

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36

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

Sam G. B. Roberts¹, Robin I.M. Dunbar², Anna I. Roberts³

¹ School of Psychology, Liverpool John Moores University, Liverpool, L3 3AF, UK

² Department of Experimental Psychology, University of Oxford, OX2 6GG, UK

³ Institute of Human Biology and Evolution, Adam Mickiewicz University, Poznan, Poland

Correspondence: anna.roberts@amu.edu.pl

Key words: Communication, cognition, social bonds, stress, goal-directed processing, stimulus-driven processing, primates

Published version:

Roberts, S. G., Dunbar, R. I., & Roberts, A. I. (2022). Communicative roots of complex sociality and cognition: neuropsychological mechanisms underpinning the processing of social information. *Philosophical Transactions of the Royal Society B*, 377, 20210295. <https://doi.org/10.1098/rstb.2021.0295>

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

39 **Abstract**

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

57 **1. Introduction**

58 Primates have unusually large brains for their body size and it has been proposed that cognitive
59 processing capacities behind tracking social relationships (represented by relative neocortex
60 size) place an upper limit on the size of groups that can be maintained as a cohesive social unit
61 [1]. Primates do not maintain equally strong social relationships with all group members, but
62 form stable, long-lasting bonds with selected related and unrelated group members [2]. One
63 of the primary mechanisms that primates use for maintaining these social bonds is grooming,
64 which can account for up to 20% of their total daytime activity budget in the most social species
65 such as gelada baboons [3]. The amount of time primates spend grooming is positively related
66 to group size [3]. However, in doing so they do not groom with more individuals; rather, they
67 devote more time to maintaining the same number of social relationships [3]. Primates also use
68 a wide range of communicative signals including vocalisations [4], gestures [5] and emotional
69 expressions [6] and these signals are important for maintaining social relationships between
70 group members [7]. In this context, social complexity is defined in terms of the network where
71 individuals interact with many different individuals across many different social contexts,
72 whilst communicative complexity is defined as systems which contain a larger number of
73 functionally distinct elements, or in which a large number of bits of information are contained
74 within signals [8]. However, the specific role that cognitive skills play in this complex
75 communication, and how in turn this relates to sociality, is still unclear. In this paper we
76 propose the hypothesis that communicative complexity is an adaptation to managing the social
77 stress of living in groups in a way that enables primates to form social bonds through complex
78 communication [9]. Thus, we will explore what makes managing social relationships
79 cognitively complex and propose that evolution of communicative complexity occurred to
80 overcome the stresses imposed by group-living [10].

81 **2. What is Social Bonding?**

82

83 Exploring the link between sociality and key features of complex communication such as
84 intentionality provides insights into how increasing flexibility in communication can facilitate
85 the emergence of social systems characterized by bonded social relationships, such as those
86 found in non-human primates (hereafter primates) and humans [8, 11]. In intentional
87 communication, the signaller communicates with a specific goal in mind and shows flexibility
88 in the pattern of communication to achieve that goal, including sensitivity to the recipients'
89 orientation, response waiting (communicating and visually monitoring recipient's response),
90 and persisting or elaborating their communication if the goal of the communication is not met
91 [12]. Intentional communication is under volitional control, as indicated by selective use of the
92 signal in response to social factors – the behavioural context, the potential recipient and wider
93 audience [10, 12]. Gestural communication, particularly in great apes [13], has shown strong
94 evidence of intentionality, although the evidence for intentionality in vocal communication in
95 other primates is more mixed [4]. However, whilst intentionality in communication has
96 traditionally been considered from the standpoint of the signaller, recent studies point to the
97 important role of intentionality from the standpoint of the recipient of the signalling [5, 14].
98 According to this perspective, intentional communication is cognitively complex because it
99 facilitates attribution of value to social relationships by the recipient through augmenting their
100 understanding of others' goals and intentions [9]. Intentional communication requires a number
101 of key cognitive skills from both signallers and receivers, including inhibition and executive
102 function to enable selective use of communicative signals and knowledge of direct and third
103 party relationships to adjust communication to the social context [12, 15]. The social cognitive
104 abilities underpinning the intentional use of communication are correlated with brain size in
105 primates [11, 16], which is also strongly correlated with group size [11]. Communication is
106 important in all group-living primates to enable them to meet the challenges of sociality [10,
107 11], but the extent to which different species of primates can communicate intentionally is still
108 debated [4, 12]. If the use of intentional communication enables primates to overcome the
109 stresses imposed by group living, we predict that more complex communication systems, and
110 the social cognition which underpins this communication, will be associated with more
111 complex social systems [8, 10, 11]

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

127 Social bonding has a psychological benefit of reducing fear during social competition (e.g. fear
128 of aggression [22]) as well as a physiological benefit (e.g. endorphin release during grooming),
129 making it inherently pleasant [21]. 'Wanting' has been characterised as the subjective emotional
130 state elicited by the representation of value, in response to the presentation of desirable stimuli of the
131 highest value to the individual goals of the recipient [23]. Further, the positive emotional state of

132 'liking' increases the power of the stimuli to excite the recipient further than the state of 'wanting'
133 [24], motivating approach behaviours as well as positively valenced emotions [23]. This contrasts
134 with the subjective emotional state elicited by undesirable events, which produces negative
135 representations of value to the individual goals of the recipient. In this case, the punishing stimulus is
136 assigned the 'not wanting' or 'not liking' attribute, leading to avoidance behaviour and negatively
137 valenced emotions [23].

