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The Evolution of Human Sociality. Categorizations, Emotions, and Friendship

Michael Windzio 

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Abstract This overview describes the ambivalent result of humans' evolution towards a social and cooperative species. The evolution of friendship, based on commitment rituals and norms, solved the problem of defection in reciprocal altruism. The social brain implies the cognitive capacity of “mentalizing” and of keeping track of the reputation of group members, but, equally as importantly, generates strong emotions depending on the degree of social integration or social exclusion. Strong emotions linked to categories of social relationships, in particular to friends who we regard as almost irreplaceable, generate commitment and reduce social transactions costs and thereby facilitate cooperation. A multilevel perspective on social categorizations reveals, however, that a similar mechanism applies between cultural groups, owing to cultural group-level selection. Humans apply categorical distinctions within and between groups. They distinguish in-group and out-group members by cultural markers, and, in addition, between friends and others. In this perspective, cultural markers generate categorizations and emotions that facilitate unconditional support if required, but can also result in out-group rejection, and, in combination with neurochemicals, in dehumanization as well.

Keywords Friendship · Social brain · Culture · Commitment · Out-group rejection

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Die Evolution der menschlichen Sozialität. Kategorisierungen, Emotionen und Freundschaft

Zusammenfassung Dieser Überblick beschreibt das ambivalente Ergebnis der Entwicklung des Menschen zu einer sozialen und kooperativen Spezies. Die Evolution der Freundschaft, die heute u. a. auf Ritualen und Normen der Bindung und Verpflichtung beruht, reduzierte das Problem der Defektion im reziproken Altruismus. Das „soziale Gehirn“ ermöglicht die kognitive Fähigkeit des „Mentalisierens“ und erzeugt Emotionen in Abhängigkeit vom Grad der sozialen (Des-)Integration. Starke Emotionen, die mit bestimmten sozialen Kategorien verbunden sind, etwa mit Freunden, die wir als nahezu unersetzlich betrachten, erzeugen stabile Bindungen, verringern die Kosten sozialer Transaktionen und erleichtern so stabile Kooperation. Eine Mehrebenenperspektive auf soziale Kategorisierungen zeigt jedoch, dass ein ähnlicher Mechanismus auch zwischen kulturellen Gruppen wirksam ist, und zwar aufgrund der kulturellen Selektion auf der Gruppenebene und der Koevolution von Biologie und Kultur. Menschen treffen kategoriale Unterscheidungen innerhalb und zwischen Gruppen. Sie unterscheiden zwischen Freunden und Anderen sowie anhand kultureller Marker zwischen Eigen- und Fremdgruppe. Aus dieser Perspektive erzeugen kulturelle Marker Kategorisierungen und Emotionen, die bei Bedarf stabile Bindungen ermöglichen, aber auch zu einer Ablehnung der Fremdgruppe führen können – und in Kombination mit Neurochemikalien sogar zu einer Dehumanisierung.

Schlüsselwörter Freundschaft · Soziales Gehirn · Kultur · Bindung · Ablehnung der Fremdgruppe

1 Introduction

Social integration and cooperation are among the most important topics in sociology. This overview is aimed at enhancing sociological thinking by introducing evolutionary perspectives on human sociality. Evolutionary perspectives assume evolved biological and cultural dispositions and relate them to ecological causes that affected humans' ancestors in the distant past. A common explanation of cooperation in evolutionary biology refers to mutual support among kin, to differences in the reproductive success of phenotypes, and to the underlying expression of genes. Yet an evolutionary explanation of close cooperative relationships or friendship among non-kin is more demanding because it must also take cultural evolution into account, in particular shared norms and taken-for-granted knowledge. Explaining the evolution of human sociality requires the boundary between the biological focus on genes and the sociological focus on culture to be blurred. The resulting concept of gene–culture co-evolution is an appropriate approach to the following question: Which mental structures shape our disposition to categorize others, e.g., as cooperators or trusted friends, and to commit us to the relationship?

This question asks for the *proximate* explanations of human sociality and friendship. Proximate factors are physical and mental dispositions that influence the repro-

duction of an organism in its current state (Marchionni and Vromen 2009, p. 90). They explain our behavior at a given moment in a given environment (Vromen 2017). Humans' "social brains" (Dunbar 2016; Crisp 2015; Lindenberg 2015b) activate emotional evaluations of different social categories, and also distinguish between cultural groups according to cultural markers, interpreted as indicators of cooperativeness, a sense of "we-ness" (Tomasello 2018, p. 91), or at least of non-hostile behavior.

Ultimate explanations, in contrast, refer to varying environmental conditions in the past, which changed humans' physical and behavioral dispositions in the long run via differences in reproductive success. As ultimate factors in the evolution of human sociality I will discuss *cultural evolution* and *gene–culture coevolution*, both driven by multilevel selection and cultural group selection (Laland and Brown 2011; Boyd 2018, p. 99; Asma and Gabriel 2019, p. 228).

This overview cannot, of course, cover all aspects of the evolution of human sociality. I focus on categories and social transaction costs, describe aspects of the "social brain" as a proximate cause of human sociality, introduce the example of friendship as a selective protective alliance among non-kin based on norms and emotions, and summarize arguments on how such protective alliances might have evolved. Protective alliances are usually linked to culturally transmitted norms and practices, which is why cultural group selection might have been of particular importance. According to the multilevel perspective, social categorizations between groups perform the same function as friendships within groups: they reduce *social transaction costs* by commitment and thereby facilitate cooperation. Finally, I give examples of how friendship varies between cultures and suggest that, although a strict definition of friendship is problematic (Brent et al. 2014), commitment to selective protective alliances (DeScioli and Kurzban 2009) could be the common denominator across cultures.

2 Commitment to Social Categories Reduces Social Transaction Costs

According to Barrett (2015), human cognition evolved by adding new capacities to existing ones. Behavior of simple organisms resulting from, for example, the perception of light evolved into the capacity of combining visual inputs with information stored in the memory and thereby enriching it with prior beliefs (Barrett 2015, p. 80). Humans classify objects based on "inductive bets" on their most likely identity and meaning. For instance, during human evolution a mind–world fit certainly required that we quickly tag objects as food or non-food, or animate or inanimate objects (Barrett 2015, pp. 90, 108; Asma and Gabriel 2019, p. 176). Given the importance of such categorizations for survival, emotions are also involved in this tagging. As social embedding in groups was crucial for early humans, we cognitively represent others' mental states or emotions, which we tag with our prior beliefs in order to generate meaning and to assess what could be consequences for us or others (Barrett 2015, p. 147). Human sociality is based on a *cognitive capacity* to tag our perceptions of other persons in order to infer their intentions (Dunbar 1998, 2016, 2021; Humphrey 2002), but it is also based on *emotions* (Turner 2000; Asma and Gabriel

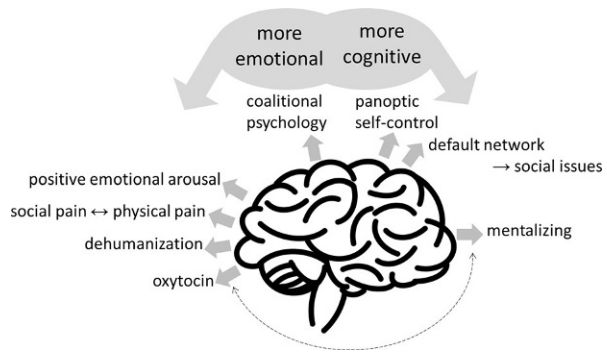
2019, p. 260) of social closeness, social approval (Turner 2007, pp. 83–84), social exclusion, or loneliness (Cacioppo and Patrick 2009; Lieberman 2013, pp. 50–51; Dunbar 2021, p. 312). Positive or negative emotional arousal is even “... one the most critical forces driving face-to-face interaction and its embeddedness” (Turner 2002, p. 67). Why are we so sensitive to emotions we experience in our social relationships? According to the commitment model humans’ evolved sociality is based on *commitment* (Frank 1988) to social categories at different levels—e.g., dyads, groups, and cultures. Commitment means limiting the number of potential exchange partners and to foreclose most behavioral options.

The *inclusive fitness theory* states that individuals cooperate because the reproduction of close relatives reproduces part of one’s own genome. According to Hamilton’s formula, genes related to altruism proliferate in a population if the benefit b weighted by the degree of relatedness r outweighs the costs c of altruistic investment ($rb > c$) (Wilson 2012, p. 167). However, altruistic action is not restricted to close relatives (Hruschka 2010, p. 80). Humans and primates also establish close ties to non-kin or distant kin (Seyfarth and Cheney 2012).

