A neurochemical hypothesis for the origin of hominids

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It has always been difficult to account for the evolution of certain human characters such as language, empathy, and altruism via individual reproductive success. However, the striatum, a subcortical region originally thought to be exclusively motor, is now known to contribute to social behaviors and "personality styles" that may link such complexities with natural selection. We here report that the human striatum exhibits a unique neurochemical profile that differs dramatically from those of other primates. The human signature of elevated striatal dopamine, serotonin, and neuropeptide Y, coupled with lowered acetylcholine, systematically favors externally driven behavior and greatly amplifies sensitivity to social cues that promote social conformity, empathy, and altruism. We propose that selection induced an initial form of this profile in early hominids, which increased their affiliative behavior, and that this shift either preceded or accompanied the adoption of bipedality and elimination of the sectorial canine. We further hypothesize that these changes were critical for increased individual fitness and promoted the adoption of social monogamy, which progressively increased cooperation as well as a dependence on tradition-based cultural transmission. These eventually facilitated the acquisition of language by elevating the reproductive advantage afforded those most sensitive to social cues.

basal ganglia | neurotransmitter | *Ardipithecus* | hominin | dopamine

Darwin struggled to account for human language, empathy, and altruism by classical natural selection. More recent attempts to do so (e.g., human self-domestication, cultural intelligence, and cultural group selection) (1–4) have relied principally on explanations rooted in features of human culture of the later Pleistocene. Common to each of these hypotheses is the presumption that major cognitive changes occurred relatively late in human evolution after major brain expansion and concurrent with the appearance of the genus *Homo*. However, Holloway (5–11) argued decades ago that brain reorganization and not mere cortical volume must have been critical to the emergence and success of early hominids (here defined as humans and their ancestors following separation from the *Pan* clade) and that this restructuring was likely coincident with other unique features such as upright walking and canine reduction. Indeed, hominid success compared with that of all other hominoids suggests that intensified social behavior must have underlain their numeric and taxonomic spread into uniquely inhospitable environments even though other hominoids remained restricted to Miocene refugia (12–17). What adaptations could have so remarkably favored these ancestors, and most critically, how did their social behavior eventually promote the adoption of articulate speech, empathy, and altruism through simple, individual reproductive success? Here we argue that selection for a prosocial neurochemistry in the basal ganglia of earliest hominids was the most probable prime mover in the emergence of our species from the last common ancestor (LCA) we shared with the ancestors of extant African apes. We also discuss how this could have contributed to subsequent expansion of the cerebral cortex in the genus *Homo*.

The basal ganglia comprise an interactive group of subcortical nuclei. These forebrain structures communicate extensively with the cerebral cortex via both motor and cognitive loops (18–22). Although originally thought to primarily subserve motor regulation, the basal ganglia are now recognized to be critical circuits in cognitive functions as well. The striatum is the primary input structure of the basal ganglia, receiving projections from virtually all parts of the cerebral cortex, thalamus, and brainstem. It contains three subdivisions: the caudate nucleus, putamen, and ventral striatum. The caudate nucleus and putamen are collectively referred to as the dorsal striatum, while the ventral striatum includes the nucleus accumbens and portions of the olfactory tubercle. Of note, some domains of the basal ganglia are activated before cortical regions during cognitively demanding tasks, highlighting their importance in directing cortico-basal ganglia loop activity (23, 24). As a consequence, lesions of the basal ganglia can mimic those of the cortex itself (25–27), thus confirming that the former modulate virtually every aspect of cognition (24).

The striatum plays a major role in social behaviors, particularly those involved in reward, with a dichotomy of function between the dorsal and the ventral striatum (28–34). The dorsal striatum is involved in internally driven, goal-directed behaviors.

Significance

Two factors vital to the human clade are our unique demographic success and our social facilities including language, empathy, and altruism. These have always been difficult to reconcile with individual reproductive success. However, the striatum, a region of the basal ganglia, modulates social behavior and exhibits a unique neurochemical profile in humans. The human signature amplifies sensitivity to social cues that encourage social conformity and affiliative behavior and could have favored provisioning and monogamy in emergent hominids, consilient with the simultaneous origin of upright walking and elimination of the sectorial canine. Such exceptional neurochemistry would have favored individuals especially sensitive to social cues throughout later human evolution and may account for cerebral cortical expansion and the emergence of language.