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

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

168 Focused attention to a target stimulus provides a means of selecting neural representations for
169 further processing and augmenting the representations favouring that target to increase the
170 magnitude and fidelity of neural signals dependent on the attentional focus [27]. The objective
171 of voluntary attention can thus be viewed as increasing specificity of representations [27].
172 Primates use relevant information such as the identity of the partner, the social relationships in
173 the group as a whole and the ongoing context (e.g. mating, aggression, travel) to form
174 representations about the goal of social interactions [15, 19]. Further, communication forms an
175 important part of the incoming information, and can make social goals of individual importance
176 more relevant, as represented in the working memory of the observer [9, 13]. This amounts to
177 making an adaptive decision about the goal of the interaction whereby access to accumulated
178 knowledge facilitates a flexible increase in the accuracy and consistency of the response to a
179 novel situation. Once the incoming information has been evaluated according to behavioural

180 rules and context, an appropriate motor plan is formed and executed based on generated
181 representation of the goal [28]. This ability is dependent on Brodmann Area 10, a region of the
182 prefrontal cortex only found in anthropoid primates [29], suggesting that primates may have
183 an advantage in goal-directed processing of social information compared to other mammals.

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

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

212 **3. The Double Jeopardy of Primate Social Life**

213 The main benefit to group-living in primates lies in reducing the risk of predation [35].
214 To maintain group cohesion over time, and thus benefit from reduction in predation risk, group
215 members must coordinate their behaviour with others over time and space, either as one single
216 group or, in fission-fusion social systems, as a set of smaller semi-independent foraging parties
217 [36]. To understand the dynamics shaping social cohesion, a detailed understanding of which
218 factors influence the ability of primates to build and maintain social relationships over time is
219 required, as this is at the heart of what makes primate life socially complex [2, 11]. Other
220 species also come together in large groups (e.g. grazing ungulates such as wildebeest and
221 buffalo), but these are loose aggregations of animals, without stable group membership and
222 long-term social relationships between individuals [21]. In contrast, primates live in groups
223 with stable membership, and form long-lasting bonds with certain individuals within the group
224 [2]. These bonds have direct fitness consequences – for example, the sociality of adult female
225 baboons (as measured by grooming and proximity to others) is positively associated with infant
226 survival [2].

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

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

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

276 [48], the cognitive constraints on forming social relationships in larger social groups imply that
277 many individuals will have weak bonds with the dominant group members [41, 49]. From the
278 point of view of cognitive and emotional distractions acting as regular stressors in primate
279 social life, it is thus important to determine the nature of the influence of these stressors on the
280 capacity of primates to process social information.

281 **4. The Influence of Stress on Processing of Social Information**

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

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

319 At the level of cognitive processing in the prefrontal cortex, reduced tonic dopamine reduces
320 the ability of the phasic bursts to activate D1 receptors in the direct pathway, leading to too
321 little updating and maintenance of relevant representations [56]. This results in reduced LTP
322 of relevant representations, but relatively enhanced LTD of irrelevant information. Conversely,
323 excessive tonic dopamine leading to reduced ability of the phasic dips to activate D2 receptors

324 in the indirect pathway would lead to excessive updating of relevant information (LTP) but
325 reduced avoidance of irrelevant information (LTD). At the level of motor performance,
326 elevated levels of dopamine result in increased potentiation of rewarding actions, but reduced
327 avoidance of aversive outcomes. On the other hand, when tonic dopamine is reduced below
328 baseline, this leads to reduced learning of rewarding actions, but relatively enhanced avoidance
329 of aversive actions as the overactive indirect pathway leads to excessive inhibition.

330 The effects of stress on dopaminergic function are not uniform, but converging lines of
331 evidence show that stress can operate as a switch between goal-directed processing mediated
332 by the prefrontal cortex and stimulus-driven processing relying on the intact striatum [30].
333 Whereas dopamine innervation is comparatively sparse in prefrontal cortex as compared to the
334 striatum, dopaminergic pathways respond differently to stress. There is evidence that
335 subcortical dopamine projections do not sensitise to chronic or acute stress and the cellular
336 activity of dopamine is greatest in prefrontal cortex, showing a 20-fold greater release of
337 dopamine in response to stress relative to the striatum. Enhanced release of dopamine in
338 response to stress in prefrontal cortex impairs processing of goal-directed behaviour, whereas
339 stimulus-driven processing in the striatum is relatively unimpaired by stress in a manner that
340 facilitates stimulus-driven processing over goal-directed processing in conditions of stress [30].
341 Both cognitive and emotional distractors take off-line working memory processes and impair
342 cognitive performance by switching the functioning to phylogenetically older brain circuits
343 [59]. Thus, in the presence of distraction causing cognitive or emotional stress, attention
344 regulation switches from slow ‘top down’ regulation by the prefrontal cortex that is focused on
345 the goal-relevant information, to the reflexive and rapid ‘bottom-up’ regulation by the sensory
346 cortex, where the physical characteristics of the stimuli (e.g. its high intensity) capture attention
347 [59]. This raises a question about possible strategies of information processing under stress.

