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Communicative roots of complex sociality and cognition: Neuropsychological mechanisms underpinning the processing of social information

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Abstract

Primate social bonds are described as being especially complex in their nature, and primates have unusually large brains for their body size compared to mammals. Communication in primates has attracted considerable attention because of the important role it plays in social bonding. It has been proposed that differentiated social relationships are cognitively complex because primates need to continuously update their knowledge about different types of social bonds. Therefore, primates infer whether an opportunity for social interaction is rewarding (valuable to individual goals) based on their knowledge of the social relationships of the interactants. However, exposure to distraction and stress have detrimental effects on the dopaminergic system, suggesting that understanding social relationships as rewarding is affected in these conditions. This paper proposes that complex communication evolved to augment the capacity to form social relationships during stress through flexibly modifying intentionality in communication (audience checking, response waiting, elaboration). Intentional communication may upregulate dopamine dynamics to allow recognition that an interaction is rewarding during stress. By examining these associations between complexity of communication and stress, we provide new insights into the cognitive skills involved in forming social bonds in primates and the evolution of communication systems in both primates and humans.

1. Introduction

Primates have unusually large brains for their body size and it has been proposed that cognitive processing capacities behind tracking social relationships (represented by relative neocortex size) place an upper limit on the size of groups that can be maintained as a cohesive social unit [1]. Primates do not maintain equally strong social relationships with all group members, but form stable, long-lasting bonds with selected related and unrelated group members [2]. One of the primary mechanisms that primates use for maintaining these social bonds is grooming, which can account for up to 20% of their total daytime activity budget in the most social species such as gelada baboons [3]. The amount of time primates spend grooming is positively related to group size [3]. However, in doing so they do not groom with more individuals; rather, they devote more time to maintaining the same number of social relationships [3]. Primates also use a wide range of communicative signals including vocalisations [4], gestures [5] and emotional expressions [6] and these signals are important for maintaining social relationships between group members [7]. In this context, social complexity is defined in terms of the network where individuals interact with many different individuals across many different social contexts, whilst communicative complexity is defined as systems which contain a larger number of functionally distinct elements, or in which a large number of bits of information are contained within signals [8]. However, the specific role that cognitive skills play in this complex communication, and how in turn this relates to sociality, is still unclear. In this paper we propose the hypothesis that communicative complexity is an adaptation to managing the social stress of living in groups in a way that enables primates to form social bonds through complex communication [9]. Thus, we will explore what makes managing social relationships cognitively complex and propose that evolution of communicative complexity occurred to overcome the stresses imposed by group-living [10].

2. What is Social Bonding?

Exploring the link between sociality and key features of complex communication such as intentionality provides insights into how increasing flexibility in communication can facilitate the emergence of social systems characterized by bonded social relationships, such as those found in non-human primates (hereafter primates) and humans [8, 11]. In intentional communication, the signaller communicates with a specific goal in mind and shows flexibility in the pattern of communication to achieve that goal, including sensitivity to the recipients' orientation, response waiting (communicating and visually monitoring recipient's response), and persisting or elaborating their communication if the goal of the communication is not met [12]. Intentional communication is under volitional control, as indicated by selective use of the signal in response to social factors – the behavioural context, the potential recipient and wider audience [10, 12]. Gestural communication, particularly in great apes [13], has shown strong evidence of intentionality, although the evidence for intentionality in vocal communication in other primates is more mixed [4]. However, whilst intentionality in communication has traditionally been considered from the standpoint of the signaller, recent studies point to the important role of intentionality from the standpoint of the recipient of the signalling [5, 14]. According to this perspective, intentional communication is cognitively complex because it facilitates attribution of value to social relationships by the recipient through augmenting their understanding of others' goals and intentions [9]. Intentional communication requires a number of key cognitive skills from both signallers and receivers, including inhibition and executive function to enable selective use of communicative signals and knowledge of direct and third party relationships to adjust communication to the social context [12, 15]. The social cognitive abilities underpinning the intentional use of communication are correlated with brain size in primates [11, 16], which is also strongly correlated with group size [11]. Communication is important in all group-living primates to enable them to meet the challenges of sociality [10, 11], but the extent to which different species of primates can communicate intentionally is still debated [4, 12]. If the use of intentional communication enables primates to overcome the stresses imposed by group living, we predict that more complex communication systems, and the social cognition which underpins this communication, will be associated with more complex social systems [8, 10, 11]