The concept of *reciprocal altruism* (Trivers 1985, p. 48) provides an explanation of cooperative behavior among non-kin: if you do me a favor, I will do one for you later. The major problem is to identify cheaters who benefit from others’ behavior but do not reciprocate. For species living in cooperative groups, it was beneficial to evolve a “... complex psychological system in which individuals regulate both their own altruistic and cheating tendencies and their responses to these tendencies in others” (Trivers 1985, p. 388). Part of this psychological system are uncontrollable emotional reactions (Seabright 2010, pp. 80–81; de Waal 2019, p. 68), such as sympathy, blushing, or voice intonation (Frank 1988, pp. 125–130, 2001, p. 62). We also manage reputation in systems of indirect reciprocity (A gives to B, B to C, and A hopes to get something back from someone else) (Nowak and Highfield 2012, p. 54). Equally as important for reciprocal altruism is our capacity to recognize signals of growing up in the same community (Dunbar 2016, p. 315; Henrich 2016, p. 201), which we interpret as indicators of shared norms and knowledge (Berreby 2008, p. 225; Boyd 2018, p. 37; Laland and Brown 2011, pp. 148–149). However, Trivers’ (1985) concept of reciprocal altruism does not explain an important aspect of protective alliances and friendships: they usually do *not* depend on balanced reciprocity. Once a relationship is defined as a friendship, we usually do not keep track of reciprocity in a *tit-for-tat* manner (de Waal 2010, p. 174).

By shifting a person into the category of a trusted cooperator to whom one is committed, humans reduce *social transaction* costs (Frank 1988). Friends are a special case of trusted cooperators. According to transaction cost economics, actors invest time, effort, and money on imperfectly transparent markets in order to make sure that economic transactions lead to the desired result. Incorporating the production process into the boundaries of an organizational hierarchy, in contrast, facilitates the surveillance and control of employees. Information asymmetry now shifts to the producer’s favor, so that governance costs within the hierarchy become lower than transaction costs on markets (Williamson 1981, p. 558). Organizations often aim for “goal congruence,” which is an overlap of organizational and individual goals, by sharing common beliefs and values (Ouchi 1980, p. 136). With reference

Fig. 1 Components of the “social brain”. (Source: author)



to Durkheim, Ouchi (1980) describes the result of goal congruence as a *clan*, where culture and norms have largely converged. By focusing on the adaptive fitness of reduced transaction costs, transaction costs economics is explicitly linked to the evolutionary literature in economics and sociology (Williamson 1981, p. 568).

Social transaction costs in our daily interactions relate to the question of whom one can trust and rely on when in need of help, support, or in cooperation. These costs are reduced if particular persons are likewise “incorporated” into a close social circle categorized as trusted collaborators or friends—a category normatively corroborated by shared taken-for-granted knowledge on what we can expect from trusted friends (Hruschka 2010, p. 170), and, related to these norms, sometimes also by ceremonies and commitment rituals (Hruschka 2010, p. 70). Social transaction costs decrease considerably when institutionalized expectation states at the group level are combined with strong emotions at the individual level. Individuals respond with strong emotions when they either violate or confirm others’ expectation states (Turner 2007, p. 83). Humans’ social brain is a fitness-enhancing result of *cognitive* capacities required to strategically manage social relationships in groups of ~50–150 persons (“~” means “approximately”), as argued by Dunbar (2016, p. 67).¹ Evolution also enhanced *emotional* capacities to integrate social relationships (Maryanski 2018, p. 234; Turner 2021, pp. 57–59; Dunbar 2021, pp. 312–313). In working groups, for instance, repeated cooperative interaction often leads to positive emotions (Lawler et al. 2015), which can result in friendship or at least in committed collegiality. Positive emotions signal commitment to the interaction and thereby “foreclose potentially valuable opportunities” (Frank 2001, p. 60), such as defecting or erratically switching to new partners. In the following, I further elaborate this argument by describing the components of the social brain.

¹ Categorizations leading to high commitment are often based on homophily. Dunbar lists six main dimensions of homophily in friendships: “shared language, shared place of origin, similar educational history, shared interests and hobbies, shared worldview (...) and shared sense of humour” (Dunbar 2016, p. 319). Later, he added a seventh “pillar” of friendship, namely “having the same musical tastes” (Dunbar 2021, p. 203, 2022, pp. 107–111).

3 Proximate Explanations of Human Sociality: Cognitions and Emotions Evolved into the “Social Brain”

Human social interaction comes along with a variety of emotions, expressed both in facial expression (Frank 1988, p. 121; Turner 2000, p. 113) and in *prosody*, which is the emotional intonation in speech (Mithen 2006, p. 55). Humans and primates rely heavily on facial expression and voice intonation (Turner 2021, p. 68) when they communicate emotional states. We experience communication as strained and awkward when an appropriate emotional connotation is absent (Turner 2000, pp. 121–122; de Waal 2010, pp. 78–82). Within weeks after birth human infants are able to read emotions and to imitate facial expressions of close family members (Tomasello and Gonzalez-Cabrera 2017; Turner 2021, p. 101). Six- to eight-month-old babies respond emotionally when they observe unfair behavior of googly-eyed geometric figures (Greene 2015, p. 46; Bloom 2013, pp. 26–27). These insights underpin the assumption that evolution wired human dispositions to emotional reactions in social interactions, to sympathy and empathy, but also to anger (Frank 1988; Turner 2007; de Waal 2010).

Neuroscientific studies of macaques revealed that observing others’ motor actions stimulates neural activities similar to those corresponding with their own execution of such actions. Although the debate on the role of *mirror neurons* in observational learning and empathy is still unsettled (Sapolsky 2018, pp. 538–541), their activation could be a first step toward mentalizing: they might contribute to the ability to mentally reproduce *what* a person is doing, which is a precondition of understanding *why* he or she is doing it (Lieberman 2013, p. 150).² Mentalizing is a cognitive adaptation to social interaction and is processed in the evolutionarily more recent frontal lobe (which is part of the neocortex) (Dunbar 2016, pp. 46, 242). Mentalizing means to have a belief about another person’s belief, and this can be extended in recursive sequences into higher *orders of intentionality*: “I *think* that you *assume* that I don’t *know* that you *tried* to *make me believe* that I *supposed* something wrong”. A minority of humans are capable of cognitively processing more than the fifth order, and differences between species correspond with differences in frontal lobe volume (Dunbar 2016, pp. 45–46, 2021, p. 121). Chimpanzees and orangutans, for instance, seem to be able to process second-order intentionality (Dunbar 2021, p. 116).

Although a clear distinction between cognition and emotion is impossible (Damasio 1994; Barrett 2015, p. 85), the social brain consists of both emotional and cognitive components, and the emotional (and often automatically processing) components often dominate (Turner 2000, 2007; see Fig. 1). From a social neuroscience perspective, Lieberman (2013) summarizes recent findings on the neural foundation

² Mentalizing is usually used synonymously with the concept of the “Theory of Mind” (Premack and Woodruff 1978). However, the “Theory of Mind” is misleading in that the chimpanzee studied by Premack and Woodruff does not have a “theory,” but is only able to “... impute wants, purposes, or affective attitudes to another individual” (Premack and Woodruff 1978, p. 526). Other authors prefer the term mindreading (Mercier and Sperber 2018, p. 94) or, like Lieberman (2013, p. 108), mentalizing. It means that we generate information about others’ mental states by interpretation and inference on the basis of our prior information on the person and the situation (Vromen 2017).