348 **5. Origin of the Sociable Primate**

349 When acutely stressed, unrewarding information may appear rewarding and a single pattern of
350 behaviour may become so robust that it causes maladaptive responding in the face of changing
351 goals or contexts [52]. Given the negative influence of acute stress on cognitive processing
352 [52], the tendency has been to highlight the strategies that facilitate positive interactions
353 through the action of opiates such as endorphins [24]. The anatomical distribution of the
354 endorphin system in areas related to aversive experience and stress such as the hypothalamus,
355 the pituitary gland, and the adrenal medulla indicates the key function of endorphin in
356 ameliorating negative effects of exposure to stress [60]. For instance, exposure to stressful,
357 aversive events is accompanied by the release of endorphins in plasma [61]. Thus, the presence
358 of aversive stimuli activates stress that can release endorphins, enabling the observer to
359 evaluate an unrewarding stimuli in a more positive or less negative way. Changes in the
360 affective colouring given to aversive stimuli can reduce sensitivity to potentially negative
361 outcomes associated with a social relationship and may aid in the search and attainment of this
362 relationship to favour the formation of positive associations, facilitating approach behaviours
363 [24]. In the case described above, the approach is achieved through endogenous release of
364 endorphins due to the internal stimulus of stress [24]. In conditions of high uncertainty or fear,
365 primates use a number of behaviours to ameliorate stress which involve endorphin system (e.g.
366 gentle biting, embracing, holding hands, kissing, stroking, lip smacks and chorusing in
367 chimpanzees, or g-g rubbing in bonobos) [62-64]. An understanding of intentions is not
368 required in these contexts, fostering social bonding on a larger scale during acute stress [41].

369 When chronically stressed, alterations to dopamine dynamics in prefrontal cortex may cause
370 the ambiguity of the goal to increase, causing incongruent responding, and the rewarding
371 information may appear unrewarding, causing inhibition [52]. In a chronic stress condition, the

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

388 Mutual visual contact appears to play an important role in forming representations of others'
389 goals by triggering the spontaneous attributions of mental states in the recipient in healthy
390 humans [70]. The process of mental attribution is shown by the effect of exchanging mutual
391 visual contact, with goal attribution highest during mutual visual contact in both the recipient
392 of gaze behaviour as well as the giver [71]. In humans, seeing another person's direct gaze was
393 associated with subsequent redirecting of movement towards the sender of the visual contact
394 [72]. Further, in a condition when gaze was received in the absence of mutual visual contact,
395 there was increase in self-awareness in the recipient of the eye gaze [66], which was associated
396 with increase in skin conductance ratings relative to no gaze condition (both sender and
397 receiver looking in opposite directions). This suggests that receiving visual attention in the
398 absence of mutual gaze is nonetheless associated with subsequent redirecting of attention
399 towards the sender of the visual contact to facilitate goal attribution [71]. Whilst in many
400 species mutual visual contact is a threat, in more egalitarian primate species eye contact is
401 tolerated [73] and plays an important role in regulating social interactions [74]. For example,
402 mutual visual contact is important in female-female sexual contact in bonobos, with sexual
403 interactions accompanied by mutual visual contact lasting longer than those without [75].
404 Overall therefore mutual visual contact plays an important role in directing attention in both
405 primates and humans.

406 When combined with mutual visual contact, manual visual gestures such as pointing induce
407 maximal activity in the hippocampus (relative to mutual visual contact alone) in humans, a
408 region known to play a role in regulating dopamine dynamics in prefrontal cortex [53, 76].
409 Further, use of right-handed gestures is controlled by the left hemisphere, increasing the
410 signaller's accuracy of movement towards the recipient of the gesture in chimpanzees [77].
411 Primates direct right-handed gestures at the individuals who display stress in presence of the
412 signaller, suggesting an important role of right-handed gestures in regulating dopamine
413 dynamics [71]. Manual visual gestures in great apes are not rigidly distinctive, but the large
414 variation and gradation in the structural components making up manual visual gestures
415 suggests that these signals might attract attention through their novelty [78]. Dopamine neurons
416 in the prefrontal cortex are excited when novel information is presented, but have weaker
417 responses to neutral events [23, 79]. Further, surprising low probability events such as
418 producing signal in non-dominant context or elaborations of communicative acts that are
419 inconsistent with prior expectations (and hence require the recipient to generate an explanation)
420 can prompt goal-directed processing and shifts in understanding [80]. Finally, neurons in the

421 orbitofrontal cortex are activated by primary, appetitive reinforcers, such as gentle sweeping
422 touch, creating representation of the pleasant stimulus in the recipient but not influencing
423 subsequent movement [81]. The orbitofrontal cortex has a direct connection with the striatum,
424 so that involvement of the habitual system could potentiate representations of goals and values
425 of the observer.

