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3 **An evolutionary perspective on paranoia**
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12 **Abstract**

13 Although paranoia is the most commonly presenting symptom of psychosis, paranoid thoughts occur
14 frequently in the general population and range widely in severity, from mild socio-evaluative
15 concerns to frank delusions about the harmful intentions of others. Furthermore, paranoia commonly
16 appears after a surprisingly diverse range of difficulties including trauma, brain injury, sleep
17 deprivation, drug use, and psychiatric and neurological disorder. Evolutionary accounts of paranoia
18 have been proposed before but have largely focused on paranoia as a misplaced threat response.
19 Although social threat is clearly a key component, the experience of paranoia is markedly more
20 complex than these accounts would lead us to believe: paranoia can involve multiple alterations in the
21 perception of the social environment, the identification of specific but seemingly arbitrary groups as
22 the source of persecution, and extended beliefs about conspiracy and complex coordination between
23 the perceived persecutors. Here, we argue for an evolutionary approach to paranoia that more fully
24 accounts for its complex social phenomenology and considers how it can be understood in light of our
25 evolved social cognition. More specifically, in terms of the ability to form coalitions and coordinate
26 between groups in situations of cooperation and competition.
27

28 **Introduction**

29 Evolutionary accounts of paranoia have been proposed before (1,2) but have largely focused on
30 paranoia as over-sensitive or misplaced social threat perception (1). Given that misperceiving social
31 threat would seem to be a serious problem for forming and maintaining productive social
32 relationships, this article focuses on an evolutionary account of why paranoid thinking is such a
33 common human characteristic and why paranoia can become intense and disabling after many forms
34 of social, psychological and neurological difficulties.

35

36 *Current conceptualisation of paranoia*

37 A persecutory belief is considered to be the central defining feature of paranoia and includes two
38 essential elements: i) a belief that harm will occur, and ii) an attribution that others intend this harm
39 (3). In the general population, such persecutory ideas can be experienced with varying degrees of
40 frequency and entertained to varying degrees of intensity. Paranoia can range from mild thoughts
41 about others' intentions to beliefs that are sufficiently unlikely, and inflexible to be classified as a
42 psychiatric symptom, most notably, as a paranoid delusion (4). One of the implicit assumptions about
43 paranoia is that it represents an exaggerated or false attribution of harmful intent to others. However,
44 given the continuum of paranoia, paranoid explanations can, and occasionally should, be accurate
45 (e.g. see (5,6)) although these are likely to be increasingly inaccurate as paranoia becomes more
46 becomes more disabling and a likely focus of clinical concern (7,8).

47

48 Epidemiological studies show that paranoia shows full taxometric continuity throughout the
49 population, indicating that categorical distinctions used in psychiatric diagnosis are not reflected in a
50 clear point of change of severity in the population (9-11). Nevertheless, this continuous distribution in
51 the population does not necessarily imply that underlying causes are fully continuous within
52 individuals, over time, or between sub-groups (12). Most current research has focused on paranoia in
53 the context of mental health, typically in people without individually diagnosable neurological
54 disorder, and has identified various risk factors and cognitive process that support paranoid thinking.
55 Indeed, paranoia has now been reliably associated with living in areas of low social cohesion (13),
56 worry (14), sleep deprivation (15,16), early life adversity and abuse, trauma (17) and victimisation
57 (16,18). Paranoia has also been found to co-occur with general cognitive biases relating to causal and
58 probabilistic reasoning and belief flexibility (19,20). However, diagnosable paranoid states can also
59 be caused by a wide range of direct disturbances to brain function. Paranoia is common in psychosis
60 following epilepsy (21), brain injury (22,23) and dementia (24). It is also one of the most frequent
61 unwanted side-effects for several classes of recreational drugs (25-27). Indeed, in terms of the causes
62 and contexts in which it appears, paranoia is perhaps most remarkable for being associated with such
63 a wide range of difficulties, impairments and stresses.

