors [130].

## 6. Biological and behavioural variation in the quality of social interactions

To date, studies of animal cognition have tended to focus on population norms: whether the members of a given species exhibit a particular trait or manifest a particular neural response. To demonstrate that a trait is linked to fitness, however, it is essential to show that variation in the trait is linked

to variation in fitness. Thus far, no studies of non-human primate cognition have been able to address this question directly. We know that individuals vary in the strength of their cooperative bonds, even when controlling for the availability of kin. However, we do not yet have a clear understanding about the degree to which this variation is owing to individual differences in skill or motivation, or whether it has a genetic basis.

What has become evident, however, is that individuals vary in the quality and frequency of their interactions with other group members and in their responses to social upheavals. This variation cannot be explained solely in terms of measures like dominance rank or the presence of kin. Instead, variation in patterns of affiliation that are correlated with fitness may result, in part, from variation in personality styles [7,9]. Female baboons who are generally more friendly to others, particularly to those of lower dominance rank, tend to form stronger social bonds than less friendly individuals [9]. These females also seem to be more motivated to anticipate challenges and to react adaptively to setbacks. They show a greater anticipatory increase in fGC levels upon the immigration of a potentially infanticidal male and a greater increase in grooming partners following the death of a close relative [11]. In contrast, females who are less friendly and who are often alone form significantly weaker bonds. The extent to which these behavioural syndromes are heritable remains unclear. In one study of baboons, close female kin did not have 'personalities' that were more alike than non-kin [132]; however, a similar study conducted on rhesus macaques suggested some heritability in personality traits [7].

A recent study in rhesus macaques found that social network position has a genetic basis [10]. Some of this variation is linked to polymorphisms in genes known to regulate serotonin signalling. Specifically, 5-HTTLPR contributes to removal of serotonin from the synapse and is polymorphic in rhesus and human; TPH2 codes for the rate-limiting enzyme in serotonin synthesis and is also polymorphic in both species. Rhesus macaques with the minor allele of both genes are socially peripheral, making fewer allies than monkeys possessing a major allele. Social isolation may arise from the influence of genetic variation in TPH2 on variation in vigilance for social threats in this same population of rhesus macaques [133]. In the laboratory, variation in 5-HTTLPR predicts elevated arousal and decreased social interest in assays of social attention and social reward [134]. Moreover, there is new evidence that serotonin and OT interact in brain circuits implicated in emotion regulation and social behaviour in humans [135], thus linking two neuromodulatory systems previously implicated in arousal and social function. Thus, although the definitive studies on the repeatability, fitness consequences and heritability of personality styles and social skills in the wild remain to be conducted, current evidence suggests that individual variation in social behaviour arises, in part, from the adaptive influence of genes on neural circuits and neuromodulatory systems mediating social function [136].

## 7. Conclusion

In this review, we have focused on cognitive mechanisms that can be attributed, wholly or in part, to selection acting within the domain of conspecific interactions. Many questions, however, remain unanswered. For example, the degree to which

the social environment presents animals with problems that are formally different or more complex than those presented by other behaviours, like foraging or predator avoidance, remains an open question. We cannot yet specify the extent to which similar neuronal mechanisms mediate both social and non-social challenges, or the ways in which social challenges are distinct from non-social ones. Similarly, although evidence suggests that the same ancestral neural circuits underlie many components of social bonding, competition and decision-making across a diverse array of taxa, other relevant brain areas may be unique to primates [2,3,4]. Finally, the degree to which sociality is heritable remains an open issue, and the epigenetic effects of social perturbations are just beginning to be examined. Several measures of gene regulation, including DNA methylation, chromatin accessibility and gene expression are known to respond to variation in environmental, developmental and social stressors [47,137]. The long-term consequences of these effects on social behaviour remain poorly understood.

In sum, non-human primates appear to be highly motivated to attend to each other's social interactions. They recognize not only other individuals' relative dominance ranks and social relationships, but also the nature and quality of recent interactions and the value of particular partners [138]. These cognitive skills enable individuals to establish strategic social bonds that, in turn, enhance fitness. Evidence suggests that, early in the evolutionary history of primates (and perhaps many mammals), selection favoured the development of genetic, neural and hormonal mechanisms that promoted not only competitive, but also cooperative, behaviour.