426 **6. Coevolution of Communicative and Social Complexity**

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

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

468 complex to more complex sociality is dependent on an increase in communication complexity
469 [10, 11].

470 It is noteworthy that, in wild chimpanzees, the size of the social network is positively correlated
471 with the diversity of social partners to whom visual contacts, manual gestures, and
472 vocalisations accompanying use of visual bodily signals (e.g. bending of the back) are directed
473 [9]. These behaviours function more effectively to direct the recipient's movement and
474 attention than visual bodily signals alone. If the formation of social bonds is cognitively
475 complex because it demands goal-directed processing of social information, then less and more
476 complex social groups will not differ in the number of social bonds primates form with group
477 members [88]. However, if use of complex communication would reduce these demands, the
478 number of social bonds that the individuals can form in more complex social groups will
479 increase [14]. For example, gelada male baboons form long-term social bonds with females,
480 whereas chacma baboons form shorter term consortships. Thus geladas have a more complex
481 social structure and they also have a larger vocal repertoire than chacmas, with derived
482 vocalisations used in affiliative interactions with the females in their reproductive unit [89].

483 Through the course of hominin evolution, there was an increase both in brain size and group
484 size, leading to selection pressures for more efficient mechanisms of social bonding than
485 grooming [1]. As group size increases, there is greater number of differentiated social
486 relationships to monitor and a greater risk of monopolisation of ecological and social resources
487 by dominant members of the group [44, 45] leading to stresses which would reduce the
488 coherence of the group in the absence of social bonding mechanisms. When humans expanded
489 into drier habitats with lower resource availability, these stresses would have increased,
490 demanding more efficient bonding mechanisms. More complex communication enables social
491 bonding at a larger scale, and thus selective pressures arising from increased group size and
492 resource scarcity may have played an important role in the evolution of human language, as
493 well as other forms of nonverbal social interaction such as laughter, singing and dancing [1,
494 10, 90]. In short, complex communication, and the cognitive skills needed for such
495 communication, may have evolved in both humans and primates to enable more efficient social
496 bonding in conditions of social stress.

497 **7. Conclusion**

498 Social bonding is essentially a process of the attribution of value, where the interactants
499 experience the emotions of 'liking' and 'wanting' due to prior experience of the social
500 relationship and the use of communication. Social bonding with regular social partners in part
501 involves value attribution through bottom up processes, where goal understanding of the social
502 interaction is not necessary. In contrast, interacting with less familiar group members requires
503 cognitive processing of the goal of the action to attribute value. We have argued that intentional
504 communication (e.g. gestural communication in great apes [77]) has the potential to reduce
505 time and cognitive demands on processing of social relationships because it can transmit value
506 information, whereby observers attribute value to the signals in repeated instances of social
507 interactions. However, chronic and acute exposure to social stressors exerts a global influence
508 on the dopaminergic system in a similar way to exposure to distraction, causing a switch from
509 goal-directed to stimulus-driven processing [30]. When animals are acutely stressed, aversive
510 stimuli may appear overly apparent and rewarding, causing maladaptive responding [52]. In
511 this context, the use of habitual signals may enable the recipient to redirect their attention on
512 the relevant, rewarding goals. In contrast, when chronically stressed, rewarding stimuli may
513 appear irrelevant and unrewarding, causing inhibition [52]. Regulating use of intentional
514 signals may enhance cognitive processing when exposed to stressors by upregulating the
515 dopamine system, which is necessary for goal-directed processing to occur during stress. In a

516 chronic stress condition, this would activate under-stimulated D1 receptors and release the
517 indirect pathway from excessive inhibition of relevant, rewarding information [53]. Future
518 studies should focus on differences in cognitive skills underpinning use of communication in
519 response to exposure to stressors to provide new insights into the evolutionary origins of
520 language.

521 **Acknowledgments**

522 This work has been funded by National Science Centre, Poland, UMO-2018/31/ D/NZ8/01144
523 ('Understanding origins of social brains and communication in wild primates') at Institute of
524 Human Biology and Evolution, Faculty of Biology, Adam Mickiewicz University, 61614,
525 Poznan, Poland