64

65 Given this diversity, the aim of this article is to ask whether paranoia might sometimes serve an
66 adaptive (fitness-enhancing) function and how an evolutionary perspective can help us to predict
67 where paranoia will be most common. To be clear, our aim is not an attempt to explain how frank
68 paranoid delusions and – by extension – psychotic spectrum disorders, have been favoured by
69 selection. Indeed, based on the lowered reproductive success of individuals with these disorders and
70 the lack of evidence of benefits to kin (see (28)), we think that this is highly unlikely. Our overarching
71 hypothesis is that the existence of paranoia can generally be understood as a consequence of selection
72 for detecting and evaluating coalitional threat. We first describe the phenomenology of paranoia and
73 argue that current evolutionary theories do not fully account for the perception of conspiracy and
74 selective identification of arbitrary persecutors that are so common in paranoia. We suggest that
75 coalitional competition, which can occur both within and between groups and which can be
76 relatively stable in some contexts and yet highly flexible in others, can help to explain why paranoia
77 takes the form it does. Our hypothesis predicts that within-individual variation in paranoid thinking
78 should occur in response to immediate context-specific changes in the perception of coalitional
79 threat (as defined by (29)), whereas stable between-individual differences in paranoia are likely to
80 emerge in response to chronic threat from others. Finally, we explore why impairments to brain
81 function also commonly predispose individuals to paranoia, and whether this is likely to be an
82 adaptive response to the environment or a maladaptive consequence of cognitive constraints.

83

84 *Understanding the full social phenomenology of paranoia*

85 Freeman and Garety's (3) definition has been useful in providing a clear operational definition of a
86 central component of paranoia. However, existing approaches to paranoia have tended to
87 conceptualise paranoia in terms of cognitive processes used to make sense of other *individuals* rather
88 than *groups*. One limitation of this approach is that it fails to account for why the experience of more
89 severe paranoia often involves the misperception of group boundaries and collective action. Indeed,
90 paranoia is frequently accompanied by other features that are common enough to be included in
91 phenomenological descriptions, both historical and modern, but are often neglected by more recent
92 cognitive approaches. These are i) the perception of a conspiracy behind the intentional harm, and ii)
93 social selectivity in terms of identifying the people perceived to be the source of intentional harm.

94

95 Conspiracy thinking is common in the general population (30) and is defined as a tendency to provide
96 "explanations for important events that involve secret plots by powerful and malevolent groups"
97 (31)). In paranoid delusions, however, conspiracy thinking often becomes self-focused, with delusions
98 commonly involving the perception of organised attempts to harm the believer, rather than malign
99 explanations for public events. The perception of a self-focused conspiracy has been identified as a
100 central characteristic of delusional paranoia from early in the history of psychiatry (32) and forms part
101 of many modern phenomenological descriptions (33,34). Cameron (1959) conceptualised this aspect

102 of paranoia as a belief in a persecutory ‘pseudo-community’ who are perceived to be united in a co-
103 ordinated undertaking against the paranoid individual but who fail to correspond to any group in
104 wider society who share the coordinated aims and actions attributed to them. Unlike public conspiracy
105 theories, these concerns are more likely to focus on the history, intentions and day-to-day activities of
106 the believer.

107

108 Although paranoia involves a belief that others intend harm to the believer, these concerns typically
109 pertain to specific individuals or social groups and also commonly involve the misperception of group
110 boundaries and coordinated group action. In increasingly severe paranoia, these concerns and
111 misperceptions become increasingly exaggerated and may present as frank persecutory delusions.
112 Studies of delusional patients indicate that the majority selectively identify specific groups as
113 responsible for their maltreatment. In a study of delusions in Korean, Korean-Chinese, and Chinese
114 patients conducted by Kim et al. (35), only 27.4%, 17.7% and 24.6% of persecutors, respectively,
115 were unspecified, while the rest were variously identified as groups such as relatives, neighbours, the
116 police, or medical personnel (see also (36)). Green et al. (37) reported that persecutory delusions
117 could be classified as focusing on individuals (e.g. “my father”), groups with defined members (“[the
118 patient’s] neighbour, his neighbour’s brother and mates”), established social groups (“the police”),
119 undefined groups (“people”, “spirits”) and all others (“everyone”) with perceived individual and
120 multiple persecutors each consisting 50% of the total.