of human sociality: first, when the brain seems to do nothing, the default neural network seems to nudge us toward thinking about social relationships (Lieberman 2013, p. 19). Second, human brains process physical pain and social pain (pain due to social distress, e.g., fear of social rejection due to norm violation) in a similar way (Panksepp and Biven 2012, p. 314). Both activate the dorsal anterior cingulate cortex, which exists in mammals but not in reptiles (Lieberman 2013, pp. 50–51), and detects whether a desired condition is met or not (Lieberman 2013, p. 62). Negative emotions resulting from our social relationships can have severe consequences for our mental and physical health (Cacioppo and Patrick 2009, p. 96), whereas positive emotional arousal in social settings, when we meet expectations (Turner 2007, p. 83) or satisfy transactional needs (Turner 2007, pp. 102–104), can improve our mental health (Cacioppo and Patrick 2009, pp. 218–219). Third, our social brains have a strong disposition to assume agency and intentions in our environment and to mentalize.³ If they do, the mentalizing network in the human brain is activated (Lieberman 2013, p. 117). Finally, there is a related, specific human cognitive component in cooperation, which Tomasello describes as “joint intentionality” (Tomasello 2018, p. 50). In humans, the creation of a cooperative “we” constitutes a new epistemic level (Tomasello 2018, p. 55): humans experience their own *self* not just as their own self-concept (“I”), but also as a concept of how the self might be perceived by others (“me”) (Mead 1934). The function of the social self (“me”) is *harmonizing* by being sensitive to responses in our social environment. We compare our concept of self (e.g., “I am a friendly person”) with the assumed view of members in significant social groups, e.g., family or colleagues (Lieberman 2013, pp. 191–192). Social selves make humans receptive to influence from their social environment and facilitate the adoption of new ideas and the compliance with social norms (Henrich 2016, pp. 214–215; Boehm 2012, p. 173). A specialized brain network in the medial prefrontal cortex deals with *panoptic self-control* (Lieberman 2013, p. 194), which is the tendency to assume that we are evaluated and judged by others. In line with Tomasello’s idea of “joint intentional activity” as a precursor of a shared sense of ‘we’ (Tomasello 2018, p. 75), panoptic self-control harmonizes our behavior with morals, norms, and expectations in our social environment and increases cooperativeness (Lieberman 2013, p. 228). A further aspect of self-control and self-regulation is the capacity to calibrate between different types of goals. Lindenberg (2015a, pp. 48–50) assumes three main overarching goals, namely the hedonic goal, the gain goal, and the group-oriented normative goal. Pursuing each overarching goal is crucial for humans’ survival. The hedonic goal is focused on immediate gratification and is usually the strongest, whereas the normative goal is weakest; thus, the latter needs institutional support (Lindenberg 2015b, p. 44). Here we see the essential tension between individual and group benefit: “... in the course of evolution, the development of the social brain took place in such a way that, among

³ Barrett (2015, p. 145) argues that the question of whether animals or human babies have the capacity of mentalizing is not simply a question of “yes” or “no”. There can be different kinds of mentalizing, which can be also context-dependent, e.g. whether food, predators, or dominant individuals are involved. Also mirror-neurons seem to respond differently conditional on the framing of a situation and the ‘prior’ information, e.g. hand reaching for a cup either in order to clean a table or in order to drink (Barrett 2015, pp. 124–125).

non-kin, sacrifices for the group would not jeopardize one's own fitness" (Lindenberg 2015b, p. 43). In order to provide the adaptive advantages for the individual, however, for example, during intergroup conflicts, groups had to institutionalize behavioral norms and thereby provide an institutional backing of the normative goal, which facilitated the generation of collective goods. This is a major argument in cultural group selection theory (see below). At the individual level, humans are highly sensitive to norms and social expectations because of their disposition to panoptic self-control.

Our reliance on trust in strong-tie relationships makes us vulnerable, so we usually regard the breaking of a behavioral norm, e.g., among friends, as a severe transgression (Dunbar 2021, p. 229). Related to that, individuals are often willing to bear the cost of punishing antisocial norm violations. We sometimes even enjoy observing what Fehr and Gächter (2002) call "altruistic punishment" (Bowles and Gintis 2011, pp. 24–26; Henrich 2016, p. 196) in "... that delicious sense of pleasure described by the German word *schadenfreude*" (Dunbar 2021, p. 241). Violating social norms could jeopardize our reproductive success (Boehm 2012, pp. 333–334; Greene 2015, p. 226), so that our panoptic self-control in combination with negative emotions ("social pain") of shame and guilt guide most of us quite successfully through our social environment.

Humans also rely on cues of shared knowledge, shared norms and group membership as cultural indicators of potential cooperative alliances, such as dialect, styles of behavior, and indicators of religion and other beliefs. This is one reason why humans tend to distinguish between in- and out-group (Tooby and Cosmides 2010; Tomasello 2018, pp. 88–98; Henrich 2016, pp. 200–201; Boyer 2018, pp. 45–46). Shared norms are essential "... to make human groups function as adaptive units, even when their members are not closely related" (Sober and Wilson 1998, p. 173). In humans, the definition of groups and collective alliances, of 'us and them', is flexible and often adapted to the needs of the current situation (Berreby 2008, pp. 212–213; Crisp 2015, pp. 84–85), which is probably also a result of our evolutionary past as hunter–gatherers living in fission–fusion arrangements (Lindenberg 2015a). Thereby, our *coalitional psychology* (Tooby and Cosmides 2010) emerged. Our propensity to apply social categorizations quickly and unconsciously (Berreby 2008, pp. 137–139) may have a genetic component, but an *actual* definition of group boundaries strongly depends on contexts, situations, and cultural markers of group membership (Kurzban et al. 2001). Commitment to cooperation, thus, has a flipside: we tend to categorize others as potentially threatening non-cooperators if they do not share our cultural markers. Humans tend to apply distinctions *within* and *between* groups in order to ensure cooperation. They do so in a similar way as they distinguish between trusted friends and others within their own group. Categorizations can lead, in the worst case, to dehumanization.

Dehumanization means the denial of others as a fully human being (Crisp 2015, pp. 45–46) and is responsible for the most severe *antisocial* atrocities humans have committed. This is also due to the ambivalent role of the neuropeptide oxytocin. Prosocial effects of oxytocin are common in mammalian parental care relationships (Hruschka 2010, p. 36), where "... *oxytocin* is a critical driver of our caregiving motivations" (Lieberman 2013, p. 92). However, oxytocin is a "momma bear" hormone

(Hare and Woods 2020, pp. 109–114)—the same hormone is released if a mother observes somebody threatening her child. The influence of oxytocin on our behavior suggests that humans’ prosocial, moral sentiments coevolved with the specific mammalian way of mother–child bonding (de Waal 2022, p. 259; Panksepp and Biven 2012, p. 289):⁴ we care intensively for those to whom we feel close, but respond at the same time highly sensitive toward perceived threats from the outside (Bloom 2013, pp. 174–175; Sapolsky 2018, pp. 116–118). Oxytocin seems to increase our willingness to blindly trust our partners and friends and to take risks with them (Hruschka 2010, p. 40), but decreases cooperation with strangers (Berreby 2008, p. 242; Haidt 2012, p. 173; Crisp 2015, p. 45). Under the influence of oxytocin we stop mentalizing, and this “... allows us to blind ourselves to the humanity of people outside our group when we feel threatened” (Hare and Woods 2020, p. 111). During raids against other groups of hunter–gatherers (Boyer 2018, pp. 58–60; Wrangham 2019, pp. 236–238; Bowles 2009; Gat 2008, pp. 116–127, Furuichi 2019, p. 110) or when parents protect their offspring from violent offences, this “blinding” relaxes the suppression of aggression. Categorizing a person as an *out-group stranger* who could be threatening (Hare and Woods 2020, p. 110) is not unlikely to turn into dehumanization: “There seems to be a special, pejorative moral ‘discount’ applied to cultural strangers—who often are not even considered to be fully human and therefore may be killed with little compunction” (Boehm 2012, p. 135).

According to these arguments, Dunbar’s (2016, p. 61) important insight into the correlation of brain (neocortex) size with group size and social complexity is just part of the story. Panksepp and Biven (2012, p. 287) complain that social scientists became interested in aspects of the social brain that are accessible by brain imaging methods but neglect the more ancient *subcortical* emotional processes, which are much more difficult to visualize. Panksepp and Biven highlight the importance of different subcortical emotional systems, which they also call “affective circuits” (Panksepp and Biven 2012, p. 35). They assume these systems to exist in all mammals and to be evolutionarily much older than the recently developed expansion of the neocortex. A system that Panksepp and Biven (2012) call PANIC/GRIEF generates the emotion of separation distress: mammalian pups are born immature, depend on nurturance and protection by their mothers, and emit emotionally driven distress vocalizations in the case of separation (Panksepp and Biven 2012, p. 320). If separation is only short and the social bond re-established, neurochemicals, also opioids and oxytocin, are elevated in infants’ brains, resulting in comfort and relaxation. As a result, “... especially the very young who are completely dependent on others, are literally addicted to social relationships” (Panksepp and Biven 2012, p. 327). The affective circuit of PLAY has a social component as well. PLAY comes along with laughter and touch, as well as joined non-aggressive rough-and-tumble activities. Although PLAY may also have non-social functions, the more play experiences animals had in their early development, the more time they spend with others, “... suggesting a social bonding (friendship) function of play” (Panksepp and Biven 2012, p. 374). Surely, most of these insights result from animal experi-

⁴ De Waal is convinced that “... the amount of ink that scientists have spent on the ‘puzzle of altruism’ could have been greatly reduced had we considered how mothers treat offspring” (de Waal 2022, p. 261).