526 **References**

- 527 [1] Dunbar, R. I. M. 1998 The social brain hypothesis. *Evolutionary Anthropology* **6**, 178-190.
528 [2] Silk, J. B. 2007 Social components of fitness in primate groups. *Science* **317**, 1347-1351.
529 (DOI:10.1126/science.1140734|ISSN 0036-8075).
530 [3] Lehmann, J., Korstjens, A. & Dunbar, R. 2007 Group size, grooming and social cohesion in
531 primates. *Animal Behaviour* **74**, 1617-1629.
532 [4] Fischer, J. & Price, T. 2017 Meaning, intention, and inference in primate vocal communication.
533 *Neuroscience & Biobehavioral Reviews* **82**, 22-31.
534 [5] Roberts, A. I., Vick, S.-J. & Buchanan-Smith, H. 2012 Usage and comprehension of manual
535 gestures in wild chimpanzees. *Animal Behaviour* **84**, 459-470. (DOI:10.1016/j.anbehav.2012.05.022).
536 [6] Florkiewicz, B. & Campbell, M. 2021 Chimpanzee facial gestures and the implications for the
537 evolution of language. *PeerJ* **9**, e12237.
538 [7] Liebal, K., Call, J. & Tomasello, M. 2004 Use of gesture sequences in chimpanzees. *American*
539 *Journal of Primatology* **64**, 377-396.
540 [8] Freeberg, T. M., Dunbar, R. I. & Ord, T. J. 2012 Social complexity as a proximate and ultimate
541 factor in communicative complexity. *Philosophical Transactions of the Royal Society B: Biological*
542 *Sciences* **367**, 1785-1801.
543 [9] Roberts, S. & Roberts, A. I. 2018 Visual attention, indicative gestures, and calls accompanying
544 gestural communication are associated with sociality in wild chimpanzees (*Pan troglodytes*
545 *schweinfurthii*). *Journal of Comparative Psychology*. (DOI:10.1037/com0000128).
546 [10] Roberts, A. & Roberts, S. G. 2019 Communicative roots of complex sociality and cognition.
547 *Biological Reviews*. (DOI:10.1111/brv.12553).
548 [11] Dunbar, R. I. & Shultz, S. 2021 Social complexity and the fractal structure of group size in
549 primate social evolution. *Biological Reviews*.
550 [12] Townsend, S. W., Koski, S. E., Byrne, R. W., Slocombe, K. E., Bickel, B., Boeckle, M., Braga
551 Goncalves, I., Burkart, J. M., Flower, T. & Gaunet, F. 2017 Exorcising G. B. S. Rice's ghost: An empirical
552 approach to studying intentional communication in animals. *Biological Reviews* **92**, 1427-1433.
553 [13] Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H. 2005 Understanding and sharing
554 intentions: the origins of cultural cognition. *Behavioural and Brain Sciences* **28**, 675-735.
555 [14] Roberts, A. I. & Roberts, S. G. B. 2016 Wild chimpanzees modify modality of gestures according
556 to the strength of social bonds and personal network size. *Scientific Reports* **6**.
557 (DOI:10.1038/srep33864).
558 [15] Silk, J. B., Seyfarth, R. M. & Cheney, D. L. 2016 Strategic use of affiliative vocalizations by wild
559 female baboons. *PLoS One* **11**, e0163978.
560 [16] Devaine, M., San-Galli, A., Trapanese, C., Bardino, G., Hano, C., Saint Jalme, M., Bouret, S., Masi,
561 S. & Daunizeau, J. 2017 Reading wild minds: a computational assay of theory of mind sophistication
562 across seven primate species. *PLoS computational biology* **13**, e1005833.
563 [17] Westbrook, A. & Braver, T. S. 2016 Dopamine does double duty in motivating cognitive effort.
564 *Neuron* **89**, 695-710.

565 [18] Skuse, D. H. & Gallagher, L. 2009 Dopaminergic-neuropeptide interactions in the social brain.
566 *Trends in cognitive sciences* **13**, 27-35.

567 [19] Adams, G. K., Ong, W. S., Pearson, J. M., Watson, K. K. & Platt, M. L. 2021 Neurons in primate
568 prefrontal cortex signal valuable social information during natural viewing. *Philosophical*
569 *Transactions of the Royal Society B* **376**, 20190666.

570 [20] Adolphs, R. 2009 The social brain: neural basis of social knowledge. *Annual review of psychology*
571 **60**, 693-716.

572 [21] Dunbar, R. I. M. & Shultz, S. 2010 Bondedness and sociality. *Behaviour* **147**, 775-803.
573 (DOI:10.1163/000579510x501151).

574 [22] Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Medoza, S. P., Saltzman, W.,
575 Snowdon, C. T., Ziegler, T. E., Banjevic, M., Garland, T., et al. 2003 Are subordinates always stressed?
576 A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*
577 **43**, 67-82. (DOI:10.1016/s0018-506x(02)00037-5).

578 [23] Bromberg-Martin, E. S., Matsumoto, M. & Hikosaka, O. 2010 Dopamine in motivational control:
579 rewarding, aversive, and alerting. *Neuron* **68**, 815-834.

580 [24] Dum, J. & Herz, A. 1987 Opioids and motivation. *Interdisciplinary Science Reviews* **12**, 180-190.

581 [25] Mayes, L. C., Magidson, J., Lejuez, C. & Nicholls, S. S. 2009 Social relationships as primary
582 rewards: The neurobiology of attachment.