Value prediction plays an important role in socially complex species because it supports the action selection processes [17]. The neural representations of value have been found in various areas of the brain such as the amygdala, orbitofrontal cortex (OFC), ventromedial prefrontal cortex (vmPFC), and ventral and dorsal striata, as well as parietal, premotor, and dorsal frontal areas [17, 18]. Among neurotransmitters such as acetylcholine, glutamate and noradrenaline, dopamine transmission has been identified as playing a particularly important role in facilitating processing of social information by assigning stimuli the attribute of value [17, 18]. Evidence from animal studies [19] and in vivo imaging studies in humans [20] indicates that these neural structures are involved in processing social information, enabling the individual to understand and predict others' behaviour. One important part of this process is value attribution, where outcomes are assessed as valuable to the individual's goals as seen in response to rewarded events, resulting in approach behaviour [19]. Hence, social bonding can be identified by the coordinated behaviours that arise as a consequence of the value attribution through tracking prior social relationships with the interactant and communication (e.g. joint resting, joint travel, proximity and visual monitoring of core social partners [21]).

Social bonding has a psychological benefit of reducing fear during social competition (e.g. fear of aggression [22]) as well as a physiological benefit (e.g. endorphin release during grooming), making it inherently pleasant [21]. 'Wanting' has been characterised as the subjective emotional state elicited by the representation of value, in response to the presentation of desirable stimuli of the highest value to the individual goals of the recipient [23]. Further, the positive emotional state of ‘liking’ increases the power of the stimuli to excite the recipient further than the state of ‘wanting’ [24], motivating approach behaviours as well as positively valenced emotions [23]. This contrasts with the subjective emotional state elicited by undesirable events, which produces negative representations of value to the individual goals of the recipient. In this case, the punishing stimulus is assigned the ‘not wanting’ or ‘not liking’ attribute, leading to avoidance behaviour and negatively valenced emotions [23].

Hedonic aspects of value representations can arise through less cognitively complex stimulus-driven processing as in habits, where the recipient’s reactions are evoked by integrating past experience with the social reward through trial and error, in a manner similar to non-social rewards such as drug addiction [25]. The reinforcing properties of previous social interactions drive primates toward a positive emotional state and approach motivation, reinforcing their desire to engage in social interaction in the future [25]. One important but greatly under-researched aspect of these interactions is communication. Primate communication can increase the likelihood of engaging in social interactions by having reinforcing properties. For example, in wild female chacma baboons, grunts produced when approaching other females are given selectively to lower-ranking females and females with infants, and increase the likelihood of affiliative interactions between the signaller and receiver [15]. Receivers therefore come to associate grunts given by signallers with a rewarding outcome. For communication associated with affiliative interactions, once the observer associates a previously neutral signal (e.g. grunt) with a rewarding value, the presentation of the signal alone may trigger excitation of dopamine-mediated processing [17]. Thus, dopamine may be released in response to the presentation of a physical property of a stimulus, giving rise to hedonic aspects of signal presentation without conscious consideration of the signaller’s goals or context. The temporal dynamics of the value-coding dopamine neuron activity support its role in facilitating conditioned responding to the signals, based on perceived value [23].

Further, hedonic aspects of value representations can involve cognitively complex goal-directed processing and arise by forming mental representation of a desired goal state, which in turn gives rise to recognition of value. According to this perspective, social interaction in socially complex species like primates is cognitively complex because it demands an understanding of intentionality, where the interactants understand that others have goals and intentions different from their own and are able to integrate in real time perception and accumulation of information to form representations of other’s future behaviour [26]. However, primates do not perceive everything: the ability of the partner to attribute goals to social interactions is dependent on the ability to allocate memory by selectively focusing on relevant information [27]. Selective attention is a basic cognitive skill that enables primates to process relevant information and filter out irrelevant information.

Focused attention to a target stimulus provides a means of selecting neural representations for further processing and augmenting the representations favouring that target to increase the magnitude and fidelity of neural signals dependent on the attentional focus [27]. The objective of voluntary attention can thus be viewed as increasing specificity of representations [27]. Primates use relevant information such as the identity of the partner, the social relationships in the group as a whole and the ongoing context (e.g. mating, aggression, travel) to form representations about the goal of social interactions [15, 19]. Further, communication forms an important part of the incoming information, and can make social goals of individual importance more relevant, as represented in the working memory of the observer [9, 13]. This amounts to making an adaptive decision about the goal of the interaction whereby access to accumulated knowledge facilitates a flexible increase in the accuracy and consistency of the response to a novel situation. Once the incoming information has been evaluated according to behavioural rules and context, an appropriate motor plan is formed and executed based on generated representation of the goal [28]. This ability is dependent on Brodmann Area 10, a region of the prefrontal cortex only found in anthropoid primates [29], suggesting that primates may have an advantage in goal-directed processing of social information compared to other mammals.