## References

- Cheney DL, Seyfarth RM. 2007 *Baboon metaphysics: the evolution of a social mind*. Chicago, IL: University of Chicago Press.
- Taborsky B, Oliveira RF. 2012 Social competence: an evolutionary approach. *Trends Ecol. Evol.* **27**, 679–688. (doi:10.1016/j.tree.2012.09.003)
- Bshary R, Oliveira RF. 2015 Cooperation in animals: toward a game theory within the framework of social competence. *Curr. Opin. Behav. Sci.* **3**, 31–37. (doi:10.1016/j.cobeha.2015.01.008)
- Connell LA, Hofmann HA. 2012 Evolution of a vertebrate social decision-making network. *Science* **336**, 1154–1157. (doi:10.1126/science.1218889)
- Pearson J, Watson KK, Platt ML. 2014 Decision making: the neuroethological turn. *Neuron* **82**, 950–965. (doi:10.1016/j.neuron.2014.04.037)
- Seyfarth RM, Cheney DL. 2012 The evolutionary origins of friendship. *Annu. Rev. Psychol.* **63**, 153–177. (doi:10.1146/annurev-psych-120710-100337)
- Brent LJN, Semple S, MacLarnon A, Ruiz-Lambides A, Gonzalez-Martinez J, Platt ML. 2014 Personality traits in rhesus macaques (*Macaca mulatta*) are heritable but do not predict reproductive output. *Int. J. Primatol.* **35**, 188–209. (doi:10.1007/s10764-013-9724-6)
- Sallet J *et al.* 2011 Social network size affects neural circuits in macaques. *Science* **334**, 697–700. (doi:10.1126/science.1210027)
- Seyfarth RM, Silk JB, Cheney DL. 2012 Variation in personality and fitness in wild female baboons. *Proc. Natl Acad. Sci. USA* **109**, 16 980–16 985. (doi:10.1073/pnas.1210780109)
- Brent LJN, Heilbronner SR, Horvath JE, Gonzalez-Martinez J, Ruiz-Lambides AV, Robinson A, Skene J, Platt ML. 2013 Genetic origins of social networks in rhesus macaques. *Sci. Rep.* **3**, 1042. (doi:10.1038/srep01042)
- Seyfarth RM, Cheney DL. 2013 Affiliation empathy and the origins of a theory of mind. *Proc. Natl Acad. Sci. USA* **110**, 10 349–10 356. (doi:10.1073/pnas.1301223110)
- Noonan M *et al.* 2014 A neural circuit covarying with social hierarchy in macaques. *PLoS Biol.* **12**, e1001940. (doi:10.1371/journal.pbio.1001940)
- Cheney DL, Seyfarth RM. 1990 *How monkeys see the world: inside the mind of another species*. Chicago, IL: University of Chicago Press.
- Silk JB, Alberts S, Altmann J, Seyfarth RM, Cheney DL. 2012 Stability of partner choice among female baboons. *Anim. Behav.* **83**, 1511–1518. (doi:10.1016/j.anbehav.2012.03.028)
- Silk JB. 1993 The evolution of social conflict among primate females. In *Primate social conflict* (eds WA Mason, S Mendoza), pp. 49–83. Albany, NY: SUNY Press.
- Cheney DL *et al.* 2004 Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *Int. J. Primatol.* **25**, 401–428. (doi:10.1023/B:IJOP.0000019159.75573.13)
- Cheney DL, Silk JB, Seyfarth RM. 2012 Evidence for intrasexual selection in wild female baboons. *Anim. Behav.* **84**, 21–27. (doi:10.1016/j.anbehav.2012.03.010)
- Chapais B. 1988 Rank maintenance in female Japanese macaques: experimental evidence for social dependency. *Behaviour* **104**, 41–59. (doi:10.1163/156853988X00593)
- Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL. 2006 Female hierarchy instability, male immigration and infanticide increase glucocorticoid levels in female chacma baboons. *Anim. Behav.* **71**, 1227–1237. (doi:10.1016/j.anbehav.2005.11.009)
- Engh AL, Hoffmeier RR, Seyfarth RM, Cheney DL. 2009 O brother, where art thou? The varying influence of older siblings in rank acquisition by female baboons. *Behav. Ecol. Sociobiol.* **64**, 97–104. (doi:10.1007/s00265-009-0824-4)
- Silk JB. 2007 The strategic dynamics of cooperation in primate groups. *Adv. Stud. Behav.* **37**, 1–42. (doi:10.1016/S0065-3454(07)37001-0)
- Silk JB, Alberts SC, Altmann J. 2003 Social bonds of female baboons enhance infant survival. *Science* **302**, 1231–1234. (doi:10.1126/science.1088580)

Recent studies of captive primates have shown that monkeys value social stimuli and that activity in several cortical areas has a direct impact on the perception of other individuals, competition and cooperation. Some areas are involved with the perception of reward generally, others are implicated specifically in social contexts. Some are active when rewards benefit the actor alone, others are active when rewards benefit both the actor and another individual. Neuronal activity appears to be modulated by hormones like OT and by the action of certain genes that may affect individual differences in behaviour. Many brain areas are homologous and show similar patterns of activity in human and non-human primates, suggesting that differences in cooperation between the two groups are a matter of degree rather than a fundamental, qualitative distinction.