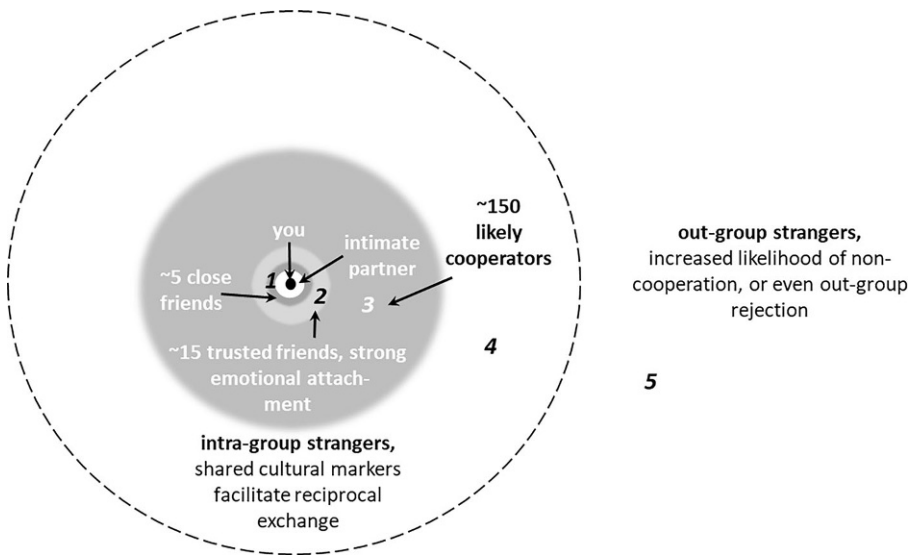


Fig. 2 Social categories of non-kin persons. (Source: author's adaptation from Dunbar 2021, p. 71)

mentation, mostly with rats. Yet humans share almost the same ancient subcortical anatomy, components, and neurochemicals. Humans' neocortex may be involved in controlling behavior when emotional systems are active (Boehm 2012, p. 173), but according to Panksepp and Biven (2012, p. 80), the neocortex itself cannot generate affects. As a result of mammalian evolution, emotional responses result from subcortical systems more or less automatically, given the appropriate stimuli, and some of these responses seem to be unconditional, that is, they are *not* learned (Panksepp and Biven 2021, p. 22). Figure 1 summarizes the components of the social brain. The link between oxytocin and mentalizing (dashed line in Fig. 1) underscores the impossibility of clearly distinguishing between emotional and cognitive components of the social brain (Barrett 2015, p. 85).⁵

How do different kinds of social categories—close, trusted friends, less close friends, strangers from the same cultural group, or out-group strangers relate to human social behavior? Dunbar (2016, 2021) suggests different categories of personal relationships among the ~150 persons we personally know quite well, which he illustrates by using a graphical representation of concentric circles. Figure 2 shows an adapted version of Dunbar's (2016, pp. 80–84, 2021, pp. 70–71) visualization.

⁵ For instance, according to Damasio (2000, pp. 75–80) a damaged amygdala (involved in the negative emotion of fear) impairs recognizing untrustworthy facial expressions, which is a *cognition*, and he assumes that the *emotional* “marking” of options, and thereby selecting from the set of alternatives, precedes decision making in general (Damasio 1994). Panksepp and Biven (2012, pp. 210–212) emphasize the role of emotions, generated by subcortical circuits, for memory and learning.

These social categorizations enable us to quickly (and often unconsciously) distinguish between

1. ~5 almost *unconditional cooperators* (close friends, and often relatives).
2. ~15 *trusted friends* who are extremely likely to cooperate, and to whom you are still emotionally so close that their “... death tomorrow would really upset you” (Dunbar 2021, p. 68).
3. Others in our ~150-*person network* of whom we have enough information to assume that they will probably cooperate, so that “... one feels one can ask a favor and expect to have it granted” (Dunbar 2003, p. 172).
4. *Intra-group strangers* who we do not know personally, but who share our cultural markers, so that we assume that they would neither behave hostile toward us nor defect in reciprocal exchange.
5. *Out-group strangers* to whom we show an increased likelihood of hostile behavior because they do not seem to share our cultural markers or norms.

According to Dunbar (2016, pp. 79–81), in contemporary Western societies, the ~150 circle, including the innermost layers, roughly includes 50% (wider) family members and 50% friends. Family is still important (Dunbar 2021, p. 94), even though large family size constrains the number of “slots” that can be filled with non-kin friends (Dunbar 2021, p. 42). The declining significance of kinship in Western societies could be the reason why there is a Western friendship “style” (see below).

The evolution of friendship is an interesting example of close ties to non-kin. Concepts of friendship exist in most cultures (Kauth 2021, pp. 64–65), and emotional commitment to selective alliances seems to be their common denominator. Yet even within the Western culture, friendship does not always mean the same. People sometimes differ in how they perceive their social relationships, just as they disagree on many other kinds of social categorizations. Empirical information about friendships in surveys is not always reciprocal—within a dyad, people do not always agree on the status of their relationship (Windzio 2018, p. 503). Consequently, scientific concepts of friendship—as used in social network studies (Windzio 2018; Leszczensky and Pink 2019)—necessarily remain somewhat diffuse too (Brent et al. 2014; Denworth 2020, pp. 22–23). This could be one reason why attempts are made in some cultures to institutionalize this form of relationship. Nevertheless, arranging social categories in concentric circles should not be misunderstood as a reification of analytic concepts. Rather, they represent ideal types with considerable fuzziness.

4 Ultimate Explanations: Cultural Group Selection Led to Commitment, Friendship, and Parochialism

According to an ultimate explanation, humans’ proximate dispositions of social behavior, today combined in our social brains, are outcomes of natural selection based on dispositions fitted to past environments (Marchionni and Vromen 2009, p. 90). Marchionni and Vromen (2009, p. 90) prefer the term “then- and now-working causes” over Mayr’s (1988) distinction between ultimate and proximate causes. In their view, ultimate causes and proximate causes of physical structure and behavior

are hard to distinguish in a longitudinal perspective because ultimate causes were proximate causes working in a species' evolutionary past. This problem becomes obvious when we try to analytically understand the proximate mechanisms described in the preceding section, which is almost impossible without referring to ultimate causes, because "... all these remarkable findings make sense in the light of evolution; they are nonsense otherwise" (Dobzhansky 1973, p. 128). Likewise, discussing the ultimate causes of social behavior requires a definition and a description of Y (what we are talking about)—as a proximate cause. Given this caveat, I will now discuss possible ultimate causes of human sociality.

4.1 From Low-Density Networks to Cooperation in Groups

The adaptive advantage of parental care (mostly, not exclusively) in mammalian species was certainly an important factor in the evolution of human pro-sociality (Hrdy 2009, p. 39; Asma and Gabriel 2019, p. 113). For 200 million years mammalian parental care imposed selective pressure on mothers to become sensitive to signals of discomfort emitted by their offspring, e.g., hunger, danger or cold (de Waal 2010, p. 67). Higher sensitivity led to better chances of successful reproduction. According to Hrdy (2009), early humans' grandmothers, siblings, older daughters, men, but also trusted non-relatives, became increasingly involved in what she calls "alloparenting." Unlike most apes, human mothers are prepared to let other persons hold their babies and give them safety and comfort in dangerous environments. Cooperation in child-care allows mothers to use their hands to care for themselves, which in turn increases the child's survival (Hrdy 2009, pp. 76–78). In Hrdy's view, it was beneficial for babies to develop a capacity to attract the emotional attention of alloparents, which also involves rudimentary mentalizing (Hrdy 2009, p. 115).

Owing to climate change 4–5 million years ago, our ancestors had to adapt to living conditions in the grasslands (von Hippel 2018, p. 33; Furuichi 2019, p. 94; Turner 2021, p. 57), but their disposition toward "... low-density networks, low sociality, high mobility, and strong individualism" (Maryanski and Turner 1992, p. 13) was inappropriate for life in the open savannah. Now, stronger social bonds and group solidarity beyond parental care provided a selective advantage in the new environment (Humphrey 2002, p. 42). Throwing stones at animals might have co-evolved with bipedalism (Turchin 2016, p. 96), but when it came to large predators, collective stone throwing might have been a better solution. Collective action required an appropriate social psychology (von Hippel 2018, p. 27), and our ancestors expanded subcortical areas of the brain (Panksepp and Biven 2012) in order to enhance the primary emotions (e.g., aversion-fear and satisfaction-happiness) with variants, mixtures, and varying intensities (Turner 2021, pp. 57–59). Part of this social psychology is human's predisposition toward commitment and friendship.