Whereas stimulus-driven control gives rise to cognitive efficiency and speed in dealing with environmental challenges, it demands that individuals adapt to challenges of the environment by having to experience them directly and this may limit the capacity of the recipient to respond flexibly in novel conditions [30]. The phylogenetically newer, cortical route mediates perception, integration and accumulation of information about social relationships from the history of prior interactions in the group to increase the accuracy of responses in the absence of prior experience with the partner [19]. In this context, understanding intentionality facilitates more complex social relationships and the acquisition of a large open-ended repertoire of signals. The process of learning is the process of inference of the goal of a social interaction, mediated in real time by higher cognitive processes such as executive function [31], which is reinforced through stimulus-driven processing. The contingencies between the signal and the goal are retrieved in the context of repeated instances of social interactions, where the agent searches through the possible signal outcomes to find the optimal solution to the current problem in a given context. Thus, when two possible goal outcomes become available, the original goal is not discarded, but the recognition of the goal depends on the additional stimulus of context, which facilitates the selection and retrieval of the goal most appropriate to the current situation [32].

Both goal-directed and stimulus-driven systems of behavioural acquisition are present in the same animals, manifesting themselves in different behaviour under different conditions. This suggests that instead of each system functioning in isolation, these two systems are mutually interdependent [33]. Phylogenetically older stimulus-driven control may benefit from the experience that comes with goal-directed processing, which may endow the stimulus-driven control with more powerful computational functions, such as the use of top down information to modify the target of reinforcement learning [33]. For instance, blood oxygenation level dependent (BOLD) responses in the striatum are influenced by information about value rather than experience [33]. When processing occurs through the goal-directed system in the early stages of communication acquisition, control may subsequently transition to the stimulus-directed system when the signal-goal links have been sufficiently sampled [34].

3. The Double Jeopardy of Primate Social Life

The main benefit to group-living in primates lies in reducing the risk of predation [35]. To maintain group cohesion over time, and thus benefit from reduction in predation risk, group members must coordinate their behaviour with others over time and space, either as one single group or, in fission-fusion social systems, as a set of smaller semi-independent foraging parties [36]. To understand the dynamics shaping social cohesion, a detailed understanding of which factors influence the ability of primates to build and maintain social relationships over time is required, as this is at the heart of what makes primate life socially complex [2, 11]. Other species also come together in large groups (e.g. grazing ungulates such as wildebeest and buffalo), but these are loose aggregations of animals, without stable group membership and long-term social relationships between individuals [21]. In contrast, primates live in groups with stable membership, and form long-lasting bonds with certain individuals within the group [2]. These bonds have direct fitness consequences – for example, the sociality of adult female baboons (as measured by grooming and proximity to others) is positively associated with infant survival [2].

One of the main variations in different social systems of primates is in the degree of temporal and spatial stability shown in group size and composition [36]. In fission-fusion social systems the broader group or community changes its size by means of the fission and fusion of subunits (known as parties or sub-groups) according to both the activity (e.g. resting, feeding) and distribution of resources [36, 37]. The term fission-fusion dynamics refers to the extent of variation in spatial cohesion and individual membership in a group over time [36]. Stable groups have a low degree of fission-fusion dynamics in that the membership of the group is stable temporally and spatially, and thus all individuals will typically encounter every member of the group every day. In contrast, in high fission-fusion dynamics, individuals form socially and geographically circumscribed communities, within which they associate in temporary subgroups (‘parties’) that vary in size, composition and duration [36]. Individuals in the wider community may thus only see each other at infrequent intervals, often weeks apart, but each individual can recognise members of their own community and is capable of maintaining long-term relationships with these individuals [36]. Increasing group size in a stable group will result in individuals simply encountering more individuals each day, whereas increasing group size in the fission-fusion social system will result in the individuals having to keep track of more indirect relationships with whom interaction may be infrequent [36, 37]. These weaker, indirect ties are cognitively challenging to manage, and this is especially true in fission-fusion social systems where the frequency of interaction between two individuals will be much lower than in stable groups [37].

In both fission-fusion and stable social systems, variation in the capacity to form and maintain social bonds will occur due to the presence of other individuals, particularly weakly bonded individuals [38, 39]. The knowledge of social relationships in the group determines how primates make decisions regarding how they should interact with other members of their group based on both the direct relationship they have with the interaction partner, as well as their ability to anticipate the behaviour of others present in the audience based on past experience [15, 37, 39]. In smaller groups, primates may be able to form relatively strong ties with all group members and predict behaviour of all others present in close proximity. However, as group size increases, the primates will experience cognitive distraction through the need to process uncertainty about social relationships, as the ties they will have with other individuals present in the audience will become increasingly weak [11]. In particular, central group members will experience cognitive distraction to a greater extent than peripheral group members, because the number of conspecifics with whom they maintain close proximity increases, and therefore the number of dyads and triads of social bonds that they manage increases [14, 40, 41].