583 [26] Pan, X., Fan, H., Sawa, K., Tsuda, I., Tsukada, M. & Sakagami, M. 2014 Reward inference by
584 primate prefrontal and striatal neurons. *Journal of Neuroscience* **34**, 1380-1396.

585 [27] Noudoost, B. & Moore, T. 2011 The role of neuromodulators in selective attention. *Trends in*
586 *cognitive sciences* **15**, 585-591.

587 [28] Chenery, H. J., Angwin, A. J. & Copland, D. A. 2008 The basal ganglia circuits, dopamine, and
588 ambiguous word processing: A neurobiological account of priming studies in Parkinson's disease.
589 *Journal of the International Neuropsychological Society* **14**, 351-364.

590 [29] Passingham, R. E. & Wise, S. P. 2012 *The neurobiology of the prefrontal cortex: anatomy,*
591 *evolution, and the origin of insight*, Oxford University Press.

592 [30] Schwabe, L., Tegenthoff, M., Höffken, O. & Wolf, O. T. 2010 Concurrent glucocorticoid and
593 noradrenergic activity shifts instrumental behavior from goal-directed to habitual control. *Journal of*
594 *Neuroscience* **30**, 8190-8196.

595 [31] Gray, J. R., Braver, T. S. & Raichle, M. E. 2002 Integration of emotion and cognition in the lateral
596 prefrontal cortex. *Proceedings of the National Academy of Sciences* **99**, 4115-4120.

597 [32] Bouton, M. E. 1994 Context, ambiguity, and classical conditioning. *Current directions in*
598 *psychological science* **3**, 49-53.

599 [33] Daw, N. D., Gershman, S. J., Seymour, B., Dayan, P. & Dolan, R. J. 2011 Model-based influences
600 on humans' choices and striatal prediction errors. *Neuron* **69**, 1204-1215.

601 [34] Gläscher, J., Daw, N., Dayan, P. & O'Doherty, J. P. 2010 States versus rewards: dissociable neural
602 prediction error signals underlying model-based and model-free reinforcement learning. *Neuron* **66**,
603 585-595.

604 [35] Shultz, S., Opie, C. & Atkinson, Q. D. 2011 Stepwise evolution of stable sociality in primates.
605 *Nature* **479**, 219.

606 [36] Amici, F., Aureli, F. & Call, J. 2008 Fission-fusion dynamics, behavioral flexibility, and inhibitory
607 control in primates. *Current Biology* **18**, 1415-1419.

608 [37] Barrett, L., Henzi, P. & Dunbar, R. 2003 Primate cognition: From 'what now?' to 'what if?'.
609 *Trends in Cognitive Sciences* **7**, 494-497.

610 [38] Roberts, S. G. & Roberts, A. I. 2020 Social and ecological complexity is associated with gestural
611 repertoire size of wild chimpanzees. *Integrative zoology* **15**, 276-292.

612 [39] Roberts, A. I. & Roberts, S. G. B. 2015 Gestural communication and mating tactics in wild
613 chimpanzees. *PLoS ONE* **10**, e0139683. (DOI:10.1371/journal.pone.0139683).

614 [40] Roberts, A. I. & Roberts, S. G. B. 2018 Persistence in gestural communication predicts sociality in
615 wild chimpanzee. *Animal Cognition*. (DOI:10.1101/365858).