4.2 The Evolution of Friendship as Protective Alliances

Friendship is an important concept—but what does this concept mean? How did friendships as protective alliances evolve? Rather than being a balanced social exchange, according to Hruschka (2010, p. 68) a friendship "... is a social relationship

in which partners provide support according to their abilities in times of need, and in which this behavior is motivated in part by positive affect between partners.” Friendship is often “... grounded in selective and exceptional help” (Hruschka et al. 2015, p. 255). These characteristics apply equally to what we commonly refer to as comradeship. However, although comradeship is often tied to close but temporary social associations, such as military units, friendship usually persists without such associations. Nevertheless, mutual support and affection among comrades and friends is similar, and comradeship can be a fertile ground for the emergence of stable friendships after, for example, a military unit has dissolved (Obeid 2010, p. 99). In line with the commitment model, friendships are social ties based on positive emotions and do not require balanced reciprocal exchange. Strong positive emotions attached to trusted friends make these relationships somehow ‘irreplaceable’ (Hruschka et al. 2015, p. 261), which is why we get upset if trusted friends die or get seriously ill (Dunbar 2021, p. 68). When providing support, trusted friends do not get the impression of being exploited, even if the exchange is not balanced. A high level of trust within Dunbar’s (2021, p. 237) ~15 layer of friends implies that a provider of support is convinced that the receiver, the friend, is really in need.

With reference to the commitment model, Tooby and Cosmides (1996, p. 140) argue that selective protective alliances make support in situations of need more likely. Paradoxically, however, the chance of supporting a person would decrease with his or her neediness if the support were based on soberly calculated social exchange. Extremely needy persons would probably be unable to return the received benefit in the future. In a similar vein, banks assume needy persons to be high-risk and are reluctant to grant them a loan, which Tooby and Cosmides (1996, p. 131) call the “banker’s paradox.” It would be fatal for individuals and groups, however, if support were denied in situations of need. Given the banker’s paradox, how can social support still be provided in threatening situations, such as infection, injury, food scarcity, or conflict? The solution to this problem lies in devoted commitment to selected persons (Frank 1988, p. 142) who, in the ideal-typical case, regard each other as *irreplaceable* (Tooby and Cosmides 1996, p. 137) and feel particularly intense emotions toward each other (Hruschka 2010, p. 62; Hruschka et al. 2015, p. 260; Asma and Gabriel 2019, p. 260). This presumably includes the layer of ~15 trusted friends in Dunbar’s (2021, p. 68) concentric circles. A prerequisite for irreplaceability is the recognition of these persons as *individuals* (Tooby and Cosmides 1996, p. 140), which corresponds, according to Christakis (2019, p. 329), with high variance in the appearance of human faces: “... in the case of friendship, our evolved psychology equips us with a sense that we are not substitutable. ... The fact that you are irreplaceable to your friends even though you are unremarkable to strangers suggests that there is a deep connection between individuality ... and friendship” (Christakis 2019, p. 284). However, time and effort you can invest in particular others whose well-being and survival is uncommonly important to you—because your well-being and survival is crucial to *them*—is limited. Tooby and Cosmides (1996, p. 136) call this the “niche limitation” of friendship. According to Christakis (2019, p. 351), the specific commitment to irreplaceable individuals becomes manifest in the fact that groups comprise networks of close social bonds with densities signifi-

cantly smaller than one—which means that many fewer than all possible friendships are realized within the respective group.

Alliances not based on balanced social exchange also exist in non-kin primates (Seyfarth and Cheney 2012, p. 158). As primates have a memory of past interaction (Seyfarth and Cheney 2012, p. 163), reciprocal altruism, e.g., with respect to grooming, is certainly one important mechanism of primate social organization. Nevertheless, in strongly bonded dyads, monkeys and primates tolerate considerable imbalance when they give and receive services. They seem to develop emotional bonds and to “... classify others according to their relationships and expectations about how they will interact” (Seyfarth and Cheney 2012, p. 167). Seyfarth and Cheney (2012, p. 170) report evidence that such enduring and close social bonds have a positive effect on reproductive success (Denworth 2020, p. 133; Kauth 2021, p. 82).

For Tooby and Cosmides (1996, p. 135), humans interpret social events as cues for others’ interest in one’s well-being. Even a minor initial signal of high valuation can suggest that the other person might be extraordinarily interested in your well-being and survival, which in turn might increase *your* interest in *his or her* well-being, so that both partners become increasingly committed to the relationship in a feedback loop (Tooby and Cosmides 1996, pp. 139–140). Likewise, Frank (2001, p. 66) describes the effect of first impressions and feedback processes when we meet new acquaintances. Given the similarity of two persons in the main domains of homophily (Dunbar 2021, p. 203), even arbitrary decisions, rituals or oaths of friendship may be enough to initiate this loop. Positive emotions, sympathy, and pleasant interaction strongly facilitate cooperation (Frank 1988, p. 143), which in turn corroborates the affective bond in a dyad. Our evolved social brains might have pre-wired us to enter into such self-reinforcing dynamics, leading into different categories, or “layers,” of social commitment. Lawler et al. (2015) describe similar processes in their “affect theory of social exchange.” According to their observation, frequent interaction in working groups based on shared responsibility often results in positive emotions, which “... leads actors to see the relation itself as a cohesive object of affective intrinsic value” (Lawler et al. 2015, p. 112), and who often become friends. If collaborators are able to control their situation, they also develop positive emotions toward the wider network, or the group, in which their interaction is embedded (Lawler et al. 2015, p. 121). In this multilevel perspective, positive *person-to-person* emotions and friendship are closely linked with positive *person-to-group* emotions, and commitment to both the dyad and the group increases.

Following from this, commitment to trusted partners and friends becomes more likely owing to positive emotions during repeated interaction. It is not trivial, however, to explain the evolution of moral emotions such as sympathy. The capacity to sympathy evolved by chance, but how could sympathy, ultimately, have been beneficial at all? According to Frank (2001, pp. 71–72), applying the powerful *tit-for-tat* strategy in social interaction requires some self-control because of the high subjective value of immediate defection against a cooperative partner—and because of the subjective discounting of future benefits. Yet mutants with a capacity for sympathy anticipate their own negative emotions resulting from their defection, which is why they start an interaction with *tit-for-tat*, that is, they start with cooperation and

then imitate the partner. Thus, Frank (2001, pp. 71–72) suggests that the ultimate motivation to apply a *rational* strategy might be to avoid negative *emotions*.

In everyday cooperation, our human ancestors chose reliable partners for cooperation in dyads or small subgroups (Tomasello 2018, p. 59). Subgroups of men often cooperated, e.g., in hunting large game (Tomasello 2018, p. 65; Kauth 2021, p. 81), subgroups of women in gathering and alloparenting (Hrdy 2009, pp. 106–107). When evaluating potential partners, “... they knew that they were being evaluated by others as well—and indeed, they could reverse roles and simulate others’ evaluations” (Tomasello 2018, p. 144). Tomasello (2018, p. 60) argues that individuals tend to regard others as being equivalent to themselves and therefore to respect their chosen partners. When cooperating, these partners are jointly committed to the role of being a partner in a supraindividual entity, the “we” (Tomasello 2018, p. 65). Again, this can easily result in a feedback loop, leading to perceiving partners as irreplaceable, simply because we assume that we are irreplaceable to them.

Trust is essential to predicting partners’ future behavior (Tomasello 2018, p. 51). The feedback loop of successful reciprocal exchange increases trust, and trust is required to put somebody into the ~ 15 layer of trusted friends (Dunbar 2021, p. 230). The other way round, defection and low trust prevent a relationship from developing into a closer friendship and from bringing it into the ~ 15 or even the ~ 5 layer.

Non-friends can be trusted cooperators as well, if, for example, you know that, for whatever reason, from a rational point of view they do not have any other option than to cooperate. However, it is the positive emotion we feel toward trusted friends that provides commitment and stabilizes the relationship, making cooperation much less dependent on situational rationality. Nevertheless, humans seem to be more generous to kin than to friends, and this is not primarily due to emotional closeness (Curry et al. 2013).⁶ With respect to very high-cost help, e.g., by donating a kidney, people seem to regard close friends like cousins (Stewart-Williams 2007, p. 195). Hence, bearing extremely high costs to help non-kin friends would also require extreme emotional closeness.