A key factor in an audience effect, more important than the mere presence of weakly bonded individuals itself, is the likelihood of physical harm received from others present in the audience [39]. Group-living involves substantial costs, as group mates have different fitness interests and compete for limited resources, including food, social partners and mates [42]; in addition, it is well-established that the stresses arising from group-living can have a direct impact on primates’ fitness [43]. The ability of dominant group members to physically harm subordinate individuals, and monopolise their resources during competition [44, 45] can act as a centrifugal force that, if unchecked, drives individuals apart and results in the group dispersing. In particular, subordinate females are exposed to higher rates of aggression from group mates, and those without access to social support have higher stress levels [46], reducing fitness through its effect on female fertility [47]. The presence of sources of anxiety such as dominant group members creates emotional distraction through being fearful of becoming a target of aggression. Although primates sometimes preferentially form social bonds with dominant group members to reduce the risk of aggression and gain a dominant’s protection

[48], the cognitive constraints on forming social relationships in larger social groups imply that many individuals will have weak bonds with the dominant group members [41, 49]. From the point of view of cognitive and emotional distractions acting as regular stressors in primate social life, it is thus important to determine the nature of the influence of these stressors on the capacity of primates to process social information.

4. The Influence of Stress on Processing of Social Information

The primary circuit for processing social information is the basal ganglia circuit [28] functionally connected with the prefrontal cortex (thereby influencing goal-directed processing), as well as the striatum (thereby influencing stimulus-driven processing) [50]. Both processes are influenced by the action of dopamine [17, 51], which acts to facilitate or suppress associations represented in the cortices by modulating activity of the basal ganglia in response to events in the environment (Fig. 1, see also Supplementary Information for the detailed description of the dopamine dynamics in basal ganglia). The extent to which individuals can effectively process different goal information is dependent on chronic and acute exposure to environmental stressors and the global influence they exert on the dopaminergic system [52]. Stress exposures demonstrate dose-response relationships in dopaminergic function in the prefrontal cortex and the striatum via activation of the hypothalamic-pituitary-adrenal (HPA) axis and the sympathetic nervous system, as part of the biological stress response [53]. In animals, aversive stimuli acting as both mild and acute stressors induce changes in the dopamine system by altering the activity of dopamine neuron populations (i.e. the numbers of neurons firing) and with regard to extracellular dopamine levels relative to baseline [54]. Single exposure to mild or acute stressors can potentiate dopaminergic activity, but also induce long-lasting changes in dopaminergic function, including altered responsivity to future stimulation associated with dopaminergic blunting [54]. Chronic stress reduces dopamine synthesis capacity, whereby reduction in baseline dopamine tone is observed following exposure to multiple stressors [55].

The prevailing baseline dopamine concentration determines the activation ratio of D1 and D2 receptor classes, which varies dynamically in response to stressors. At all levels of dopamine, the receptors are activated, but the importance of one state over the other differs depending on the prevailing dopamine concentration [56]. The D1/D2 receptor activation ratio takes the form of an inverted U-shape: at very low or very high concentrations of tonic dopamine, the network dynamics are dominated by the D2 state, whereas at intermediate concentrations of dopamine, the D1 state prevails [57]. Consistent with this model, recent evidence indicates that the influence of stress associated with increased or decreased dopaminergic output and polarity of the synaptic plasticity that can be induced in the network has profound effects on the induction of synaptic plasticity, such as long-term potentiation (LTP) and depression (LTD) in both the prefrontal cortex and the striatum. Increased tonic dopamine in response to a short period of exposure to acute stress facilitates induction of long-term potentiation, which depends on D1 activation. When levels of tonic dopamine are lower following exposure to chronic stress, LTP is impaired, instead resulting in the induction of LTD. Using Parkinson disease as a model, Frank [58] showed that these findings are mirrored in deficits in information processing in patients with altered dopamine synthesis in the prefrontal cortex and the striatum who show both cognitive and motor effects.