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In contrast, the ventral striatum, part of a system that regulates emotions and includes the orbitofrontal cortex and amygdala, is more sensitive to social and environmental cues. It regulates externally guided conduct and facilitates behavioral flexibility. In humans, the ventral striatum is thought to mediate social conformity—that is, altering one's behavior to be consistent with that of others—even if it is not the optimal choice (35–38). In humans, the underlying drive for such ventral striatal activity is thought to stem from a desire to comply with and/or gain social approval from others (39). The conventional, albeit anthropocentric, term for these social behaviors is "personality style," and we will use this phrase here to conform to long-standing literature.

Early studies in rats, mice, cats, and long-tailed monkeys (*Macaca fascicularis*) have revealed that individual personality styles are dependent on relative activity levels of the dorsal and ventral regions of the striatum (reviewed in refs. 29 and 40). Macaque studies have shown that individuals with high dorsal striatal activity are internally driven and exhibit a high level of autonomy (40). In addition, they tend to have only a superficial (contextual) knowledge of their environment (e.g., as demonstrated by a failure to adjust behavior in response to novel stimuli) and are more aggressive, dominant, and comparatively unresponsive to social events (29). In contrast, individuals who are ventral striatum-dominant are more externally driven. They tend to be subordinate in social interactions and are heavily influenced by the actions of others (40). They also explore their environment more thoroughly and are less aggressive. The two extremes of these personality styles exist on a continuum within each species that reflect each unique striatal neurochemical profile (29).

The concentrations of the major neurotransmitters within the striatum—dopamine (DA), acetylcholine (ACh), serotonin (5HT), and neuropeptide Y (NPY)—are influential in the expression of personality style on this continuum. ACh has a major impact on the activity balance of the dorsal (externally guided) versus ventral (internally guided) striatum-associated behaviors and can be pharmacologically manipulated (40, 41). Injections of ACh antagonists into the striatum of long-tailed macaques increased their externally motivated behaviors. Conversely, injecting an ACh agonist increased behaviors considered internally driven. In addition, individuals with higher baseline striatal ACh became more dominant members of their social groups. These results suggest that high ACh concentrations cause internal drive to dominate responses to social stimuli.

Functional brain imaging studies in humans have revealed that high concentrations of 5HT within the striatum also favor increased activity in its dorsal region (42, 43) and appear to promote internally driven behavioral control. High striatal 5HT in rhesus monkeys and vervets mediates behavioral inhibition and cognitive control with respect to emotions—factors that underlie social strategic skills necessary for bonding and partnership (e.g., refs. 44 and 45). Conversely, low striatal 5HT levels are associated with increased external drive, reduced levels of inhibition, increased impulsiveness, and underdeveloped social skills (44). By favoring cognitive control, 5HT decreases impulsive acts such as aggressive outbursts. High levels of 5HT may help buffer the emotional impact of group living and contribute to the cognitive flexibility necessary for successful membership in complex social groups (29). Striatal DA promotes social living and increases reward emanating from social interactions, including conformity behaviors in a wide variety of species (35, 46). Concentrations of DA and 5HT metabolites in the cerebrospinal fluid have been associated with social and behavioral differences between hamadryas baboons (*Papio hamadryas*) and olive baboons (*Papio anubis*) (47, 48). Subsequent molecular analyses of these two closely related baboon species have revealed that differences in the DA pathway related to social reward are critical in mediating species-specific behaviors (49). High concentrations of DA combined with low concentrations of ACh within the striatum favor social behavior that is externally driven with an increased sensitivity to social cues (29, 40, 42, 43, 50). The role of striatal NPY in social behaviors is not well known, but one recent study reported a positive correlation of NPY concentrations in cerebrospinal fluid with social competence in schizophrenic subjects (51).