Conceivably, friendships within groups can also undermine group cohesion, for instance, if two actors mutually exchange social approval instead of approval for compliance with group norms (Flache and Macy 1996). Yet *successful* groups were able to coordinate social interactions by institutionalizing “supraindividual social structures,” in particular, group norms and taken-for-granted knowledge (Tomasello 2018, p. 119). In the empirical world, institutionalizing norms of trust and cooperation owing to commitment among friends may have been to the benefit of the group—which is an assumption in cultural group selection theory (Boyd 2018, see below). For instance, having trusted friends facilitates childcare and gives mothers more opportunities to care for themselves. Although alloparenting usually involved close kin in most hunter–gatherer groups, non-related confidants were also involved (Hrdy 2009, p. 195). In addition, the more a male hunting group could rely on each

⁶ Friends tend to be genetically more similar than nonfriends—on average they resemble fourth cousins. Christakis (2019, p. 291) explains this genetic similarity, which is just a correlation, with a functional relatedness. This means that both persons interact with the environment in a similar way and mutually benefit from their cooperation in this functional niche—e.g., during a stag hunt (Tomasello 2009, p. 54).

individual, the higher the likelihood of success. As women had a preference for successful hunters, developing more social and cooperative hunting skills could have increased reproductive success for male individuals (Kauth 2021, p. 95). In dangerous and complex hunting, "... what I do ... depends on what I think you will do and vice versa, recursively, which means that we must be able to communicate and trust one another sufficiently" (Tomasello 2009, p. 54). This is much easier among committed friends who consider each other to be irreplaceable (Tooby and Cosmides 1996, p. 133). The same holds for violent intergroup conflicts, which often happened in the form of raiding or ambushing in small parties of 5–10 men (Wrangham 2019, p. 237). In such situations, it is extremely important to rely almost unconditionally on your trusted cooperators, who easily establish joint goals and joint intentionality as well as an agreement on functional roles (Tomasello 2014, pp. 38–40).

In Kauth's (2021, pp. 64–65) view, most cultures have institutionalized norms of how to behave in protective alliances and friendships. Their languages contain words for friends. Yet culture and norms are not individual attributes but group characteristics, which is why multilevel selection (see below) may have played an important role in the evolution of human sociality and friendship.

4.3 The Group Level: Institutional Embeddedness of Social Emotions

Selective protective alliances constitute social niches individuals built around themselves (Tooby and Cosmides 1996, p. 136), and these niches, in turn, changed the environment of others in the group (Christakis 2019, p. 270). If being more social became increasingly important for the survival of the individual, this could have resulted in a runaway process at the group level too: the more social a species is, the more social it becomes (Christakis 2019, p. 325), and the more successful the group will be in intergroup competition and conflict (Turchin 2007, pp. 127–128; Lindenberg 2015b, p. 44). Humans' increasing sociality may have facilitated the creation of collective goods within the group. In combination with institutionalized and culturally transmitted norms of how to behave in friendship alliances, selection may have become stronger at the group level owing to group differences in patterns of social interaction.

In many cultures, and probably also in small groups of hunter–gatherers during human evolution, groups try to institutionalize protective alliances and friendships. The same is true for 'blood brothers' or 'sworn brotherhood' (Kauth 2021, pp. 86–87; Hruschka 2010, p. 70), or making a particular gift as a symbol of friendship. For instance, the biologists J.B.S. Haldane and Julian Huxley became school friends at Eaton after Huxley gave Haldane an apple—a "... ritualistic mark of friendship at Eaton" (Dugatkin 2006, p. 64). The idea of such rituals is to generate reliable co-operative interaction, which then often results in positive person-to-person ties, and, eventually, positive person-to-group ties and group cohesion (Lawler et al. 2015). Negative or positive emotions often result from the (dis-)confirmation of social expectations (Turner 2007, pp. 83–84), e.g., joy due to social approval or fear of social rejection. Categorizing somebody as a trusted friend usually corresponds with strong emotions in most cultures, namely empathy, respect, pleasure, loyalty, honesty of emotional expression, and trust (Kauth 2021, p. 83; Hruschka 2010, p. 10; Hruschka

et al. 2015, p. 262). Once a ritual has been performed, non-cooperation or betrayal triggers much stronger emotions than betrayal by others (Nesse 2001, pp. 30–31; Hruschka 2010, p. 163). In trusted friendships among almost irreplaceable partners, lying and betrayal easily trigger moralistic aggression (Trivers 1985, p. 388), which “... often seems out of proportion to the offence that is committed” (Trivers 1985, p. 388). Although the victim feels sadness and anger, and perhaps also a persistent loss in self-esteem, the betrayer may feel shame and/or guilt (Turner 2021, pp. 76–77).

Groups with institutionalized norms of trust and cooperation may have had a competitive advantage over other groups, in particular if friendship is already part of a group’s *culture* and based on commitment rituals (Tooby and Cosmides 1996, p. 140; Hruschka 2010, pp. 70–73; Henrich 2016, pp. 171–174), and if dyadic interaction among cooperators also strengthens ties to the group (Lawler et al. 2015). Hence, the evolution of friendship norms may have been favored by *cultural group selection* similar to the evolution of altruism (Nowak and Highfield 2012, p. 89; Wilson 2014, pp. 38–39). Although the issue of group selection is still controversial in evolutionary biology (Sober and Wilson 1998; Wilson 2014), it now seems to be established with regard to culture, in particular with respect to behavioral norms (Richerson and Boyd 2005, p. 212; Boyd 2018, p. 99). Accordingly, processes at several levels facilitate cooperation by providing commitment and limiting the set of behavioral options: at the level of the group, institutions and norms define how to behave toward trusted friends and provide the foundation of social expectations. At the level of the individual, our innate dispositions to panoptic self-control and to experiencing positive or negative emotional arousal when meeting expectations (or not), or when properly behaving toward allies and trusted friends (or not), guide our behavior (Asma and Gabriel 2019, p. 250). In combination, institutions and the social brain reduce social transaction costs.

4.4 Cultural Evolution, Cultural Group Selection and Gene-Culture Co-Evolution

Multilevel selection may have contributed to the stabilization of an altruistic and cooperative psychology in groups of early humans (Turchin 2016, p. 81; Wilson 2012, pp. 52–56, 2014; Nowak and Highfield 2012; Boyd 2018), and the same might be true for friendship. Multilevel selection means that natural “... selection can simultaneously act on individuals within groups and on whole groups” (Turchin 2016, p. 82).

Multilevel selection can be illustrated by an experiment on the egg-laying productivity of hens living in cages with 4 to 8 other hens (Wilson 2019, pp. 84–86). In the first variant of this experiment, researchers selected the most productive hen in each cage to breed the next generation. After several generations, however, the productivity in the cages of the subsequent generations declined because the top-performing hens achieved their productivity by bullying other hens. Each subsequent generation inherited the bullying trait of the most productive individuals. Housed together in a cage, descendants of high-performing hens became aggressive and bullied and even killed each other. High strain levels were the reason for the decline in productivity. In the second variant of the experiment, the *whole group* with

the highest average performance was selected to reproduce. Its descendants stayed healthy and increased their productivity by 160%. According to the multilevel selection argument elaborated in the Price equation,⁷ the higher the variation in the prevalence of a relevant trait between groups $\text{var}(p_{Aj})$ relative to its within group variation $\text{var}(p_{Aij})$, the more important the selection becomes at the between-group level (Turchin 2016, p. 87).

Applied to human evolution, multilevel selection means that cooperative groups could outcompete less cooperative groups, either by resource competition in overlapping niches or by violent inter-group conflict and war (Turchin 2016, p. 116). Early humans lived and cooperated in manageable groups, which Dunbar assumes to comprise ~150 individuals, in varying constellations of fission and fusion (Dunbar 2016, pp. 67, 174). By cooperating, humans created niches on which their lives strongly depended (Laland 2017, p. 230), and antisocial behavior, such as extreme selfishness or bullying, came under the control of the group. According to Boehm (2000, pp. 72–73), when individuals strived for dominance and exploitation of others, collective action kept these upstart dominants under control by severe sanctions, ranging from gossip and ridicule over ostracism to capital punishment (Wrangham 2019, pp. 146–153). This could explain the egalitarian order among adult male hunter–gatherers. Owing to punishment by the group, most humans acquired the capacity of self-inhibition, self-control, and even a conscience. If this capacity resulted from gene-culture co-evolution in increasingly normative environments, the self-inhibition capacity will now have a genetic component (Boehm 2012, p. 237), even though the strong influence of culture and socialization on norm compliance is out of the question (Haidt 2012).