At the level of cognitive processing in the prefrontal cortex, reduced tonic dopamine reduces the ability of the phasic bursts to activate D1 receptors in the direct pathway, leading to too little updating and maintenance of relevant representations [56]. This results in reduced LTP of relevant representations, but relatively enhanced LTD of irrelevant information. Conversely, excessive tonic dopamine leading to reduced ability of the phasic dips to activate D2 receptors in the indirect pathway would lead to excessive updating of relevant information (LTP) but reduced avoidance of irrelevant information (LTD). At the level of motor performance, elevated levels of dopamine result in increased potentiation of rewarding actions, but reduced avoidance of aversive outcomes. On the other hand, when tonic dopamine is reduced below baseline, this leads to reduced learning of rewarding actions, but relatively enhanced avoidance of aversive actions as the overactive indirect pathway leads to excessive inhibition.

The effects of stress on dopaminergic function are not uniform, but converging lines of evidence show that stress can operate as a switch between goal-directed processing mediated by the prefrontal cortex and stimulus-driven processing relying on the intact striatum [30]. Whereas dopamine innervation is comparatively sparse in prefrontal cortex as compared to the striatum, dopaminergic pathways respond differently to stress. There is evidence that subcortical dopamine projections do not sensitise to chronic or acute stress and the cellular activity of dopamine is greatest in prefrontal cortex, showing a 20-fold greater release of dopamine in response to stress relative to the striatum. Enhanced release of dopamine in response to stress in prefrontal cortex impairs processing of goal-directed behaviour, whereas stimulus-driven processing in the striatum is relatively unimpaired by stress in a manner that facilitates stimulus-driven processing over goal-directed processing in conditions of stress [30]. Both cognitive and emotional distractors take off-line working memory processes and impair cognitive performance by switching the functioning to phylogenetically older brain circuits [59]. Thus, in the presence of distraction causing cognitive or emotional stress, attention regulation switches from slow ‘top down’ regulation by the prefrontal cortex that is focused on the goal-relevant information, to the reflexive and rapid ‘bottom-up’ regulation by the sensory cortex, where the physical characteristics of the stimuli (e.g. its high intensity) capture attention [59]. This raises a question about possible strategies of information processing under stress.

5. Origin of the Sociable Primate

When acutely stressed, unrewarding information may appear rewarding and a single pattern of behaviour may become so robust that it causes maladaptive responding in the face of changing goals or contexts [52]. Given the negative influence of acute stress on cognitive processing [52], the tendency has been to highlight the strategies that facilitate positive interactions through the action of opiates such as endorphins [24]. The anatomical distribution of the endorphin system in areas related to aversive experience and stress such as the hypothalamus, the pituitary gland, and the adrenal medulla indicates the key function of endorphin in ameliorating negative effects of exposure to stress [60]. For instance, exposure to stressful, aversive events is accompanied by the release of endorphins in plasma [61]. Thus, the presence of aversive stimuli activates stress that can release endorphins, enabling the observer to evaluate an unrewarding stimuli in a more positive or less negative way. Changes in the affective colouring given to aversive stimuli can reduce sensitivity to potentially negative outcomes associated with a social relationship and may aid in the search and attainment of this relationship to favour the formation of positive associations, facilitating approach behaviours [24]. In the case described above, the approach is achieved through endogenous release of endorphins due to the internal stimulus of stress [24]. In conditions of high uncertainty or fear, primates use a number of behaviours to ameliorate stress which involve endorphin system (e.g. gentle biting, embracing, holding hands, kissing, stroking, lip smacks and chorusing in chimpanzees, or g-g rubbing in bonobos) [62-64]. An understanding of intentions is not required in these contexts, fostering social bonding on a larger scale during acute stress [41].

When chronically stressed, alterations to dopamine dynamics in prefrontal cortex may cause the ambiguity of the goal to increase, causing incongruent responding, and the rewarding information may appear unrewarding, causing inhibition [52]. In a chronic stress condition, the use of intentional communication, as indicated by the presence of behaviours such as audience checking, response waiting and persistence accompanying the communication [12, 65], may reduce ambiguity in the recipient and facilitate responding to rewarding stimuli. One possible route for this is activation of under-stimulated D1 receptors to excite the thalamus and release the indirect pathway from excessive inhibition of relevant rewarding information [53]. The enhanced processing in conditions of chronic stress might occur through the influence of communication on arousal (when the functioning is not a disorder). These behaviours would expose the recipient to a single dose of a mild stressor, which in turn would potentiate dopamine dynamics and goal directed processing [66]. It is well established that oculomotor control, and specifically the saccadic system, influences the magnitude and fidelity of neural signals involved in forming representations, dependent on selective attention functions in the prefrontal cortex [67]. This activity largely overlaps with the activity of the locus coeruleus-norepinephrine system (LC-NE), playing a key role in working memory capacity through regulating the balance between the selective attention state and arousal [68]. Dopamine in the prefrontal cortex plays a crucial functional role for anticipatory, visual reorienting responses but not for sensory-driven movement [69].