We posit that a variety of unique contextual and historic factors initially favored selection for greater social cohesion in the earliest hominids, shortly after their separation from the LCA, and that increased cooperation and bonding was achieved via pivotal changes in the neurochemistry of the striatum. We suggest that these early shifts enhanced sociality in emerging hominids and that associated underlying changes in the basal ganglia would later lead to the appearance of creative thought and language (i.e., speech). In support of this hypothesis, we describe the striatal neurochemical profiles of DA, ACh, 5HT, and NPY of extant humans, African apes, and monkeys and show that human striatal neurochemical organization is both unique among primates and consistent with our distinctive social behavior.

Our model is consistent with what has been termed a "ventral striatum-tilted personality" (29). We argue that selection for this particular personality style, and its underlying neurochemical profile, may have ultimately initiated a positive feedback loop favoring the emergence and eventual greater dependence on culture and language. We posit that changes in the striatum were critical to the original emergence of our lineage and represent neural reorganization that facilitated (but did not require) expansion of the cerebral cortex. We posit that these changes in neurochemistry and personality style were catalysts, rather than consequences, of our evolution.

The Human Striatal Neurochemical Profile

We obtained the comparative striatal neurochemical profiles reported here by sampling regions within the caudate nucleus and putamen of humans, chimpanzees, gorillas, baboons, macaques, and capuchins (Fig. 1). Our current results (Fig. 2 and *SI Appendix*), combined with our previous data (52–54), provide strong support

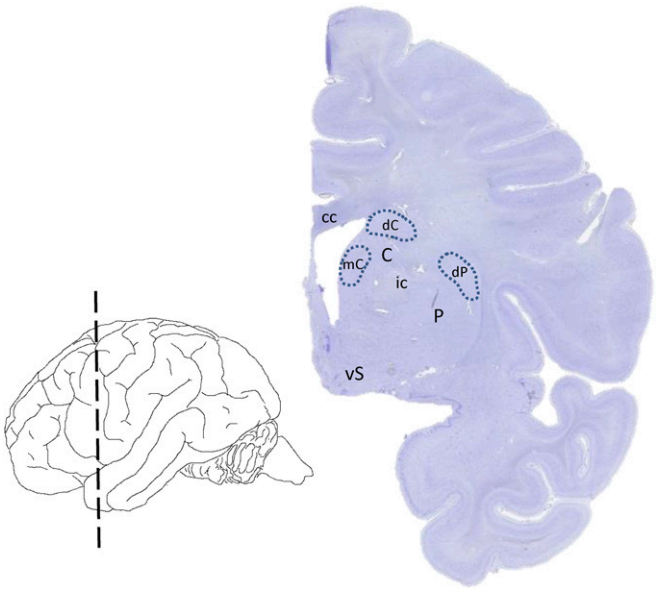

Fig. 1. Nissl-stained coronal section from the left hemisphere of a chimpanzee showing the regions sampled for neurotransmitter densities. Those regions included the dorsal caudate nucleus (dC), medial caudate nucleus (mC), and dorsal putamen (dP). C, caudate nucleus; cc, corpus callosum; ic, internal capsule; P, putamen; vS, ventral striatum. To the left of the Nissl-stained image is a tracing of a chimpanzee brain, with a dotted line indicating the approximate level of the coronal section.