Humans evolved into a highly cooperative and social species because “cultural group selection” (Boyd 2018, p. 99) worked in addition to individual selection. To some extent, *cultural evolution* follows its own inherent logic. It proceeds by the transmission of information among individuals (Richerson and Boyd 2005, pp. 68–69; Dennett 2017, pp. 210–211). Although not independent of its biological foundation in the human brain, cultural evolution facilitated a rapid response to

⁷ We can describe Price’s equation in a simplified way as a multilevel regression model (Snijders and Bosker 1999), with the effect of altruism at the level of genes, at the level of organisms, of groups, tribes, and so on. Take the example of two levels, the individual and the group (Bowles and Gintis 2011, p. 53): w_{ij} is the fitness of individual i in group j , p_{Aj} is the average share of altruists (A) in group j , p_{Aij} is the probability (or tendency) of individual i being an altruist. As altruism is costly for the individual, the effect of β_i on fitness w_{ij} is negative, whereas β_j is positive if the (on average) more altruistic group j outcompetes other groups with respect to average fitness.

$$w_{ij} = \beta_0 + \beta_j p_{Aj} - \beta_i p_{Aij}$$

In this two-level model, altruism prevails in the long run if the effect β_j at the group level outweighs the individual level effect β_i , and if the between-group variance of A_j (the distribution of A between groups) is higher than its within-group variance (the individual probability of being A_{ij}) (Turchin 2016, p. 82):

$$|\beta_j| > |\beta_i| \cap \text{var}(p_{Aj}) > \text{var}(p_{Aij})$$

More generally, the evolution of altruism depends on the *relative proportions* of these four quantities. The share of altruists will increase if the ratio of between-group $\text{var}(p_{Aj})$ to within-group variance $\text{var}(p_{Aij})$ of A is greater than the ratio of the selection strength β_i on individuals to the selection strength on groups β_j (Turchin 2016, p. 82):

$$\frac{\text{var}(p_{Aj})}{\text{var}(p_{Aij})} > \frac{\beta_i}{\beta_j}.$$

ecological change, and allowed the inhabitation of extremely diverse niches, ranging from tropical rainforest (Yanomami), the Kalahari desert (San) to the Arctic (Inuit). Survival in ecological niches requires specific knowledge that must be maintained through learning and teaching (Henrich 2016; Laland 2017, p. 190; Christakis 2019, p. 411). Active transmission of knowledge becomes even more important in rapidly changing environments where cultural adaptation is much faster than genetic adaptation (Richerson and Boyd 2005, p. 43). Part of a culture are social norms, e.g., cooperation in terms of sharing perishable meat in hunter–gatherer groups (Henrich 2016, p. 157). Groups strongly benefit from norms that increase the likelihood of within-group cooperation, but norms only persist conditional on practices of sanctioning norm violators. If individuals are prepared to bear the costs of sanctioning, the degree of cooperation in groups increases substantially (Fehr and Gächter 2002; Vromen 2017). Humans' individual reproductive success became dependent on the ability "... to acquire and navigate a social landscape governed by culturally transmitted local rules" (Henrich 2016, p. 187). As soon as this ability has a genetic component, a self-reinforcing runaway process (Richerson and Boyd 2005, pp. 183–184) of *gene–culture co-evolution* became likely: environments becoming more cultural and normative favored individuals who were more capable of norm-compliance, and who, in turn, contributed to the emergence of more sophisticated normative and cultural environments. The fact that many people feel positive emotions when punishing norm violators or complying with norms themselves might be a result of such self-reinforcing self-domestication owing to gene–culture co-evolution (Henrich 2016, p. 196; Richerson and Boyd 2005, p. 214).

Such emotions are related to an emotional bond with the group, or a sense of a "cultural we" (Tomasello 2018, p. 109). Social psychology has repeatedly shown how easy it is to create artificial collective categorizations and group boundaries, and thereby to induce coalitional thinking and in-group favoritism (Berreby 2008, p. 210; Kurzban et al. 2001; Crisp 2015, p. 35). Strong emotional bonds to the group facilitate cooperation with group members, and these bonds become corroborated by collective emotional arousal during group rituals (Maryanski 2018, p. 261), which Durkheim described as "collective effervescence." The stronger peoples' sense of "we-ness," and the more people therefore comply with group-specific norms, the more cooperative the group (Mithen 2006, p. 215). Groups also had to make sure that products of their joint collaboration were not open-access resources for outsiders who did not contribute to the collective good (Greene 2015, p. 49; Tomasello and Gonzalez-Cabrera 2017, p. 285). Is a strong sense of "we-ness" accompanied by hostility against out-group members (Laland and Brown 2011, pp. 182–183)? As group-level selection was driven by competition and even conflict between groups, and groups with a stronger sense of "we-ness" were more cooperative and more successful, it is not unlikely that we developed a tendency toward hostility against out-groups (Richerson and Boyd 2005, p. 196).

Between group selection gains in importance when success in between-group competition requires efficient cooperation within groups, e.g., in resource exploitation, resource competition, or during violent inter-group conflicts (Turchin 2016, pp. 82–90; Richerson and Boyd 2005, p. 208; Henrich 2016, pp. 171–172). Altruism based on phenotypes could emerge only in rare situations of comparatively

strong between-group selection (Boehm 2000, p. 206; Bowles 2009, p. 1294). Archaeological data on adult mortality due to prehistoric warfare and violence seem to support the proposition that group-level selection was sufficiently strong (Bowles 2009; Wilson 2012, pp. 72–73), although the significance of prehistoric warfare for human evolution is among the most controversial issues in anthropology (Fry 2015). Nevertheless, it is a strong argument in cultural evolution theory to consider *cultural* group selection to be a driving force of remarkable differences in norms between groups (Boyd 2018; Henrich 2016; Turchin 2007, p. 127). If cultural differences in norms of cooperation are substantial, the reproduction of the inferior group's culture declines and disappears in the long run during periods of ongoing competition between groups, sometimes by extinction, but often by dispersion and assimilation into the superior group's culture (Boyd 2018, p. 103; Turchin 2016, pp. 116–117). Cultural evolution allowed us to inhabit various ecological niches, but with the consequence that our environments became progressively cultural and normative.

4.5 Cultural Transmission, Cultural Group Differences, and Humans' Coalitional Psychology

“Conformist transmission” of knowledge and culture became crucial for cooperation and for the creation of a viable niche: humans often copy dominant cultural practices without testing potential alternatives themselves (Richerson and Boyd 2005, p. 121; Henrich 2016, p. 48; Boyd 2018, pp. 40–41). If individuals follow simplified rules of whom to copy from, e.g., conformist transmission or copying from the most successful members of the group (Richerson and Boyd 2005, p. 124; Boyd 2018, pp. 36–37), individuals become more similar to each other within their groups, but at the same time more dissimilar to other groups (Turchin 2016, p. 93). Imitation and social learning drive cultural evolution at the group level and consolidate cultural boundaries between groups, also by the transmission of norms and ways of how to spot and avoid norm violations (Henrich 2016, p. 189). Various elements of a particular culture had to fit together to form a viable niche-specific system of knowledge and practices. It was even dangerous not to conform to norms and practices of, for example, hunting, food preparation, tool construction, or other elements of the evolved culture. An illustrative example consists of food taboos among Fiji islanders. Pregnant women avoid marine species containing pathogens (Henrich 2016, p. 158), but in most cases they are unable to give reasons why they do so. They report that other persons, mostly elderly women, told them to avoid eating this food (Boyd 2018, p. 24). The individual in its particular ecological niche just had “... to conform to this right way of doing things” (Tomasello 2018, p. 86). Again, this is a social commitment, but now to norms and taken-for-granted knowledge of the cultural group, on which individuals so strongly depend.

In order to ensure whose stock of knowledge fits into a tribe's symbolic universe, human cognition relied on “difficult-to-fake” observable markers such as body ornament, language, or dialect, in order to decide from whom one should learn and who is likely to share the same norms of cooperation (Henrich 2016, p. 201; Tomasello 2014, pp. 82–84). Cultural markers serve as signals for coalition and alliance and

indicate within-coalition cooperation, but also potential between-coalition conflict (Tooby and Cosmides 2010, pp. 206–207). Group-level selection operates basically on culture, shared knowledge, norms, routines, and practices, and not primarily on genes, given that environmental change is too fast for genetic adaptation and slow enough for the intergenerational transmission of adaptive practices (Turchin 2016, p. 92; Richerson and Boyd 2005, p. 131). Thereby, human “... social groups became maximally distinctive from one another in language, dress, and customs, and they competed with one another. Those with the most effective social practices thrived relative to others” (Tomasello 2009, p. 94). Owing to the selection of cultures at the between-group level, cultural evolution proceeded much faster than genetic evolution, although both processes were not independent (Henrich 2016; Richerson and Boyd 2005, pp. 196–197). The gene–culture co-evolution perspective suggests that our capacity to quickly and unconsciously decode cultural markers might be an important part of our innate coalitional psychology, which is responsible for the construction and salience of group boundaries (Tooby and Cosmides 2010), so that ethnic-cultural boundaries sometimes hamper the transition of inter-group social exchange into more stable relationships (Windzio 2020).