121

122 *Evolutionary approaches to paranoia*

123 Attempts to answer the question of why some people are more paranoid than others have typically
124 appealed to proximate level explanations (Box 1) such as genetics, life history or cognitive biases (4).
125 Nevertheless, these approaches do not answer the issue of why we have a cognitive capacity for
126 paranoid thinking (Box 2) and whether between-individual variation in paranoid thinking might, in
127 some environments, be selectively advantageous in fitness terms. From a Darwinian perspective, a
128 fearful response to danger, whether actual or potential, is likely to carry significant fitness benefits
129 and to have been subject to strong selection in many species (38). Nevertheless, not all individuals
130 show an equivalent magnitude of response to the same threatening stimulus or context: levels of
131 fearfulness differ markedly across individuals, even within a species. The question of how stable,
132 between-individual differences in fearful responses might arise and be stabilised by selection falls
133 under a broader banner of research on the evolution of stable behavioural types. Research in this field
134 has shown that the evolution of variation in behavioural types stems from trade-offs in pursuing
135 different fitness-relevant activities. For example, investing in growth (e.g. via foraging) often comes
136 with an attendant increased risk of predation (39,40) and so strategies aimed at increasing growth are
137 likely to be traded-off against strategies that reduce predation risk. Organisms must therefore balance
138 the rewards of investment in growth against the increased mortality risk; the optimal resolution of

139 such trade-offs in different environments or for different individuals can therefore select for variation
140 in fearfulness, aggression, risk appetite and so on, which broadly dictate individual life history
141 strategies and associated behaviour.

142

143 In addition to balancing such trade-offs, organisms must also effectively manage costs from errors
144 that occur due to perceptual uncertainty ('error management theory', (41), Box 3). Specifically, error
145 management theory predicts that when there are asymmetries in the costs of false-positive and false-
146 negative error types, then selection will favour strategies that minimise the chance of making the
147 costlier error, even if this produces many behavioural mistakes. Following the logic of error
148 management theory, previous evolutionary accounts (1,41) have suggested that paranoia is an evolved
149 psychological mechanism shaped by the selective pressures of catastrophic harm from others that is
150 tuned to have a low threshold for detecting social threat. Individual variation in the relative
151 asymmetry of error types is proposed to account for variation in paranoia across the full spectrum (see
152 Box 3 for a critique).

153

154 *Shortcomings of existing evolutionary theories: accounting for paranoia beyond social anxiety*

155 Nevertheless, existing evolutionary theories of paranoia based solely on social threat detection do not
156 fully account for the complex phenomenology of paranoia. Specifically, we have to ask why a
157 mechanism aimed at detecting and avoiding social threats does not solely result in variation in
158 avoidance and/or submissive and appeasement behaviours (as is also observed in many non-human
159 species, see (42) and also discussed elsewhere, (43,44)), but also incorporates more complex features
160 that are not adequately explained by this approach. Namely, selective identification of a specific (yet
161 often seemingly arbitrary) group of persecutors, the attribution of unobservable malign intentions and
162 motives to these individuals, and the formulation of hypothetical narratives rendering these
163 attributions subjectively plausible. Below, we focus on the first of these features but see Box 2 for a
164 discussion of the evolution of inferential causal reasoning abilities (including mental state attribution)
165 in humans.