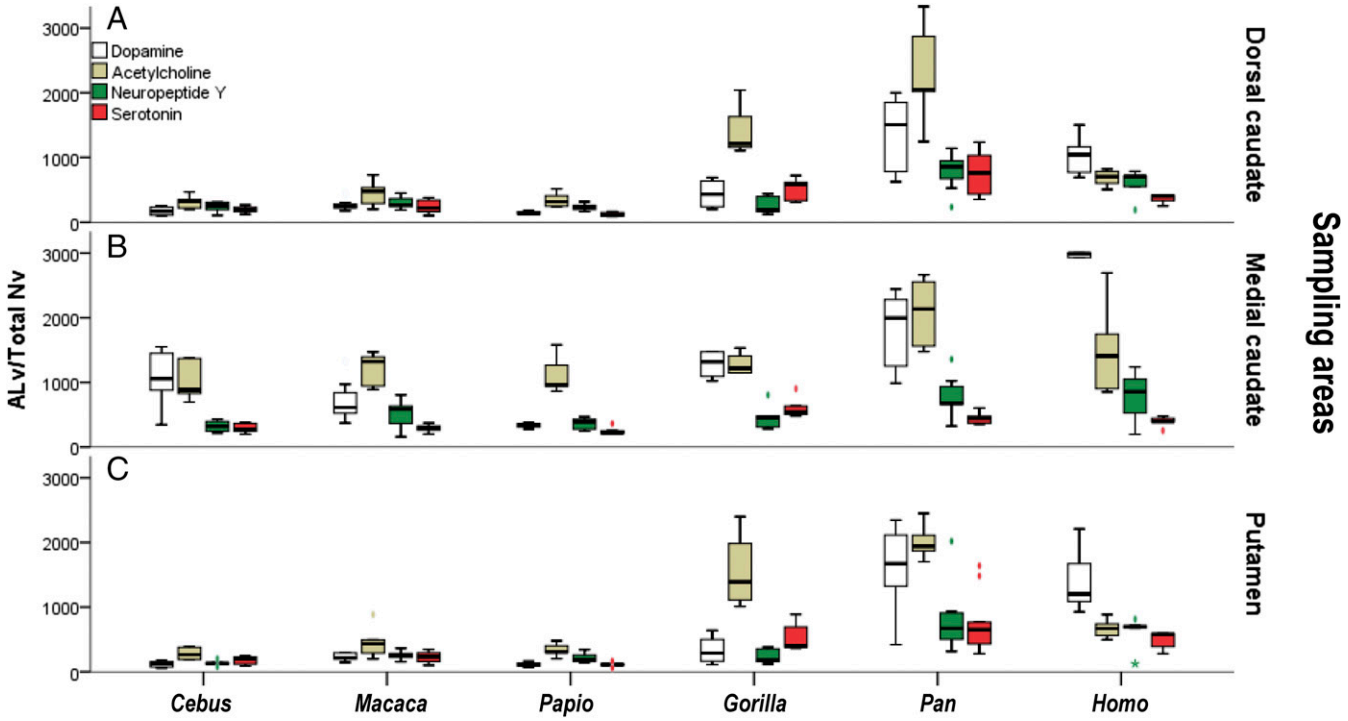

Fig. 2. The neurochemical profile of each species within the caudate nucleus [dorsal caudate nucleus (*A*) and medial caudate nucleus (*B*)] and putamen (*C*) for capuchin, pig-tailed macaque, olive baboon, gorilla, chimpanzee, and human. NPY (green box plots) and 5HT transporter (red box plots) data are from the present study and are shown in *SI Appendix*, Fig. S1. ACh data (as measured by choline acetyltransferase-immunoreactive axons; beige box plots) are from ref. 53, and DA (as measured by TH-immunoreactive axons; white box plots) are from ref. 52. Dopaminergic innervation was highest in human medial caudate nucleus, the striatal region involved in social reward, and humans are the only species to have higher DA relative to ACh content in all three striatal sampling regions. Interestingly, DA within the human medial caudate nucleus was consistently high, with little interindividual variation. ACh was elevated in humans and apes, but humans possessed lower concentrations relative to the apes. Asterisks indicate outliers.

for our hypothesis. Humans possess dramatically higher DA innervation, as measured by the density of tyrosine hydroxylase (TH) expressing axons, in the medial caudate nucleus than do nonhuman primates (52). This is particularly striking because the medial caudate nucleus is active during behaviors that involve social reward (reviewed in ref. 31) and also in speech and language (55–57). Increased levels of striatal DA are associated with social group formation in various species, and this region of the striatum is selectively altered in individuals carrying *FOXP2* mutations that accompany language deficits (55–57). *FOXP2* is an important gene that has consistently been associated with human speech and language, and the insertion of the human sequence in mice alters DA concentrations within their striatum (58–62).