**Authors' contributions.** M.L.P., D.L.C. and R.M.S contributed equally to the writing of the paper.

**Competing interests.** We have no competing interests

**Funding.** We received no funding for this study.

**Acknowledgements.** We are grateful to two anonymous reviewers for very helpful comments on the manuscript. R.M.S. and D.L.C. thank the Office of the President of the Republic of Botswana and the Botswana Department of Wildlife and National Parks for permission to conduct research in the Moremi Reserve, where research was supported by the National Science Foundation, the National Institutes of Health, the Leakey Foundation, the National Geographic Society and the University of Pennsylvania. M.L.P. thanks the following funding sources: R01 MH096875, R01 MH095894, SFARI 304935, R01 NS088674, R21 HD080498 and Ajinomoto Inc. Research was approved by the Institutional Animal Care and Use Committees of Duke University and the University of Pennsylvania.

23. Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2009 The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proc. R. Soc. B* **276**, 3099–3104. (doi:10.1098/rspb.2009.0681)
24. Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2010 Strong and consistent social bonds enhance the longevity of female baboons. *Curr. Biol.* **20**, 1359–1361. (doi:10.1016/j.cub.2010.05.067)
25. Archie EA, Tung J, Clark M, Altmann J, Alberts SC. 2014 Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proc. R. Soc. B* **281**, 20141261. (doi:10.1098/rspb.2014.1261)
26. Alberts SC. 2012 Magnitude and sources of variation in male reproductive performance. In *The evolution of primate societies* (eds JC Mitani, J Call, PM Kappeler, RA Palombit, JB Silk), pp. 412–431. Chicago, IL: University of Chicago Press.
27. Schülke O, Bhagavatula J, Vigilant L, Ostner J. 2010 Social bonds enhance reproductive success in male macaques. *Curr. Biol.* **20**, 2207–2210. (doi:10.1016/j.cub.2010.10.058)
28. Young C, Majolo B, Schülke O, Ostner J. 2014 Male social bonds predict partner recruitment in cooperative aggression in wild Barbary macaques. *Anim. Behav.* **80**, 675–682.
29. Snyder-Mackler N, Alberts SC, Bergman TJ. 2012 Concessions of an alpha male? Cooperative defense and shared reproduction in multi-male primate groups. *Proc. R. Soc. B* **279**, 3788–3795. (doi:10.1098/rspb.2012.0842)
30. Duffy KG, Wrangham RW, Silk JB. 2007 Male chimpanzees exchange political support for mating opportunities. *Curr. Biol.* **17**, 585–587. (doi:10.1016/j.cub.2007.06.001)
31. Gilby IC, Brent LNJ, Wroblewski EE, Rudicell RS, Hahn BH, Goodall J, Pusey AE. 2013 Fitness benefits of coalitionary aggression in male chimpanzees. *Behav. Ecol. Sociobiol.* **67**, 373–381. (doi:10.1007/s00265-012-1457-6)
32. Wittig RM, Crockford C, Lehmann J, Whitten PL, Seyfarth RM, Cheney DL. 2008 Focused grooming networks and stress alleviation in wild female baboons. *Horm. Behav.* **54**, 170–177. (doi:10.1016/j.yhbeh.2008.02.009)
33. Beehner JC, Bergman TJ, Cheney DL, Seyfarth RM, Whitten PL. 2005 The effect of new alpha males on female stress in free-ranging baboons. *Anim. Behav.* **69**, 1211–1221. (doi:10.1016/j.anbehav.2004.08.014)
34. Brent LNJ, Semple S, Dubuc C, Heistermann M, MacLarnon A. 2011 Social capital and physiological stress levels in free-ranging adult female rhesus macaques. *Physiol. Behav.* **102**, 76–83. (doi:10.1016/j.physbeh.2010.09.022)
35. Fürtbauer I, Heistermann M, Schülke O, Ostner J. 2014 Low female stress hormone levels are predicted by same- or opposite-sex sociality depending on season in wild Assamese macaques. *Psychoneuroendocrinology* **48**, 19–28. (doi:10.1016/j.psyneuen.2014.05.022)
36. Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL. 2006 Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proc. R. Soc. B* **273**, 707–712. (doi:10.1098/rspb.2005.3378)
37. Taylor SE, Cousino Klein L, Lewis BP, Gruenewald TL, Gurung RA, Updegraff JA. 2000 Biobehavioral responses to stress in females: tend-and-befriend not fight-or-flight. *Psychol. Rev.* **107**, 411–429. (doi:10.1037/0033-295X.107.3.411)
38. Tops M, van Peer JM, Korf J, Wijers AA, Tucker DM. 2007 Anxiety, cortisol, and attachment predict plasma oxytocin. *Psychophysiology* **44**, 444–449. (doi:10.1111/j.1469-8986.2007.00510.x)
39. Cheney DL, Seyfarth RM. 2009 Stress and coping mechanisms in female primates. *Adv. Stud. Behav.* **39**, 1–35. (doi:10.1016/S0065-3454(09)39001-4)
40. Ebitz RB, Watson KK, Platt ML. 2013 Oxytocin blunts social vigilance in the rhesus macaque. *Proc. Natl Acad. Sci. USA* **110**, 11 630–11 635. (doi:10.1073/pnas.1305230110)