166

167 An important feature of human social groups is the presence of coalitions: any situation where two or
168 more individuals unite in competition against a third party or parties (45,46). Coalitionary conflict in
169 human groups can manifest in the form of lethal aggression ('lethal raids' reviewed in (47)) but can
170 also include non-lethal and non-aggressive conflict, such as stigmatization, ostracism, exclusion, and
171 derogation. For example, witchcraft accusations have been (and still are) used to identify individuals
172 or groups for ostracism, persecution or even death (48,49). In modern industrialised societies, similar
173 forms of indirect aggression are used by coalitions to damage the reputation of (often higher-ranking)
174 rival, for example via gossip or derogation (see (50,51)).

175

176 This persistent risk of persecution selects for what Boyer (29) has named a ‘coalitional psychology’
177 that anticipates and deflects these threats by integrating oneself within a coalition or coalition(s),
178 recognising and categorizing others as allies or potential competitors; and using these categorizations
179 to predict how others might behave or react in specific social interactions (29,52-55). One might
180 expect social threat detection mechanisms to be sensitive to reliable indicators of coalitional threat,
181 such as dominance hierarchies, signals of group membership and the cohesiveness of rival coalitions
182 (29,53) and, accordingly, experimental evidence shows that exposing people to these different forms
183 of social threat does increase the tendency to make paranoid attributions (56,57).

184
185 Nevertheless, paranoia often involves the selective identification of a (seemingly arbitrary) group of
186 persecutors, where malign intent is attributed to some individuals (or groups) but not others (e.g. ‘I’m
187 being persecuted by the CIA’ [and not FBI] or ‘I’m being persecuted by my family’ [but not my
188 neighbours]’). We suggest that this arbitrary selectivity might reflect the fact that coalition boundaries
189 in human groups are themselves highly fluid and flexible and can be formed in the absence of any
190 stable group identifiers (58). The fact that coalitions can be formed on the basis of minimal cues or
191 markers of similarity in turn selects for cognitive machinery that readily and flexibly categorizes
192 people into groups on the basis of such ‘minimal’ cues (59,60). Indeed, humans readily form and
193 detect minimal groups, even from a young age (60) and the perception of these groups fundamentally
194 alters expectations about the intentions and behaviour of individuals within them (reviewed in (61)).
195 Assuming that paranoia builds on this existing cognitive machinery helps to explain the seemingly
196 arbitrary selectivity in the identification of perceived persecutors. This raises an interesting theoretical
197 question as to the extent to which increasingly severe paranoia reflects variation in cognitive
198 processes involved in perceiving coalitions and alliances, as opposed to processes involved in the
199 attribution of (harmful) intent to others. We suggest that disambiguating these processes and how they
200 vary across the paranoia spectrum will be a fruitful avenue for further research.

201
202 *Predictions deriving from a coalitional psychology model of paranoia*

203 A coalitional perspective suggests that variation in paranoia could function to protect individuals from
204 coalitional threat in specific contexts and therefore serve an adaptive function when either the
205 probability and/or the costs of harm from others are high. A prediction of this hypothesis is therefore
206 that variation in paranoid thinking will reflect the background probability and/or costs of coalitional
207 conflict. Epidemiological evidence supports this prediction: an increased tendency for paranoid
208 thinking has been documented in general population groups that are involved in higher-than-average
209 rates of coalitional aggression, such as gang members (62) and army veterans (63,64). The
210 probability of inter-coalitional violence is increased under conditions of resource scarcity (65) and,
211 as expected, living in poverty is also associated with increased tendency for paranoid thinking (66).

212

213 Variation in paranoia should also be sensitive to the perceived costs of receiving inter-coalitional
214 aggression, which escalate with low coalitional support, low social rank or increasing power
215 imbalances between coalitions (67,68). In support of this prediction, risk for psychosis (for which
216 paranoia is the most common delusional theme) is higher among people who have small social
217 networks (69) or who are socially isolated, both of which are proxies for low coalitional support.
218 Epidemiological evidence supports the idea that perceived power imbalances can raise the risk for
219 psychosis and, by extension, can also increase the probability for paranoid thinking. For example, low
220 social rank (both perceived and objective) is an important predictor for increased paranoia (70) – a
221 finding that has recently been supported by experimental work where participants’ social status
222 relative to that of a partner was experimentally manipulated (56). Similarly, being part of a
223 marginalised social group (e.g. a low status immigrant, or an ethnic minority) is a risk factor for
224 paranoia (71), which can be ameliorated by living in increased densities within the marginalised
225 group (72). A coalitional psychology perspective on paranoia would predict this otherwise
226 paradoxical ‘ethnic density effect’ since living at higher ethnic densities with perceived coalition
227 members should be associated with an increased perception of coalitional support.