DA is the major modulator of basal ganglia function and is the principal neurotransmitter within the brain's reward system, including socially mediated responsiveness. Our sampling regions have been restricted to the dorsal striatum, but we predict that humans will also exhibit increased dopaminergic innervation within ventral striatal regions as well. Support for this prediction comes from recent positron emission tomography (PET) studies that have found higher levels of dopaminergic $D_{2/3}$ receptor binding in the human ventral striatum and that these are associated with less indirect aggression (63). Furthermore, individuals considered to be socially detached also have reduced endogenous DA within their ventral striatum (64). Of critical importance is that DA actions within the ventral striatum are thought to be critical for monogamy and that increased striatal DA levels are characteristic of monogamous species (65). The dorsal striatum is also active in the formation of pair bonds and is at least partially mediated by opioids such as endorphins (66).

Our data show that striatal serotonergic axon density is relatively higher in humans and great apes than in monkeys. Increased striatal 5HT would be expected in group-living animals to reduce aggression by mediating the emotional impact of close contact with other individuals (reviewed in ref. 29). However, all of the primates in our sample are social, suggesting that elevated striatal 5HT innervation in apes and humans does more than simply reduce aggression. Interestingly, it is possible to manipulate striatal 5HT levels by depleting dietary tryptophan, a precursor (67). In humans, dietary depletion of 5HT increases retaliatory behavior, and functional imaging has revealed that it increases dorsal and reduces ventral activity in the striatum. Striatal 5HT levels are positively correlated with a greater degree of cognitive control over emotions. Such control may promote the strategic skills necessary to negotiate support and apparent trust from social partners (29, 68). Apes and humans exhibit heightened social complexity and intelligence relative to other primate species (69, 70), and their shared increase in striatal 5HT may facilitate such bonding. Furthermore, the increased NPY concentrations that we have observed in the striatum of humans and chimpanzees may also support the increased social competence in both species. Taken together, increased 5HT and NPY support high levels of sociality and sufficient behavioral inhibition to reduce within-group aggression. Both are common to gorillas, chimpanzees, and humans.

Cholinergic innervation in the striatum is relatively higher in apes and humans than in monkeys, although apes have higher striatal ACh levels than do humans (53). Because striatal ACh supports learning and memory as well as cognitive flexibility, we did not at first anticipate this finding. However, given the impact of reduced striatal ACh on social behavior, this finding is not unexpected; while higher striatal ACh concentrations favor internally motivated behavior, lower levels are associated with more external guidance. The lower striatal ACh in humans relative to that in African

apes contributes to our reduced aggression and greater willingness to respond to social cues (i.e., group-directed conformity). Humans are also unique in having higher DA concentrations relative to those of ACh in the striatum (52, 53). This may be a critical element for human-specific behaviors, because the ratio of ACh to DA is more exaggerated in our male gorilla sample, potentially contributing to the intense territoriality typical of single-male groups.

Also of particular interest here is the finding that such a ventral-striatum–dominant personality style is associated with a more thorough knowledge of the environment (29, 40), a factor that is likely to have been crucial to early hominids. Moreover, as just noted, the human DA-dominated striatum (hereafter DDS) personality style strongly favors externally motivated behaviors. The combination of lowered ACh and elevated DA may further exaggerate the DDS personality style. This is consistent with humans being the singularly most cooperative mammal, with infants being innately skilled in tasks that require shared intentionality before their first birthdays (71, 72). Combined with our ability and willingness to cooperate, our DDS may have been pivotal to the evolution of human-styled cognition (72, 73).