- 616 [41] Roberts, S. G. B. & Roberts, A. I. 2016 Social brain hypothesis, vocal and gesture networks of
617 wild chimpanzees. *Frontiers in Psychology* **7**. (DOI:10.3389/fpsyg.2016.01756).
- 618 [42] Clutton-Brock, T. & Janson, C. 2012 Primate socioecology at the crossroads: past, present, and
619 future. *Evolutionary Anthropology: Issues, News, and Reviews* **21**, 136-150.
- 620 [43] Dunbar, R. I. & Shultz, S. 2021 The Infertility Trap: the fertility costs of group-living in
621 mammalian social evolution. *FRONTIERS IN ECOLOGY AND EVOLUTION* **9**.
- 622 [44] Georgiev, A. V., Klimczuk, A. C., Traficante, D. M. & Maestripieri, D. 2013 When violence pays: a
623 cost-benefit analysis of aggressive behavior in animals and humans. *Evolutionary psychology* **11**,
624 147470491301100313.
- 625 [45] Knofe, H., Engelmann, J., Tomasello, M. & Herrmann, E. 2019 Chimpanzees monopolize and
626 children take turns in a limited resource problem. *Scientific reports* **9**, 1-7.
- 627 [46] Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Saltzman, W.,
628 Snowdon, C. T., Ziegler, T. E., Banjevic, M. & Garland Jr, T. 2003 Are subordinates always stressed? A
629 comparative analysis of rank differences in cortisol levels among primates. *Hormones and behavior*
630 **43**, 67-82.
- 631 [47] Dunbar, R. I. M. & Shultz, S. 2021 The Infertility Trap: The Fertility Costs of Group-Living in
632 Mammalian Social Evolution. *Frontiers in Ecology and Evolution* **9**. (DOI:10.3389/fevo.2021.634664).
- 633 [48] Schino, G. 2007 Grooming and agonistic support: a meta-analysis of primate reciprocal altruism.
634 *Behavioral Ecology* **18**, 115-120. (DOI:10.1093/beheco/arl045).
- 635 [49] Seyfarth, R. M. 1980 The distribution of grooming and related behaviours among adult female
636 vervet monkeys. *Animal behaviour* **28**, 798-813.
- 637 [50] Yin, H. H., Knowlton, B. J. & Balleine, B. W. 2004 Lesions of dorsolateral striatum preserve
638 outcome expectancy but disrupt habit formation in instrumental learning. *European journal of*
639 *neuroscience* **19**, 181-189.
- 640 [51] Ott, T. & Nieder, A. 2019 Dopamine and cognitive control in prefrontal cortex. *Trends in*
641 *Cognitive Sciences* **23**, 213-234.
- 642 [52] Arnsten, A. F. 2009 Stress signalling pathways that impair prefrontal cortex structure and
643 function. *Nature reviews neuroscience* **10**, 410-422.
- 644 [53] Goto, Y., Otani, S. & Grace, A. A. 2007 The Yin and Yang of dopamine release: a new perspective.
645 *Neuropharmacology* **53**, 583-587.
- 646 [54] Baik, J.-H. 2020 Stress and the dopaminergic reward system. *Experimental & Molecular*
647 *Medicine* **52**, 1879-1890.
- 648 [55] Abercrombie, E. D., Keefe, K. A., DiFrischia, D. S. & Zigmond, M. J. 1989 Differential effect of
649 stress on in vivo dopamine release in striatum, nucleus accumbens, and medial frontal cortex.
650 *Journal of neurochemistry* **52**, 1655-1658.
- 651 [56] Meyer-Lindenberg, A. & Weinberger, D. R. 2006 Intermediate phenotypes and genetic
652 mechanisms of psychiatric disorders. *Nature reviews neuroscience* **7**, 818-827.
- 653 [57] Williams, G. V. & Goldman-Rakic, P. S. 1995 Modulation of memory fields by dopamine D1
654 receptors in prefrontal cortex. *Nature* **376**, 572-575.
- 655 [58] Frank, M. J. 2005 Dynamic dopamine modulation in the basal ganglia: a neurocomputational
656 account of cognitive deficits in medicated and nonmedicated Parkinsonism. *Journal of cognitive*
657 *neuroscience* **17**, 51-72.
- 658 [59] Buschman, T. J. & Miller, E. K. 2007 Top-down versus bottom-up control of attention in the
659 prefrontal and posterior parietal cortices. *science* **315**, 1860-1862.
- 660 [60] Girardot, M.-N. & Holloway, F. A. 1985 Naltrexone antagonizes the biobehavioral adaptation to
661 cold water stress in rats. *Pharmacology Biochemistry and Behavior* **22**, 769-779.
- 662 [61] Cohen, M. R., Pickar, D., Dubois, M. & Cohen, R. M. 1986 Studies of the endogenous opioid
663 system in the human stress response. In *Enkephalins and Endorphins* (pp. 35-45, Springer).
- 664 [62] Dunbar, R. I. M. 2010 The social role of touch in humans and primates: Behavioural function and
665 neurobiological mechanisms. *Neuroscience & Biobehavioral Reviews* **34**, 260-268.
- 666 [63] Dunbar, R. I. & Shultz, S. 2010 Bondedness and sociality. *Behaviour* **147**, 775-803.

667 [64] Hashimoto, C. & Furuichi, T. 1996 Social Role and Development of Noncopulatory Sexual
668 Behavior. *Chimpanzee cultures*, 155.

669 [65] Roberts, A. I., Roberts, S. G. B. & Vick, S.-J. 2014 The repertoire and intentionality of gestural
670 communication in wild chimpanzees. *Animal Cognition* **17**, 317 - 336. (DOI:10.1007/s10071-013-
671 0664-5).

672 [66] Myllyneva, A. & Hietanen, J. K. 2016 The dual nature of eye contact: to see and to be seen.
673 *Social Cognitive and Affective Neuroscience* **11**, 1089-1095.

674 [67] Xing, B., Li, Y.-C. & Gao, W.-J. 2016 Norepinephrine versus dopamine and their interaction in
675 modulating synaptic function in the prefrontal cortex. *Brain research* **1641**, 217-233.

676 [68] Zahrt, J., Taylor, J. R., Mathew, R. G. & Arnsten, A. F. 1997 Supranormal stimulation of D1
677 dopamine receptors in the rodent prefrontal cortex impairs spatial working memory performance.
678 *Journal of neuroscience* **17**, 8528-8535.

679 [69] Billino, J., Hennig, J. & Gegenfurtner, K. R. 2016 The Role of Dopamine in Anticipatory Pursuit
680 Eye Movements: Insights from Genetic Polymorphisms in Healthy Adults. *Eneuro* **3**.