41. Bernardo J. 1996 Maternal effects in animal ecology. *Am. Zool.* **36**, 83–105. (doi:10.1093/ich/36.2.83)
42. Sanchez MM. 2006 The impact of early adverse care on HPA axis development: non-human primate models. *Horm. Behav.* **50**, 623–631. (doi:10.1016/j.yhbeh.2006.06.012)
43. Onyango PO, Gesquiere LR, Wango EO, Alberts SC, Altmann J. 2008 Persistence of maternal effects in baboons: mother's dominance rank at son's conception predicts stress hormone levels in sub-adult males. *Horm. Behav.* **54**, 319–324. (doi:10.1016/j.yhbeh.2008.03.002)
44. Weinstock M. 2008 The long-term behavioural consequences of prenatal stress. *Neurosci. Biobehav. Rev.* **32**, 1073–1086. (doi:10.1016/j.neubiorev.2008.03.002)
45. Champagne FA, Curley JP. 2009 Epigenetic mechanisms mediating the long-term effects of maternal care on development. *Neurosci. Biobehav. Rev.* **33**, 593–600. (doi:10.1016/j.neubiorev.2007.10.009)
46. Champagne FA. 2013 Early environments, glucocorticoid receptors, and behavioral epigenetics. *Behav. Neurosci.* **127**, 628–636. (doi:10.1037/a0034186)
47. Runcie DE, Wiedmann RT, Archie EA, Altmann J, Wray GA, Alberts SC, Tung J. 2013 Social environment influences the relationship between genotype and gene expression in wild baboons. *Phil. Trans. R. Soc. B* **368**, 20120345. (doi:10.1098/rstb.2012.0345)
48. Bshary R, Zuberbühler K, van Schaik C. 2016 Why mutual helping in most natural systems is neither conflict-free nor based on maximal conflict. *Phil. Trans. R. Soc. B* **371**, 20150091. (doi:10.1098/rstb.2015.0091)
49. Gomes CM, Mundry R, Boesch C. 2009 Long-term reciprocation of grooming in wild West African chimpanzees. *Proc. R. Soc. B* **276**, 699–706. (doi:10.1098/rspb.2008.1324)
50. Mitani JC. 2009 Male chimpanzees form enduring and equitable social bonds. *Anim. Behav.* **77**, 633–640. (doi:10.1016/j.anbehav.2008.11.021)
51. Cheney DL. 2011 The extent and limits of cooperation in animals. *Proc. Natl Acad. Sci. USA* **108**, 10 902–10 909. (doi:10.1073/pnas.1100291108)
52. Wittig RM, Crockford C, Wikberg E, Seyfarth RM, Cheney DL. 2007 Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proc. R. Soc. B* **274**, 1109–1115. (doi:10.1098/rspb.2006.0203)
53. Engh AL, Hoffmeier RR, Cheney DL, Seyfarth RM. 2006 Who, me? Can baboons infer the target of vocalisations? *Anim. Behav.* **71**, 381–387. (doi:10.1016/j.anbehav.2005.05.009)
54. Wittig RM, Crockford C, Langergraber KE, Zuberbühler K. 2014 Triadic social interactions operate across time: a field experiment with wild chimpanzees. *Proc. R. Soc. B* **281**, 20133155. (doi:10.1098/rspb.2013.3155)
55. Deaner RO, Khera AV, Platt ML. 2005 Monkeys pay per view: adaptive valuation of social images by rhesus macaques. *Curr. Biol.* **15**, 543–548. (doi:10.1016/j.cub.2005.01.044)
56. Hayden BY, Parikh PC, Deaner RO, Platt ML. 2007 Economic principles motivating social attention in humans. *Proc. R. Soc. B* **274**, 1751–1756. (doi:10.1098/rspb.2007.0368)
57. Watson KK, Ghodasra J, Furlong MA, Platt ML. 2012 Visual preferences for sex and status in female rhesus macaques. *Anim. Cogn.* **15**, 401–407. (doi:10.1007/s10071-011-0467-5)
58. Bickart KC, Wright CI, Dautoff RJ, Dickerson BC, Barrett LF. 2011 Amygdala volume and social network size in humans. *Nat. Neurosci.* **14**, 163–164. (doi:10.1038/nn.2724)
59. Powell J, Lewis PA, Roberts N, García-Fiñana M, Dunbar RIM. 2012 Orbital prefrontal cortex volume predicts social network size: an imaging study of individual differences in humans. *Proc. R. Soc. B* **279**, 2157–2162. (doi:10.1098/rspb.2011.2574)
60. Lewis PA, Rezaie R, Brown R, Roberts N, Dunbar R. 2011 Ventromedial prefrontal volume predicts understanding of others and social network size. *Neuroimage* **57**, 1624–1629. (doi:10.1016/j.neuroimage.2011.05.030)
61. Kanai R, Bahrami B, Roylance R, Rees G. 2011 Online social network size is reflected in human brain structure. *Proc. R. Soc. B* **282**, 20111959. (doi:10.1098/rspb.2011.1959)
62. Adolphs R. 2009 The social brain: neural basis of social knowledge. *Annu. Rev. Psychol.* **60**, 693–716. (doi:10.1146/annurev.psych.60.110707.163514)
63. Frith CD. 2007 The social brain? *Phil. Trans. R. Soc. B*, **362** 671–678. (doi:10.1098/rstb.2006.2003)
64. Rushworth MFS, Mars RB, Sallet J. 2013 Are there specialized circuits for social cognition and are they unique to humans? *Curr. Opin. Neurobiol.* **23**, 436–442. (doi:10.1016/j.conb.2012.11.013)
65. Gross CG, Bender DB, Rocha-Miranda CE. 1969 Visual receptive fields of neurons in inferotemporal cortex of the monkey. *Science* **166**, 1303–1306. (doi:10.1126/science.166.3910.1303)
66. Gross CG, Rocha-Miranda CE, Bender DB. 1972 Visual properties of neurons in inferotemporal