Additional support for the critically important role of a DDS in human behavior comes from studies of those neuropathological processes that are associated with dysfunctional social behaviors. Individuals with autism are thought to be deficient in their ability to understand the nuances of social behavior, communication, and social meaning (74). These individuals are exceptionally internally driven and exhibit a correspondingly altered neurochemical profile (i.e., decreased DA and 5HT, abnormal cholinergic striatal cholinergic interneurons, and decreased cholinergic striatal innervation) (75–79). Recent PET imaging has revealed a negative association of striatal 5HT with hostility (i.e., combativeness and global irritability) in individuals with impulsive aggressive personality disorder (80). In addition, there is evidence of abnormal glucose metabolism and decreased 5HT synthesis in the striatum of individuals with borderline personality disorder (BPD) (81, 82), and dopaminergic involvement is also expected (83), with a DA transporter polymorphism linked to BPD risk (84).

A Hypothesis: The Neurochemistry of Human Origins

Human striatal neurochemistry has almost certainly long been modified by natural selection, and while the fossil record cannot provide access to the neurochemistry of extinct species, we propose that selection for a DDS personality style probably began in our earliest ancestors and has led to its exaggerated form in modern humans. It is obvious that humans are in many ways a unique species, and it is equally obvious that at some point our ancestors must have begun to differ from other hominoids in ways that promoted our unique evolutionary success (Fig. 3). The issue here is identification of that point in time when at least a partial DDS must have begun its human-like transformation in our genome.

We argue that anthropoid primates are already intensely social; it is therefore necessary that hominid success was in some way more deeply interwoven with novel social behaviors that could have qualified as "breakthrough adaptations." What these were, when they emerged, and why they have provided such an expanded avenue for the success of the human lineage has long remained a mystery whose solution has traditionally been assigned to the emergence of *Homo* and principally attributable to a greatly enlarged cerebral cortex (1–3).

However, our knowledge of the LCA has now matured by virtue of the recovery of *Ardipithecus ramidus*, which evolved as a low canopy clamberer and terrestrial biped sometime before 4.4 Mya (14, 16). *Ardipithecus* was uniquely equipped with a relatively primitive (late Miocene-like) postcanine dentition combined with a substantially reduced sectorial canine complex (14, 85). Essentially an omnivore, it is inferred to have relied significantly on forest floor foods requiring a search-intensive collection strategy (14, 86–88).

The primate canine is a "social tooth" typically used to assert dominance and aggression, and its reduction in the earliest hominids indicates a major shift in social behavior (85, 89). Further, upright walking is a peculiar mode of locomotion for any primate, and it has been hypothesized to have been initiated by intense selection for the act of carrying food. It has no energetic advantage (90, 91), it greatly increases the probability of musculoskeletal injury, and even modern human "running" is energetically costly and exceptionally clumsy and torpid. Thus, transitional, facultatively bipedal hominids were likely to have been exceptionally easy targets for predation. Despite these relatively immense disadvantages, the likely immediate descendant of *Ardipithecus*, *Australopithecus*, erupted into geographic abundance, readily spreading into novel ecological niches throughout much of Africa (15). Together, these data collectively imply that reduced intrasocial aggression, dedicated carrying behavior, and unusual demographic success occurred together in a hominoid whose life history strategy was also hampered by a need for unusually intense parental care and thus prolonged birth spacing (i.e., a K strategist). All other hominoid taxa with such life history strategies became more geographically restricted or went extinct. The neurochemical data presented above provide a potential solution to this mystery.

Two major K-associated demographic factors that limited Miocene hominoids were prolonged interbirth intervals and the difficulty of successfully raising overlapping offspring. To overcome these obstacles and increase reproductive success, males and females must have employed novel strategies that differed from those of other hominoids. Female hominids can be inferred to have been either pregnant or nursing for much of their adult lives (13, 17) and therefore only rarely impregnable. Males that continued to rely on a strategy of coitus with females only during the periovulatory period would have therefore had very limited reproductive success (92, 93). An alternative strategy of eliminating or dominating all other reproductive-aged males would have greatly limited the dominant male's capacity to prevent predation of females saddled with helpless offspring, bipedality, reduced access to the arboreal canopy, and a search-intensive diet. Females were therefore unlikely to have chosen males attempting such a strategy.