Mutual visual contact appears to play an important role in forming representations of others' goals by triggering the spontaneous attributions of mental states in the recipient in healthy humans [70]. The process of mental attribution is shown by the effect of exchanging mutual visual contact, with goal attribution highest during mutual visual contact in both the recipient of gaze behaviour as well as the giver [71]. In humans, seeing another person's direct gaze was associated with subsequent redirecting of movement towards the sender of the visual contact [72]. Further, in a condition when gaze was received in the absence of mutual visual contact, there was increase in self-awareness in the recipient of the eye gaze [66], which was associated with increase in skin conductance ratings relative to no gaze condition (both sender and receiver looking in opposite directions). This suggests that receiving visual attention in the absence of mutual gaze is nonetheless associated with subsequent redirecting of attention towards the sender of the visual contact to facilitate goal attribution [71]. Whilst in many species mutual visual contact is a threat, in more egalitarian primate species eye contact is tolerated [73] and plays an important role in regulating social interactions [74]. For example, mutual visual contact is important in female-female sexual contact in bonobos, with sexual interactions accompanied by mutual visual contact lasting longer than those without [75]. Overall therefore mutual visual contact plays an important role in directing attention in both primates and humans.

When combined with mutual visual contact, manual visual gestures such as pointing induce maximal activity in the hippocampus (relative to mutual visual contact alone) in humans, a region known to play a role in regulating dopamine dynamics in prefrontal cortex [53, 76]. Further, use of right-handed gestures is controlled by the left hemisphere, increasing the signaller's accuracy of movement towards the recipient of the gesture in chimpanzees [77]. Primates direct right-handed gestures at the individuals who display stress in presence of the signaller, suggesting an important role of right-handed gestures in regulating dopamine dynamics [71]. Manual visual gestures in great apes are not rigidly distinctive, but the large variation and gradation in the structural components making up manual visual gestures suggests that these signals might attract attention through their novelty [78]. Dopamine neurons in the prefrontal cortex are excited when novel information is presented, but have weaker responses to neutral events [23, 79]. Further, surprising low probability events such as producing signal in non-dominant context or elaborations of communicative acts that are inconsistent with prior expectations (and hence require the recipient to generate an explanation) can prompt goal-directed processing and shifts in understanding [80]. Finally, neurons in the orbitofrontal cortex are activated by primary, appetitive reinforcers, such as gentle sweeping touch, creating representation of the pleasant stimulus in the recipient but not influencing subsequent movement [81]. The orbitofrontal cortex has a direct connection with the striatum, so that involvement of the habitual system could potentiate representations of goals and values of the observer.

6. Coevolution of Communicative and Social Complexity

The formation of social bonds in complex social settings is cognitively demanding because audience characteristics impose social stresses, meaning that social bonding is less likely to be successful than in simpler social settings (Fig. S1). For signallers, adjusting their communication according to the characteristics of both the recipient and the audience is a more complex cognitive challenge in groups with a larger number of differentiated social relationships [8]. As social complexity increases, there are more direct and third-party relationships for the signaller to keep track of (e.g. judging both the dominance status of audience members and their alliance status to the recipient [39, 82]). Under chronic stress, primates tend to avoid interactions with unfamiliar conspecifics and focus their limited time budgets on a small number of strong social bonds where the reward has already been experienced [83] . For example, during a period of instability in the male dominance hierarchy, female chacma baboons focused their grooming on a small number of preferred partners, and this reduction in grooming diversity was associated with a reduction in stress as measured by glucocorticoid levels [84]. In contrast, provisioned rhesus macaques widened their social networks after a hurricane [85], suggesting that events which disrupt the ecological habitat of the whole group through loss of green vegetation and shade may have different effects than social stressors, for which a strong set of social bonds provides an important buffer [84]. When social bonds become weaker under chronic stress, this creates need for more innovation through communication to capture others' attention. Complex, intentional communication involves the signaler monitoring the recipient's attention and adjusting their communication to achieve the intended goal [12, 86]. This augments goal-directed processing of information by the recipients, allowing individuals to perceive social interactions as relevant and rewarding during chronic stress. As dyad partners repeatedly interact in a goal-directed way through complex communicative signals, the cognitive control may transfer to the habitual system, giving rise to social coordination based on an automatic perception of value. This allows an effective means to maintain social relationships when the challenges of group-living demand reallocation of cognitive resources from the recipient onto the external environment during chronic stress, when primates prioritize processing of information relevant to the stressor, at the expense of processing information relevant to rewarding goals.