228

229 Paranoia also varies within individuals and is fine-tuned to the degree of coalitional threat in the
230 current interaction. For example, experimental work where people interact with a political affiliate or
231 with a political adversary shows that harmful intent attributions, the fundamental component of live
232 paranoid ideation (Box 4) are stronger for the dissimilar than for the similar interaction partner, as
233 expected (56). Paranoid thinking should also respond flexibly to the cohesiveness of coalitions since
234 cohesive coalitions are more able to work together to harm rivals (29). As expected, recent work has
235 shown that paranoid attributions increase when participants interact with a cohesive pair of opponents
236 compared to a pair of non-cohesive opponents (57). Thus, observational and experimental evidence
237 suggests that paranoid thinking is flexible and responsive to social context in both the short and long-
238 term, as would be expected if paranoia is the output of a mechanism for detecting and avoiding
239 coalitional threat.

240

241 Paranoia also varies widely across the lifespan, emerging in adolescence, being most pronounced in
242 early adulthood (73) and declining as individuals age (74). Indeed, if paranoia is an output of a
243 coalitional psychology, then its emergence should coincide with onset of coalitional threat. Empirical
244 evidence suggests that coalitional competition begins to emerge when individuals reach puberty and is
245 most intense during late adolescence and early adulthood (75). Competition during adolescence may
246 play an important role in the formation of and integration into coalitions that ultimately determine
247 individuals’ status, access to resources (including mates) and reproductive success. In modern tribal
248 societies, such as the *Nyangatom*, men form close alliances with same-age individuals during
249 adolescence. It is also at this time that men begin to join lethal raiding excursions to neighbouring

250 groups (usually with members of their coalition), continuing to participate in these raids until they end
251 their reproductive careers (c. age 45, (76)). More generally, interaction with peers increases markedly
252 during adolescence (77), leading also to an increase in social competition at this age. For example,
253 bullying – which can be construed as a form of coalitional competition - is prevalent across all world
254 cultures (and also in pre-industrialised societies) and increases in frequency as children enter
255 adolescence (78), peaking around the age of 14 (79). Other work has shown that adolescence is a
256 period that is characterised by increased sensitivity to social threat, social risks and social exclusion
257 (80-82), as well as being a common onset period for many mental health problems, including
258 psychotic-spectrum disorders (73,83). Thus, we suggest that the developmental trajectory of paranoia
259 reflects a selective process that balances sensitivity to threat in line with fitness-relevant outcomes.

260

261 Individuals may also experience sensitive periods during development, where cues from the (social)
262 environment exert exaggerated effects on subsequent development. Sensitive periods are expected to
263 evolve whenever the early environment can reliably predict future conditions and when there are
264 constraints on plasticity (84). The conditions experienced during a sensitive period of development
265 can act as a ‘weather forecast’, guiding subsequent development along different trajectories and
266 generating adaptive matches between the environment and the individual’s phenotype (84-88). It has
267 been suggested that adolescence could be one such sensitive period in development (84,89,90), with
268 the evolutionary relevance being that individuals receive more reliable cues about the kind of social
269 world they will inhabit and their place in it during adolescence than earlier in development (see (84)).
270 One of the key outstanding questions with respect to paranoia will be to determine whether social
271 threat shapes responses across the lifetime, or whether there are sensitive periods of development
272 during which exposure to social threat exerts lasting consequences on social cognition and behaviour.
273 If the latter, then identifying when these sensitive periods are and how they vary in response to the
274 stochasticity of the social environment (e.g. (88,91)) will also be fruitful.