An alternative "behavior" with greater probability of male and female reproductive success may have been for males to habitually copulate with a specific female, regardless of any ovulatory signaling. In its earlier form, this strategy would have been especially effective during the latter phases of lactational amenorrhea when other males remained relatively "uninterested" (94). As reported elsewhere, males of the genus *Pan* occasionally share food with females in return for an offer of, or at least acceptance of, associated copulation (95, 96). Females choosing to regularly mate with such "provisioning" males would enjoy substantial benefits that increase their own reproductive fitness. Their own search time and travel would have been substantially reduced, allowing them to intensify infant care and to more successfully avoid predators. Their intake of relatively rare, high-protein/fat foods would have substantially increased depending on the skills of their "provisioner(s)." Females' choice of males with the greatest environmental awareness would be under intense selection, as would a male's capacity to carry exceptionally valuable foods for significant distances. Males maintaining a principal strategy of competing with other males for copulation with females in estrous were also those that were most likely to have retained larger canines and were therefore also less likely to have been chosen by females as potential provisioners. In addition, canine reduction may have also been related to complex hormonal changes that corresponded to striatum prosociality. However, if this

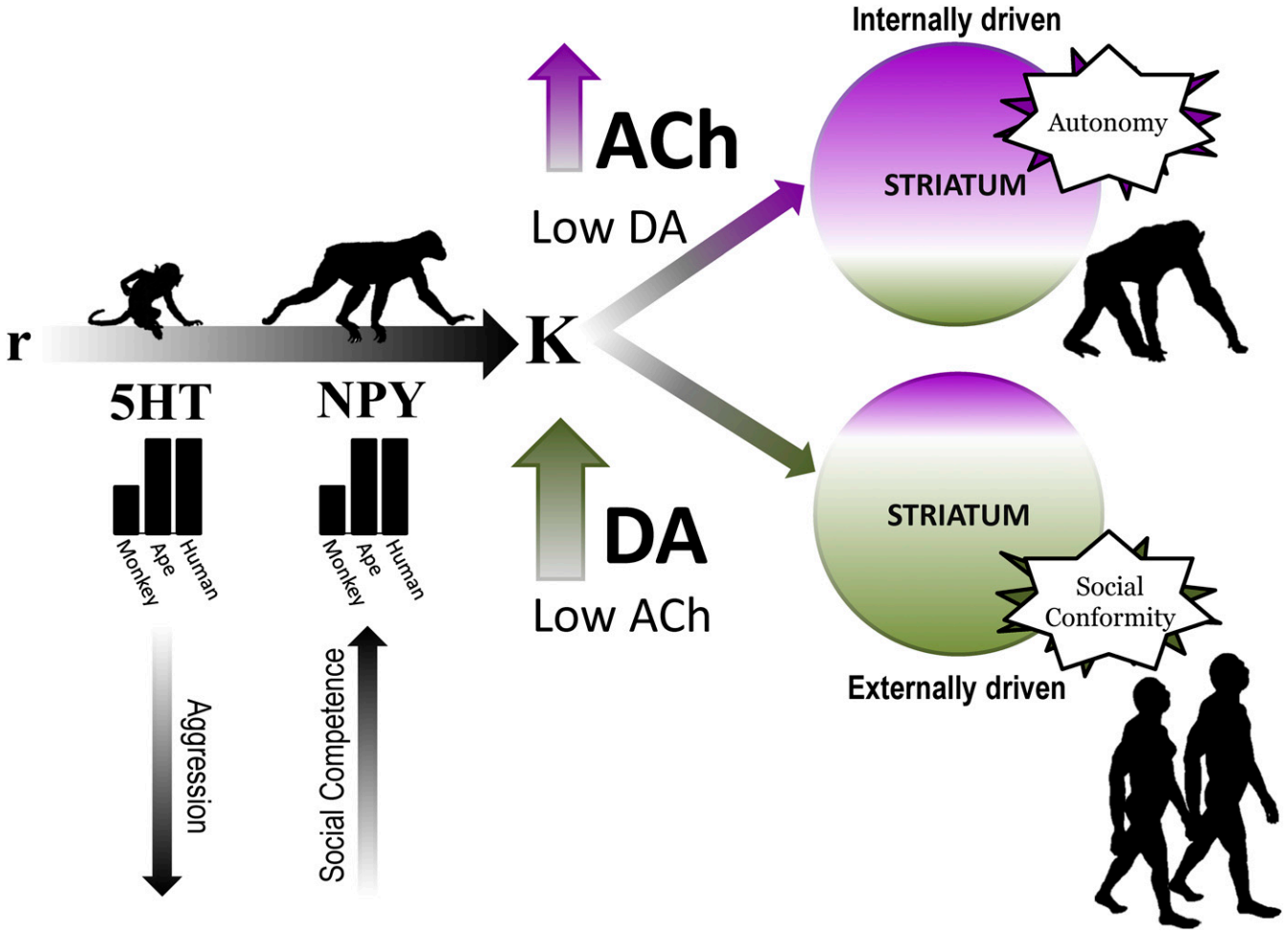

Fig. 3. Role of striatum neurochemistry in human origins. As primates moved from an r-to K-life history strategy, striatal 5HT levels increased to buffer against aggression and striatal NPY levels also rose, at least in some species, to facilitate increased social competence. In our sample, humans, chimpanzees, and gorillas show increased 5HT relative to other primates within sampled striatal regions, and humans and chimpanzees also share increased NPY. Extant apes now exhibit high striatal cholinergic innervation and low DA, a combination that is associated with personality styles that are externally motivated and characterized by aggressiveness, dominance, low motivation to alter ongoing behaviors in response to social or environmental stimuli, as well as a relatively superficial knowledge of the environment. In contrast, humans now possess high striatal DA and low ACh innervation, a unique profile that is accompanied by increased externally motivated behaviors. The human profile is associated with conformity behaviors that are more responsive to social and environmental cues, decreased aggression, and a more sophisticated knowledge