- cortex of the macaque. *J. Neurophysiol.* **35**, 96–111.
67. Kanwisher N, McDermott J, Chun MM. 1997 The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* **17**, 4302–4311.
68. McCarthy G, Puce A, Gore JC, Allison T. 1997 Face-specific processing in the human fusiform gyrus. *J. Cogn. Neurosci.* **9**, 605–610. (doi:10.1162/jocn.1997.9.5.605)
69. Tsao DY, Freiwald WA, Tootell RB, Livingstone MS. 2006 A cortical region consisting entirely of face-selective cells. *Science* **311**, 670–674. (doi:10.1126/science.1119983)
70. Meadows JC. 1974 The anatomical basis of prosopagnosia. *J. Neurol. Neurosurg. Psychiatr.* **37**, 489–501. (doi:10.1136/jnnp.37.5.489)
71. Behrmann M, Avidan G. 2005 Congenital prosopagnosia: face-blind from birth. *Trends Cog. Sci.* **9**, 180–187. (doi:10.1016/j.tics.2005.02.011)
72. Duchaine BC, Nakayama K. 2006 Developmental prosopagnosia: a window to content-specific face processing. *Curr. Opin. Neurobiol.* **16**, 166–173. (doi:10.1016/j.conb.2006.03.003)
73. Smith DV, Hayden BY, Truong TK, Song AW, Platt ML, Huettel SA. 2010 Distinct value signals in anterior and posterior ventromedial prefrontal cortex. *J. Neurosci.* **30**, 2490–2495. (doi:10.1523/JNEUROSCI.3319-09.2010)
74. Aharon I, Etcoff N, Ariely D, Chabris CF, O'Connor E, Breiter HC. 2001 Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron* **32**, 537–551. (doi:10.1016/S0896-6273(01)00491-3)
75. Levy DJ, Glimcher PW. 2012 The root of all value: a neural common currency for choice. *Curr. Opin. Neurobiol.* **22**, 1027–1038. (doi:10.1016/j.conb.2012.06.001)
76. Klein J, Deaner RO, Platt ML. 2008 Neural correlates of social target value in macaque parietal cortex. *Curr. Biol.* **18**, 419–424. (doi:10.1016/j.cub.2008.02.047)
77. Watson KK, Platt ML. 2012 Social signals in primate orbitofrontal cortex. *Curr. Biol.* **22**, 2268–2273. (doi:10.1016/j.cub.2012.10.016)
78. Klein J, Platt ML. 2013 Social information signalling by neurons in primate striatum. *Curr. Biol.* **23**, 691–696. (doi:10.1016/j.cub.2013.03.022)
79. Adams GK, Watson KK, Pearson JM, Platt ML. 2012 Neuroethology of decision-making. *Curr. Opin. Neurobiol.* **22**, 982–989. (doi:10.1016/j.conb.2012.07.009)
80. Chang SW, Brent LJJ, Adams GK, Klein JT, Pearson JM, Watson KK, Platt ML. 2013 Neuroethology of primate social behavior. *Proc. Natl Acad. Sci. USA* **110**, 10 387–10 394. (doi:10.1073/pnas.1301213110)
81. Kumar D, Melo HL, Duzel E. 2012 The emergence and representation of knowledge about social and nonsocial hierarchies. *Neuron* **76**, 653–666. (doi:10.1016/j.neuron.2012.09.035)
82. Wilson M. 2002 Six views of embodied cognition. *Psychon. Bull. Rev.* **9**, 625–636. (doi:10.3758/BF03196322)
83. Shadlen MN, Kiani R. 2007 Neurology: an awakening. *Nature* **448**, 539–540. (doi:10.1038/448539a)
84. Kubanek J, Snyder LH. 2015 Reward-based decision signals in parietal cortex are partially embodied. *J. Neurosci.* **35**, 4869–4881. (doi:10.1523/JNEUROSCI.4618-14.2015)
85. Chance MR, Mead AP. 1953 Social behaviour and primate evolution. *Symp. Soc. Exp. Biol.* **7**, 395–439.
86. Zink CF, Tong Y, Chen Q, Bassett DS, Stein JL, Meyer-Lindenberg A. 2008 Know your place: neural processing of social hierarchy in humans. *Neuron* **58**, 273–283. (doi:10.1016/j.neuron.2008.01.025)
87. Bauman MD, Lavenex P, Mason WA, Capitanio JP, Amaral DG. 2004 The development of social behavior following neonatal amygdala lesions in rhesus monkeys. *J. Cogn. Neurosci.* **16**, 1388–1411. (doi:10.1162/0898929042304741)
88. Kawashima R, Sugiura M, Kato T, Nakamura A, Hatano K, Ito K, Fukuda H, Kojima S, Nakamura K. 1999 The human amygdala plays an important role in gaze monitoring: a PET study. *Brain* **122**, 779–783. (doi:10.1093/brain/122.4.779)
89. Baron-Cohen S, Ring HA, Wheelwright S, Bullmore ET, Brammer MJ, Simmons A, Williams SC. 1999 Social intelligence in the normal and autistic brain: an fMRI study. *Eur. J. Neurosci.* **11**, 1891–1898. (doi:10.1046/j.1460-9568.1999.00621.x)
90. Kling A, Cornell R. 1971 Amygdalectomy and social behavior in the caged stump-tailed macaque (*Macaca speciosa*). *Folia Primatol.* **14**, 190–208. (doi:10.1159/000155350)