275

276 *When does paranoia become pathological?*

277 Having argued so far in favour of viewing variation in paranoia as part of a normally-functioning,
278 naturally selected human psychology, we now address the question of when paranoia might be best
279 viewed as a disorder and, therefore, under negative selection. The definition of mental disorder is
280 historically controversial and beyond the scope of this article: here we adopt the ‘Harmful
281 Dysfunction’ definition proposed by Wakefield (92) which states that a) mental disorders are
282 conditions that cause harm to the person as judged by the standards of the person’s culture, and b) that
283 the condition results from the inability of some internal mechanisms (psychological or physiological)
284 to perform its natural function, wherein a natural function is an effect that is part of the evolutionary
285 explanation of the existence and structure of the mechanism. Importantly, as with many other
286 biological continuities (e.g. weight), it may be difficult (if not impossible) to provide precise cut-offs

287 that demarcate the boundary between ordered and disordered paranoia (93) without denying clear
288 pathology within this range.

289

290 An analogy may be helpful: fever helps the body fight off pathogens and can therefore be viewed as
291 part of a normally-functioning body's evolved responses to infection. Nevertheless, the underlying
292 mechanisms regulating temperature can become impaired or fail, leading to increasingly dysregulated
293 fever that can sometimes be fatal. Clearly, in the latter case, fever would be viewed as pathological
294 (i.e. disordered) despite that fact that, under normal circumstances, fever is an adaptive response to
295 infection. Based on this logic, we suggest that as paranoia becomes increasingly severe and therefore
296 less responsive to threat in the immediate environment, it is increasingly likely to stem from
297 dysfunction in the underlying cognitive mechanisms that support threat evaluation and so is likely to
298 fit the definition of disorder (being, by implication, maladaptive). We remain agnostic about the
299 precise cut-off point for separating ordered from disordered paranoia, as well as about the magnitude
300 and linearity / non-linearity of fitness costs involved.

301

302 At this point however, it is also instructive to raise another question. Paranoia is increased by a wide
303 range of brain injuries and impairments, including substance use and abuse, sleep deprivation,
304 traumatic head injury, and dementia: do these impairments imply that the resulting paranoia is
305 necessarily disordered? We argue that it need not be the case. Rather, we suggest that it is possible
306 that increased paranoia in response to brain impairment reflects the correct functioning of a 'cognitive
307 failsafe' because cognitive impairment renders people at higher risk of being exploited by others
308 whom were previously allies or makes them less able to incur the costs of being exploited (e.g. see
309 (94,95)) and therefore a bias toward developing paranoia, rather than other socio-affective states, after
310 impairment may have a protective effect. Thus, this might constitute an adaptive response rather than
311 a disorder. Nevertheless, following the fever analogy above, this hypothesis allows that in some
312 individual contexts, impairments to the mechanisms of the cognitive failsafe can lead to increasingly
313 severe and disordered paranoia, resulting in worse or even catastrophic outcomes for an individual.

314

315 *Conclusions*

316 We argue that an evolutionary approach can help make sense of otherwise puzzling features of
317 paranoia. These include a population continuum of paranoia that includes both context-sensitive
318 paranoid thinking and inflexible, unlikely paranoid delusions, as well as the tendency to selectively
319 identify seemingly arbitrary groups of persecutors, and to perceive that one is the target of conspiracy.
320 We also note that our approach highlights some key areas of future research. The first is on the
321 phenomenology of paranoia and we suggest that the content of delusions in severe paranoia should
322 often reflect common sources of coalitionary threat (e.g. coordinated groups and cliques, higher status
323 individuals, physical harm, threats to reputation). For some individuals, different threats may be more

324 salient or more likely and this might well be reflected in the content of delusions across individuals
325 (e.g. see (96)). Secondly, we suggest additional focus is needed on how people perceive social groups,
326 including processes relating to identification with in-group and categorising others as out-group, and
327 how these processes may be altered in people experiencing severe paranoia. We also note that
328 paranoia has received surprisingly little attention from evolutionary scientists in comparison to other
329 psychiatric difficulties and we hope it becomes of further interest in the field, given its clear relevant
330 to fitness concerns, its diverse presentation and ubiquity in human history.