681 [70] von dem Hagen, E. A., Stoyanova, R. S., Rowe, J. B., Baron-Cohen, S. & Calder, A. J. 2014 Direct
682 gaze elicits atypical activation of the theory-of-mind network in autism spectrum conditions.
683 *Cerebral cortex* **24**, 1485-1492.

684 [71] Jarick, M. & Bencic, R. 2019 Eye contact is a two-way street: Arousal is elicited by the sending
685 and receiving of eye gaze information. *Frontiers in Psychology* **10**, 1262.

686 [72] Hietanen, J. K., Leppänen, J. M., Peltola, M. J., Linna-aho, K. & Ruuhiala, H. J. 2008 Seeing direct
687 and averted gaze activates the approach–avoidance motivational brain systems. *Neuropsychologia*
688 **46**, 2423-2430.

689 [73] Harrod, E. G., Coe, C. L. & Niedenthal, P. M. 2020 Social structure predicts eye contact tolerance
690 in nonhuman primates: evidence from a crowd-sourcing approach. *Scientific Reports* **10**, 1-9.

691 [74] Emery, N. J. e. a. 2000 The eyes have it: the neuroethology, function and evolution of social
692 gaze. *Neuroscience & Biobehavioral Reviews* **24**, 581-604.

693 [75] Annicchiarico, G., Bertini, M., Cordonni, G. & Palagi, E. 2020 Look at me while having sex! Eye-to-
694 eye contact affects homosexual behaviour in bonobo females. *Behaviour* **157**, 949-970.

695 [76] Conty, L. & Grèzes, J. 2012 Look at me, I'll remember you: the perception of self-relevant social
696 cues enhances memory and right hippocampal activity. *Human brain mapping* **33**, 2428-2440.

697 [77] Roberts, A. I., Murray, L. & Roberts, S. G. B. 2019 Complex sociality of wild chimpanzee can
698 emerge from laterality of manual gesture. *Human Nature*. (DOI:10.1007/s12110-019-09347-3).

699 [78] Roberts, A. I., Vick, S.-J., Roberts, S. G. B., Buchanan-Smith, H. M. & Zuberbühler, K. 2012 A
700 structure-based repertoire of manual gestures in wild chimpanzees: Statistical analyses of a graded
701 communication system. *Evolution and Human Behavior* **33**, 578-589.
702 (DOI:10.1016/j.evolhumbehav.2012.05.006).

703 [79] Berridge, K. C. & Robinson, T. E. 1998 What is the role of dopamine in reward: hedonic impact,
704 reward learning, or incentive salience? *Brain research reviews* **28**, 309-369.

705 [80] Pezzo, M. 2003 Surprise, defence, or making sense: What removes hindsight bias? *Memory* **11**,
706 421-441.

707 [81] Rolls, E. T., O'Doherty, J., Kringelbach, M. L., Francis, S., Bowtell, R. & McGlone, F. 2003
708 Representations of pleasant and painful touch in the human orbitofrontal and cingulate cortices.
709 *Cerebral cortex* **13**, 308-317.

710 [82] Bergman, T. J., Beehner, J. C., Cheney, D. L. & Seyfarth, R. M. 2003 Hierarchical classification by
711 rank and kinship in baboons. *Science* **302**, 1234-1236.

712 [83] Dunbar, R. I. M. & Dunbar, P. 1988 Maternal time budgets of gelada baboons *Animal Behaviour*
713 **36**, 970-980.

714 [84] Wittig, R. A., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M. & Cheney, D. L. 2008
715 Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior*
716 **54**, 170-177. (DOI:10.1016/j.yhbeh.2008.02.009).

717 [85] Testard, C., Larson, S. M., Watowich, M. M., Kaplinsky, C. H., Bernau, A., Faulder, M., Marshall,
718 H. H., Lehmann, J., Ruiz-Lambides, A. & Higham, J. P. 2021 Rhesus macaques build new social
719 connections after a natural disaster. *Current biology* **31**, 2299-2309. e2297.
720 [86] Roberts, A. I., Roberts, S. G. B. & Vick, S.-J. 2014 The repertoire and intentionality of gestural
721 communication in wild chimpanzees. *Animal Cognition* **17**, 317-336.
722 [87] Roberts, A. I., Vick, S.-J., Roberts, S. G. B. & Menzel, C. R. 2014 Chimpanzees modify intentional
723 gestures to coordinate a search for hidden food. *Nature Communications* **5** **3088**.
724 (DOI:10.1038.ncomms4088).
725 [88] Dunbar, R. 2018 Network Structure and Social Complexity in Primates. *bioRxiv*, 354068.
726 [89] Gustison, M. L., le Roux, A. & Bergman, T. J. 2012 Derived vocalizations of geladas
727 (*Theropithecus gelada*) and the evolution of vocal complexity in primates. *Philosophical Transactions*
728 *of the Royal Society B: Biological Sciences* **367**, 1847-1859.
729 [90] Dunbar, R. I. M. 2014 *Human Evolution*, Oxford University Press.

730

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

739

740

741

742

743

744

745

746

747

748

749

750

751

752

753

754

755