This capacity builds more complex social bonding in terms of both a greater range of social interactions and a greater range of social partners [5, 8, 87]. The association between brain size and group size in primates consists of a series of socio-cognitive grades rather than a single linear relationship, with cognitive abilities such as inhibition and executive function that are important in communication complexity increasing across the grades [11]. The multi-level structure found in larger groups such as baboons and chimpanzees is dependent on maintaining both strong social bonds within sub-groups and weaker ties across the whole group, thus maintaining overall group cohesion [11]. More complex, intentional communication may play an important role in this process, allowing social bonding on a larger scale, by creating an efficient form of attribution of value, overcoming the bias to bond with a narrow range of closely related conspecifics [84]. Given the importance of communication in the daily interactions of socially complex primates, this would suggest that a phase transition from less complex to more complex sociality is dependent on an increase in communication complexity [10, 11].

It is noteworthy that, in wild chimpanzees, the size of the social network is positively correlated with the diversity of social partners to whom visual contacts, manual gestures, and vocalisations accompanying use of visual bodily signals (e.g. bending of the back) are directed [9]. These behaviours function more effectively to direct the recipient's movement and attention than visual bodily signals alone. If the formation of social bonds is cognitively complex because it demands goal-directed processing of social information, then less and more complex social groups will not differ in the number of social bonds primates form with group members [88]. However, if use of complex communication would reduce these demands, the number of social bonds that the individuals can form in more complex social groups will increase [14]. For example, gelada male baboons form long-term social bonds with females, whereas chacma baboons form shorter term consortships. Thus geladas have a more complex social structure and they also have a larger vocal repertoire than chacmas, with derived vocalisations used in affiliative interactions with the females in their reproductive unit [89].

Through the course of hominin evolution, there was an increase both in brain size and group size, leading to selection pressures for more efficient mechanisms of social bonding than grooming [1]. As group size increases, there is greater number of differentiated social relationships to monitor and a greater risk of monopolisation of ecological and social resources by dominant members of the group [44, 45] leading to stresses which would reduce the coherence of the group in the absence of social bonding mechanisms. When humans expanded into drier habitats with lower resource availability, these stresses would have increased, demanding more efficient bonding mechanisms. More complex communication enables social bonding at a larger scale, and thus selective pressures arising from increased group size and resource scarcity may have played an important role in the evolution of human language, as well as other forms of nonverbal social interaction such as laughter, singing and dancing [1, 10, 90]. In short, complex communication, and the cognitive skills needed for such communication, may have evolved in both humans and primates to enable more efficient social bonding in conditions of social stress.

7. Conclusion

Social bonding is essentially a process of the attribution of value, where the interactants experience the emotions of 'liking' and 'wanting' due to prior experience of the social relationship and the use of communication. Social bonding with regular social partners in part involves value attribution through bottom up processes, where goal understanding of the social interaction is not necessary. In contrast, interacting with less familiar group members requires cognitive processing of the goal of the action to attribute value. We have argued that intentional communication (e.g. gestural communication in great apes [77]) has the potential to reduce time and cognitive demands on processing of social relationships because it can transmit value information, whereby observers attribute value to the signals in repeated instances of social interactions. However, chronic and acute exposure to social stressors exerts a global influence on the dopaminergic system in a similar way to exposure to distraction, causing a switch from goal-directed to stimulus-driven processing [30]. When animals are acutely stressed, aversive stimuli may appear overly apparent and rewarding, causing maladaptive responding [52]. In this context, the use of habitual signals may enable the recipient to redirect their attention on the relevant, rewarding goals. In contrast, when chronically stressed, rewarding stimuli may appear irrelevant and unrewarding, causing inhibition [52]. Regulating use of intentional signals may enhance cognitive processing when exposed to stressors by upregulating the dopamine system, which is necessary for goal-directed processing to occur during stress. In a chronic stress condition, this would activate under-stimulated D1 receptors and release the indirect pathway from excessive inhibition of relevant, rewarding information [53]. Future studies should focus on differences in cognitive skills underpinning use of communication in response to exposure to stressors to provide new insights into the evolutionary origins of language.