331
332 **Box 1. Proximate and Ultimate level explanations**
333

334 It is worth clearly delineating between proximate and ultimate levels of explanation. In evolutionary
335 biology, an answer to the question of ‘why’ an individual behaves in a certain way can take two
336 broad, non-mutually exclusive forms: proximate and ultimate level explanations (97-100). Ultimate
337 level explanations provide the answer to ‘why’ the behaviour exists: they describe the function of the
338 behaviour in question and show how such behaviour, on average, is associated with fitness increases.
339 Proximate level explanations, on the other hand, are concerned with ‘how’ the behaviour is
340 implemented. For example, proximate level explanations could describe the psychological
341 mechanisms that support or constrain the behaviour but could also include the hormonal or
342 physiological basis of behaviour. For example, one might answer the question of why a lioness chases
343 a zebra by saying that the lioness needs to eat and is motivated by hunger, or that she has babies to
344 feed, or that she is joining the other lionesses in the pride in the hunt – these would all be valid
345 proximate-level explanations. An ultimate level explanation for hunting behaviour is that lionesses
346 who attempt to hunt and kill prey have more surviving offspring than those who do not partake in
347 hunting and so this behaviour has been selected for in lion populations over evolutionary time.
348 Clearly, the two explanations are not mutually exclusive. However, a proximate level answer cannot
349 be posed as the solution to an ultimate question of why behaviour exists.

350
351 **Box 2. Which features of paranoia are unique to humans and why?**

352 Evidence for the sort of inter-coalition competition that we propose results in selective pressure for
353 variation in paranoia is also present for other species, raising the question of to what extent features of
354 paranoia may be present in non-humans animals. For example, lethal intergroup competition in the
355 form of lethal raiding occurs also in chimpanzees(47), and more subtle forms of coalitional
356 competition have also been observed in many other social non-human species (see (46) for a review).
357 There is also convincing evidence for variation in social anxiety in non-human species (42). However,
358 we would argue that the key cognitive mechanism that underlies the ability for paranoid thinking:
359 namely the ability to reason about unobservable causal mechanisms to explain why events have
360 occurred in the past or might occur in the future seems to be, for the most part, unique to humans
361 (101). The ability to attribute intentions to others (also key in paranoia and arguably absent in non-

362 human species, (102)) might represent an instantiation of this ability for inferential causal reasoning,
363 albeit one that is specific to the social domain (103). The question of what selective pressures are
364 most likely to have favoured the human-specific propensity to seek diagnostic causal explanations for
365 phenomena humans is hotly debated (see (103,104)) and a full discussion is beyond the scope of this
366 article. Specifically, it remains an open question whether the human tendency to seek and draw causal
367 inferences evolved in response to social selection pressures, or whether this is more likely to have
368 evolved in response to ecological selection pressures, being subsequently co-opted and used in the
369 social domain.