91. Mason WA, Capitanio JP, Machado CJ, Mendoza SP, Amaral DG. 2006 Amygdalectomy and responsiveness to novelty in rhesus monkeys (*Macaca mulatta*): generality and individual consistency of effects. *Emotion* **6**, 73–81. (doi:10.1037/1528-3542.6.1.73)
92. Antoniadis EA, Winslow JT, Davis M, Amaral DG. 2007 Role of the primate amygdala in fear-potentiated startle: effects of chronic lesions in the rhesus monkey. *J. Neurosci.* **27**, 7386–7396. (doi:10.1523/jneurosci.5643-06.2007)
93. Chance MR. 1967 Attention structure as the basis of primate rank orders. *Man* **2**, 503–518. (doi:10.2307/2799336)
94. Cai X, Padoa-Schioppa C. 2014 Contributions of orbitofrontal and lateral prefrontal cortices to economic choice and the good-to-action transformation. *Neuron* **81**, 1140–1151. (doi:10.1016/j.neuron.2014.01.008)
95. Tomasello M, Carpenter M, Call J, Behne T, Moll H. 2005 Understanding and sharing intentions: the origins of cultural cognition. *Behav. Brain Sci.* **28**, 675–691. (doi:10.1017/S0140525X05000129)
96. Silk JB, House BR. 2011 Evolutionary foundations of human prosocial sentiments. *Proc. Natl Acad. Sci. USA* **108**, 10 910–10 917. (doi:10.1073/pnas.1100305108)
97. Warneken F. 2013 The development of altruistic behavior: helping in children and chimpanzees. *Soc. Res.* **80**, 431–442.
98. Warneken F, Tomasello M. 2014 The development and evolutionary origins of human helping and sharing. *Oxford Handbooks Online*. (doi:10.1093/oxfordhb/9780195399813.013.007)
99. Saxe R, Kanishwer N. 2003 People thinking about thinking people: the role of the temporo-parietal junction in “theory of mind”. *Neuroimage* **19**, 1835–1842. (doi:10.1016/S1053-8119(03)00230-1)
100. Shepherd SV. 2010 Following gaze: gaze-following behavior as a window into social cognition. *Front. Integr. Neurosci.* **4**, 5.
101. Mosher CP, Zimmerman PE, Gothard KM. 2014 Neurons in the monkey amygdala detect eye contact during naturalistic social interactions. *Curr. Biol.* **24**, 2459–2464. (doi:10.1016/j.cub.2014.08.063)
102. Roy A, Shepherd SV, Platt ML. 2012 Reversible inactivation of pSTS suppresses social gaze following in the macaque (*Macaca mulatta*). *Soc. Cogn. Affect. Neurosci.* **9**, 209–217. (doi:10.1093/scan/nss123)
103. Shepherd SV, Klein J, Platt ML. 2009 Mirroring of attention by neurons in macaque parietal cortex. *Proc. Natl Acad. Sci. USA* **106**, 9489–9494. (doi:10.1073/pnas.0900419106)
104. Klein J, Shepherd SV, Platt ML. 2009 Social attention and the brain. *Curr. Biol.* **19**, 958–962. (doi:10.1016/j.cub.2009.08.010)
105. Chang SW, Winecoff A, Platt ML. 2011 Vicarious reinforcement in rhesus macaques (*Macaca mulatta*). *Front. Dec. Neurosci.* **5**, 27.
106. Craig AD. 2009 How do you feel – now? The anterior insula and human awareness. *Nat. Rev.* **10**, 59–70. (doi:10.1038/nrn2555)
107. Waytz A, Zaki J, Mitchell JP. 2012 Response of dorsomedial prefrontal cortex predicts altruistic behavior. *J. Neurosci.* **32**, 7646–7650. (doi:10.1523/JNEUROSCI.6193-11.2012)
108. Chang SW, Platt ML. 2014 Amygdala: eyes wide open. *Curr. Biol.* **24**, R1000–R1002. (doi:10.1016/j.cub.2014.08.044)
109. Carter CS. 1998 Neuroendocrine perspectives on social attachment and love. *Psychoneuroendocrinology* **23**, 779–818. (doi:10.1016/S0306-4530(98)00055-9)
110. Bartz JA, Hollander E. 2006 The neuroscience of affiliation: forging links between basic and clinical research on neuropeptides and social behavior. *Horm. Behav.* **50**, 518–528. (doi:10.1016/j.yhbeh.2006.06.018)
111. Snowdon C, Pieper B, Boe C, Cronin K, Kurian A, Ziegler T. 2010 Variation in oxytocin is related to variation in affiliative behavior in monogamous pairbonded tamarins. *Horm. Behav.* **58**, 614–618. (doi:10.1016/j.yhbeh.2010.06.014)
112. Crockford C, Wittig RM, Langergraber KE, Ziegler TE, Zuberbühler K, Deschner T. 2013 Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proc. R. Soc. B* **280**, 20122765. (doi:10.1098/rspb.2012.2765)
113. Wittig RM, Crockford C, Deschner T, Langergraber KE, Ziegler TE, Zuberbühler K. 2014 Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proc. R. Soc. B* **281**, 20133096. (doi:10.1098/rspb.2013.3096)