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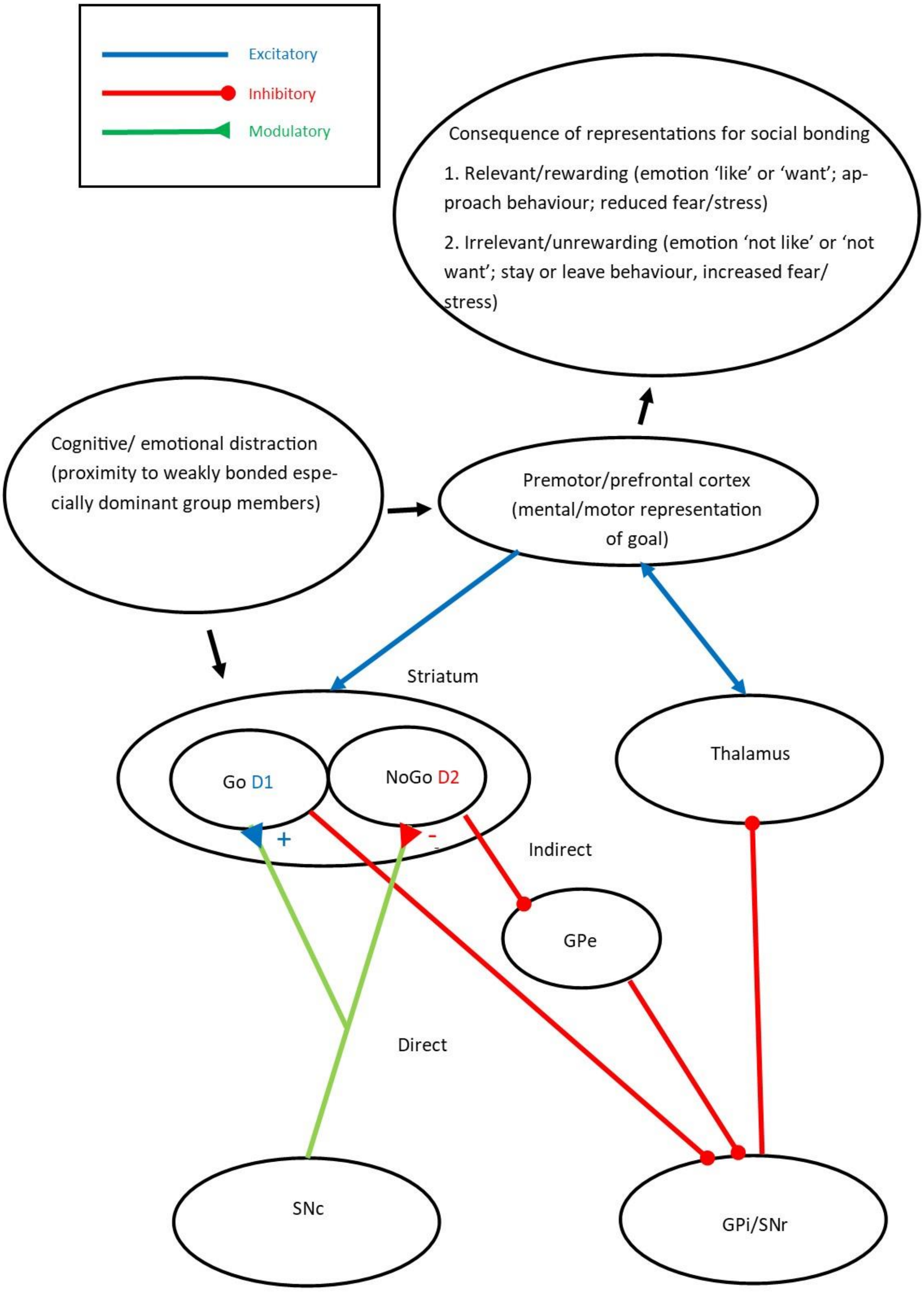
Fig. 1. The function of cortico-striato-thalamo-cortical loops of the basal ganglia in processing of social information, composed of the direct (Go) pathways, modulated by D1 dopamine receptors and indirect pathways (NoGo) modulated by D2 dopamine receptors. The role of Go cells is to disinhibit the thalamus to facilitate the execution of the actions represented in the cortex via the internal segment of the globus pallidus (GPi). The inhibition of the thalamus, to suppress actions from being performed is executed by the NoGo cells. Dopamine projects to the dorsal striatum from substantia nigra pars compacta (SNc) to excite Go cells via D1 receptors and inhibit NoGo cells via D2 receptors. Adapted from Frank [58].


Excitatory
Inhibitory
Modulatory
Consequence of representations for social bonding
1. Relevant/rewarding (emotion 'like' or 'want'; approach behaviour; reduced fear/stress)
2. Irrelevant/unrewarding (emotion 'not like' or 'not want'; stay or leave behaviour, increased fear/stress)
Cognitive/ emotional distraction (proximity to weakly bonded especially dominant group members)
Premotor/prefrontal cortex (mental/motor representation of goal)
Striatum
Thalamus
Go D1
NoGo D2
+
-
Indirect
GPe
Direct
SNc
GPi/SNr