370

371 **Box 3. Error-management theory**

372 Error management theory (41) states that the existence of asymmetric error costs can favour the
373 evolution of strategies that err on the side of caution, thereby protecting individuals from catastrophic
374 errors, and may be presented as cognitive biases – that is, psychological mechanisms that result in
375 inaccurate perceptions of the true environment but that can shape behaviour in on-average beneficial
376 ways (see (105-108) for discussion). For example, it may be better to mistake a stick for a snake, than
377 a snake for a stick, because the latter mistake is more likely to be fatal. False alarms of this sort are
378 abundant in nature, in humans and non-human species (28,41). Crucially, selection is not expected to
379 produce perfectly optimal behaviour under all circumstances but rather to produce strategies that are
380 on average successful over the lifetime and within a population. From an evolutionary perspective,
381 many behavioural ‘mistakes’ (mistaking sticks for snakes) would be permitted under a broadly
382 adaptive strategy of ‘all snake-shaped things should be initially treated as if they could be snakes’.
383 The strength of such biases (whether behavioural or cognitive) should therefore reflect the asymmetry
384 in error costs: the greater the risk that one error type will produce a catastrophic outcome in
385 comparison to the other, the more likely individuals are to be biased towards making the least costly
386 of the error types. Nevertheless, it is worth noting a shortcoming in the typical application of error
387 management theory to paranoia: in social groups, the asymmetric costs in terms of misperceiving
388 social motivations may depend on context (41). The costs of wrongly treating someone as trustworthy
389 who actually wants to do you harm may be severe. However, the costs of wrongly treating a coalition
390 member as untrustworthy may also be severe due to the fact non-cooperation often results in
391 reciprocal defection (109), punishment (110,111), or exclusion (112,113). Indeed, mistakenly treating
392 others as if they might harm you can jeopardize the future of potentially mutually-beneficial
393 partnerships, to the extent that the costs associated with such errors have been posited as the basis for
394 the extraordinarily high levels of human trust and cooperation in seemingly anonymous, one-shot
395 interactions (when the potential for cheating and being exploited is rife) (114) (but see (115)). So,
396 while it may be adaptive to consistently err on the side of misperceiving a snake for a stick – as in the
397 traditional formulation of error management theory – the costs are highly asymmetric in comparison
398 to human threat examples in large part because you cannot form a coalition with a snake or

399 incorrectly reject it as an ally. Importantly, the exact distribution of cost asymmetry that drives
400 selection in these situations is an empirical question and it is possible that the costs of under-
401 perceiving hostile intent in others is still on average higher than the costs of over-perceiving hostile
402 intent in allies. However, the fact that the latter is well-established as having costs in human social
403 groups suggests that cost asymmetry will not mirror contexts that are most commonly cited as
404 selective pressures that drive the evolution of cognitive biases (sticks, snakes etc).

405

406 **Box 4. Measuring paranoia in experiments involving genuine social interactions**

407 Paranoia by definition affects how we form and update impressions of others in social interactions. It
408 is therefore instructive to attempt to measure paranoia in settings where participants experience
409 genuine social interactions with others. Game theory tasks – typically used in experimental and
410 behavioural economics - provide many paradigmatic examples of stylized social interactions that can
411 be used to infer or measure social behaviour and preferences and these tasks are now being used to
412 great effect to better understand how social cognition and behaviour vary in paranoia. Many game
413 theoretic tasks operationalise pro-social behaviour as the willingness to forego financial earnings in
414 the task in order to benefit the partner(s) in the interaction. Games can be one-shot or repeated, occur
415 among pairs or groups of individuals and allow for various forms of social behaviour, including
416 cooperation and punishment. In particular, many game theoretic tasks allow us to measure paranoid
417 attributions since the motives underpinning the decisions to cooperate or not in these tasks are often
418 murky. Consider, for example, the Dictator Game. In this two-player game, one person (the ‘dictator’)
419 is given a sum of money and can choose whether to send some to the partner (the ‘receiver’) or to
420 keep all the money for themselves. The receiver has no active role in this game and must accept
421 whatever share the dictator offers. Importantly, the motives underpinning a dictator’s decision to keep
422 all the money are ambiguous. One might infer that the dictator is motivated by greed (or self-interest).
423 Alternatively, one might also infer that the dictator is motivated by a desire to deny the receiver any
424 money (i.e. intent to harm). Inferring harmful intent in such an interaction is a reliable proxy for
425 paranoid thinking and, in a series of studies using participants from the general population
426 (56,57,116), it has been shown that people who have higher tendency for paranoid thinking make
427 stronger harmful intent attributions in these tasks. The degree to which individuals attribute harmful
428 intent to others in turn predicts their willingness to punish their interaction partners (117).

429

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