114. Baumgartner T, Heinrichs M, Vonlanthen A, Fischbacher U, Fehr E. 2008 Oxytocin shapes the neural circuitry of trust and trust adaptation in humans. *Neuron* **58**, 639–650. (doi:10.1016/j.neuron.2008.04.009)
115. Kosfeld M, Heinrichs M, Zak PJ, Fischbacher U, Fehr E. 2014 Oxytocin increases trust in humans. *Nature* **435**, 673–676. (doi:10.1038/nature03701)
116. Modahl C, Green L, Fein D, Morris M, Waterhouse L, Feinstein C, Levin H. 1998 Plasma oxytocin levels in autistic children. *Biol. Psychiatr.* **43**, 270–277. (doi:10.1016/S0006-3223(97)00439-3)
117. Wu S *et al.* 2005 Positive association of the oxytocin receptor gene (*OXTR*) with autism in the Chinese Han population. *Biol. Psychiatr.* **58**, 74–77. (doi:10.1016/j.biopsych.2005.03.013)
118. Jacob S, Brune CW, Carter CS, Leventhal BL, Lord C, Cook EH. 2007 Association of the oxytocin receptor gene (*OXTR*) in Caucasian children and adolescents with autism. *Neurosci. Lett.* **417**, 6–9. (doi:10.1016/j.neulet.2007.02.001)
119. Andari E, Duhamel JR, Zalla T, Herbrecht E, Leboyer M, Sirigu A. 2010 Promoting social behavior with oxytocin in high-functioning autism spectrum disorders. *Proc. Natl Acad. Sci. USA* **107**, 4389–4394. (doi:10.1073/pnas.0910249107)
120. Chang SW, Barter JW, Ebitz RB, Watson KK, Platt ML. 2012 Inhaled oxytocin amplifies both vicarious reinforcement and self reinforcement in rhesus macaques (*Macaca mulatta*). *Proc. Natl Acad. Sci. USA* **109**, 959–964. (doi:10.1073/pnas.1114621109)
121. De Dreu CK, Greer LL, Handgraaf MJ, Shalvi S, Van Kleef GA, Baas M, Ten Velden FS, Van Dijk E, Feith SW. 2010 The neuropeptide oxytocin regulates parochial altruism in intergroup conflict among humans. *Science* **328**, 1408–1411. (doi:10.1126/science.1189047)
122. Young LJ, Wang Z, Insel TR. 1998 Neuroendocrine bases of monogamy. *Trends Neurosci.* **21**, 71–75. (doi:10.1016/S0166-2236(97)01167-3)
123. Vargas-Pinilla P *et al.* 2015 Evolutionary pattern in the OXT-OXTR system in primates: coevolution and positive selection footprints. *Proc. Natl Acad. Sci. USA* **112**, 88–93. (doi:10.1073/pnas.1419399112)
124. Parker KJ *et al.* 2014 Plasma oxytocin concentrations and *OXTR* polymorphisms predict social impairments in children with and without autism spectrum disorder. *Proc. Natl Acad. Sci. USA* **111**, 12 258–12 263. (doi:10.1073/pnas.1402236111)
125. Bartz JA, Zaki J, Bolger N, Ochsner KN. 2011 Social effects of oxytocin in humans: context and person matter. *Trends Cogn. Sci.* **15**, 301–309.