During human evolution, when most humans lived as hunter–gatherers, there was certainly not much opportunity to meet a person whose skin color was significantly different (Greene 2015, pp. 52–53; Boyer 2018, p. 48). The assumption that racism is not part of our biological dispositions is in line with empirical findings on 3-year-old children. For them, skin color does not matter with regard to whom to accept a toy from or with whom to join an activity (Bloom 2013, p. 114). However, humans are sensitive to *cultural* markers as indicators of group boundaries (Kurzban et al. 2001). In an experiment, young babies could switch between audio tracks with different languages by sucking on a pacifier. As a result, these babies showed high preferences for hearing the language they are used to (Bloom 2013, pp. 110–111). Moreover, babies prefer looking at persons who speak without accent. Taken together, this indicates that our sensitivity to cultural markers may have become an innate trait. We are probably wired for a coalitional psychology (Tooby and Cosmides 2010; Hare and Woods 2020, p. 95), that is, for flexible and context-dependent in-group vs out-group distinctions (Kurzban et al. 2001; Berreby 2008, pp. 225–230). In this perspective, cultural markers at the between-group level perform the same function as commitment rituals within groups. They reduce social transaction costs by generating categorizations and emotions, they facilitate cooperation and norm compliance, and, in the case of close friendship, strong commitment to support if required.

5 Varieties of Friendship

The difficulty of defining friendship (Hruschka 2010, p. 29; Denworth 2020, pp. 22–23) may also result from the historical and cultural variance in “styles” of friendship. Nevertheless, Kauth (2021, p. 64) lists concepts of “friends” from various cultures and languages. In combination with emotional closeness, the willingness to help altruistically may be a universal core of friendship (Dunbar 2021, p. 93). However, the onset of sedentariness and agriculture dramatically changed humans’

social organization, and thus probably also friendship. Along with rising population density and mobility, the division of labor became more differentiated. Informal social control makes potential norm violators suspect that there might be someone somewhere who observes the incident, and who then will punish the violator. Most modern institutions rely on such a suspicion. For instance, we take it as given that there is a judge who does not simply decide "... in favour of the party who can pay her the most" (Seabright 2010, p. 69). Accordingly, modern institutions consolidate cooperation in an anonymous way.

The degree of legitimacy of modern institutions co-evolved with a long-term historical process of individualization. Monotheistic religions, their all-seeing and all-knowing moralistic gods (Dunbar 2022, pp. 193–195), in combination with a contingent afterlife (Henrich 2020, p. 128), surely contributed to a cultural extension of humans' *panoptic self-control* (Lieberman 2013, pp. 216–217). Humans always lived in culturally constructed niches and relied on norms, but the need for well-functioning institutions became even stronger in densely populated civilizations. A mind–world fit (Barrett 2015, p. 106) in such social contexts required us to tame our tendency to regard strangers with suspicion. Humans had to develop what Lindenberg (2015a, p. 54) calls "weak solidarity", namely the capacity to comply with social norms, while at the same time putting a much stronger weight on pursuing own interests than we do in strong-tie relationships among close friends or relatives.

Henrich and colleagues suppose that the marriage and family policies of the Western Church during the Middle Age (Catholic and later Protestant, but not Orthodox) have paved the way for the Western individualistic, universalistic, and institution-oriented culture and psychology (Henrich 2020; Schulz et al. 2019), which they describe using the acronym WEIRD (western, educated, industrialized, resourceful, and democratic) (Henrich et al. 2010). By taking action against polygyny and cousin marriages, the Western Church dissolved networks of distant kinship and thereby repressed clan-based social self-organization. People reorganized themselves into voluntary associations, such as guilds, universities, and monasteries (Henrich 2020, p. 355), where they got used to cooperating with strangers. Although there is not a simple WEIRD vs non-WEIRD dichotomy (Henrich 2020, p. 31), Westerners tend more toward individualism, non-conformity, feelings of guilt instead of shame, universalism, and impersonal pro-sociality (Henrich 2020, pp. 194–209) than people from other cultures.

Dunbar's (2016, pp. 61–64) hypothesis that a social species' group size is constrained by its cognitive capacity to process behavioral information of group members implies a natural constraint in humans too. He assumes that humans are cognitively limited to ~150 persons who they know well enough to ask for a favor. The erosion of clan-based social organization and extended family structures thus opened "slots" within the ~150 layer previously occupied by many family members (Dunbar 2021, p. 42). Enhanced options to make a choice about one's friends could have led to more individualistic friendship styles in WEIRD cultures.

Hruschka (2010, pp. 57–68) contrasts concepts of friendship in WEIRD cultures with data from a wide-ranging ethnographic record. Friends in WEIRD cultures often share personal issues and even secrets. Thereby, they signal trust and intensify potential coalitions. In contrast, self-disclosure is an essential part of a friendship in

only one third of societies in the cross-cultural data set. In some societies, friends even avoid self-disclosure. Friendship based on mutual trust allows a high degree of informality in WEIRD cultures, but there are limits, e.g., with respect to using nicknames and joking. Although friends do not keep track of support and helping in reciprocal exchange, they sometimes exchange *symbolic* gifts that underscore the status of their relationship—and balance in this exchange between friends can be *very* important in some cultures. Moreover, there are differences regarding the influence of third parties on friendships. Although WEIRD individualism implies the norm that individuals choose friends themselves, in other cultures, third parties, e.g., parents or shamans, sometimes arrange friendships. Often, the wider community can influence a friendship, e.g., by reinforcing norms, gossip, shaming, and punishing violations of friendship norms, and the community can also influence the termination of a friendship (Hruschka 2010, pp. 57–68).

Concepts of friendship differ between cultures and also between genders (Denworth 2020, pp. 157–158; de Waal 2022, pp. 229–232), but the basic function is very similar: the reduction of *social transactions costs* by categorizing persons as almost irreplaceable, and thereby increasing the likelihood of commitment and support.

6 Summary and Conclusion

In this overview, the commitment model (Frank 1988; Nesse 2001) has been extended to the different layers of concentric circles of persons with whom we interact and cooperate. Based on emotions generated by the social brain, commitment increases cooperation. According to this model, our social brains rely on these categories in order to reduce social transaction costs. The flipside of the coin is boundary spanning against cultural out-groups. My major argument on the evolution of human sociality and friendship focuses on cultural group selection and gene–culture co-evolution as ultimate explanations of the evolution of the social brain at the micro-level and culture at the macro-level. In line with gene–culture co-evolution theory, a mutual reinforcement of cultural change and genetic adaptation paved the way for the proximate psychological mechanisms of social behavior.

Categorizing others as friends based on emotions and commitment rituals and the categorization of persons as out-group members based on cultural markers and a sense of “we-ness” perform similar functions (Fig. 2): at different levels, in dyads within groups, and in between-group interaction, social–emotional categories imply varying levels of commitment and facilitate cooperation and selective alliances. Shared cultural markers facilitate reciprocal exchange among strangers. This line of argumentation is complex, but appropriate to the complexity of the subject under study. An evolutionary perspective provides a better understanding of humans’ social behavior, why and how we tend to respond to particular cues in our social environments, and why we tend to apply social categories. These insights can endow sociology with new ideas on conditions of cooperation, social cohesion, but also of cultural boundaries and intergroup conflict. An evolutionary perspective on human sociality and friendship can contribute to micro-sociology, in particular to studies on adolescents’ friendship networks (Leszczensky and Pink 2019), but also to stud-

ies on intergroup relations and polarization in attitudes. Sociologists can learn with whom they are dealing: gaining an insight into how the social brain works illustrates humans' emotional, social, and cooperative dispositions, but also humans' tendency to distinguish between in- and out-groups. Rather than organizing their social relationships by market-like social exchange, they categorize their social relationships according to different levels of commitment.

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Declarations

Conflicts of interest M. Windzio declares that he has no competing interests.

Ethical standards This is a conceptual paper that does not involve any human or animal test subjects. This research was conducted with an ethic of respect for cultures, communities, the individual/person, and independent knowledge. I ensure that this research was conducted in accordance with ethical principles.

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