126. Young LJ, Wang Z. 2004 The neurobiology of pair bonding. *Nat. Neurosci.* **7**, 1048–1054. (doi:10.1038/nn1327)
127. Freeman SM, Inoue K, Smith AL, Goodman MM, Young LJ. 2014 The neuroanatomical distribution of oxytocin receptor binding and mRNA in the male rhesus macaque (*Macaca mulatta*). *Psychoneuroendocrinology* **45**, 128–141. (doi:10.1016/j.psyneuen.2014.03.023)
128. Freeman SM, Walum H, Inoue K, Smith AL, Goodman MM, Bales KL, Young LJ. 2014 Neuroanatomical distribution of oxytocin and vasopressin 1a receptors in the socially monogamous coppery titi monkey (*Callicebus cupreus*). *Neuroscience* **273**, 12–23. (doi:10.1016/j.neuroscience.2014.04.055)
129. Owen SF, Tuncdemir SN, Bader PL, Tirko NN, Fishell G, Tsien RW. 2013 Oxytocin enhances hippocampal spike transmission by modulating fast-spiking interneurons. *Nature* **500**, 458–462. (doi:10.1038/nature12330)
130. Stoop R. 2012 Neuromodulation by oxytocin and vasopressin. *Neuron* **76**, 142–159. (doi:10.1016/j.neuron.2012.09.025)
131. Liu Y, Wang ZX. 2003 Nucleus accumbens oxytocin and dopamine interact to regulate pair bond formation in female prairie voles. *Neuroscience* **121**, 537–544. (doi:10.1016/S0306-4522(03)00555-4)
132. Seyfarth RM, Silk JB, Cheney DL. 2014 Social bonds in female baboons: the interaction between personality, kinship and rank. *Anim. Behav.* **87**, 23–29. (doi:10.1016/j.anbehav.2013.10.008)
133. Watson KK, Li D, Brent LJJ, Horvath JE, Gonzalez-Martinez J, Ruiz-Lambides A, Robinson AG, Skene J, Platt ML. 2015 Genetic influences on social attention in free-ranging rhesus macaques. *Anim. Behav.* **103**, 267–275. (doi:10.1016/j.anbehav.2015.02.012)
134. Watson KK, Ghodasra JH, Platt ML. 2009 Serotonin transporter genotype modulates social reward and punishment in rhesus macaques. *PLoS ONE* **4**, e4156. (doi:10.1371/journal.pone.0004156)
135. Mottolese R, Redouté J, Costes N, Le Bars D, Sirigu A. 2014 Switching brain serotonin with oxytocin. *Proc. Natl Acad. Sci. USA* **111**, 8637–8642. (doi:10.1073/pnas.1319810111)
136. Brent LJJ, Chang SW, Garipey JF, Platt ML. 2014 The neuroethology of friendship. *Ann. NY Acad. Sci.* **1316**, 1–17. (doi:10.1111/nyas.12315)
137. Tung J, Gilad Y. 2013 Social environmental effects on gene regulation. *Cell. Mol. Life Sci.* **70**, 4323–4339. (doi:10.1007/s00018-013-1357-6)
138. Seyfarth RM, Cheney DL. 2015 Social cognition. *Anim. Behav.* **103**, 191–202. (doi:10.1016/j.anbehav.2015.01.030)