of the environment. High concentrations of striatal DA are also associated with pair bonds (i.e., monogamy). The progressive evolution of increasing DA combined with decreasing ACh (to reduce aggression) accounts for why humans can display social, rather than territorial, monogamy. We posit that an earlier manifestation of this profile was central to the success of human ancestors and helped initiate social monogamy in post-LCA hominids.

behavioral complex were to have become fixed, the resulting group would have become composed of multiple pair-bonded dyads. All other monogamous primates are territorial pair-dwellers. The answer to how such a shift could occur may be in alterations of the neurochemistry of early hominids.

The roles of the neuropeptides oxytocin and vasopressin in social behaviors, parenting, and monogamy across species ranging from voles to marmosets are well-established (97–100). Both are involved in human pair-bonding, and genetic studies show that receptor variation is associated with levels of promiscuity in human males and relationship quality in females (101–105). However, it has been argued that human social relationships would require a different neurochemical base (106). Pearce et al. (106) recently showed that DA, 5HT, β-endorphin, and testosterone receptor variation also influence human social and sexual relationships. While a host of additional cues (and their associated genes) are undoubtedly necessary to firmly establish modern human-like monogamy, it is still true that "a single gene can have a profound influence on the expression of complex behaviors defining reproductive strategies" (ref. 107, p. 98). Further, both regions of the striatum are key factors in regulating monogamy, with elevated levels of DA in its ventral portion (in concert with oxytocin and vasopressin) and opioids in its dorsal part both favoring pair bond formation (66, 97, 108). Suffice it to say that pair bonding has developed in other mammals and could have done so easily in *Ardipithecus* or a predecessor, but with one caveat. As noted above, other monogamous primates behave aggressively toward species members that are not their chosen mates or contemporary offspring. What could have "rescued" pair-bonded hominids from the same fate?

Our model is outlined in Figs. 3 and 4. While humans exhibit increased DA innervation in striatal regions associated with social reward (far more so in humans than in any other species; Fig. 2), we predict that nonhuman primates that also pair bond exhibit elevated ACh content, consistent with their pronounced territoriality. However, a gene complex similar to that found in prairie voles in combination with the unique human DDS personality style (Fig. 4) would provide an alternative group reproductive

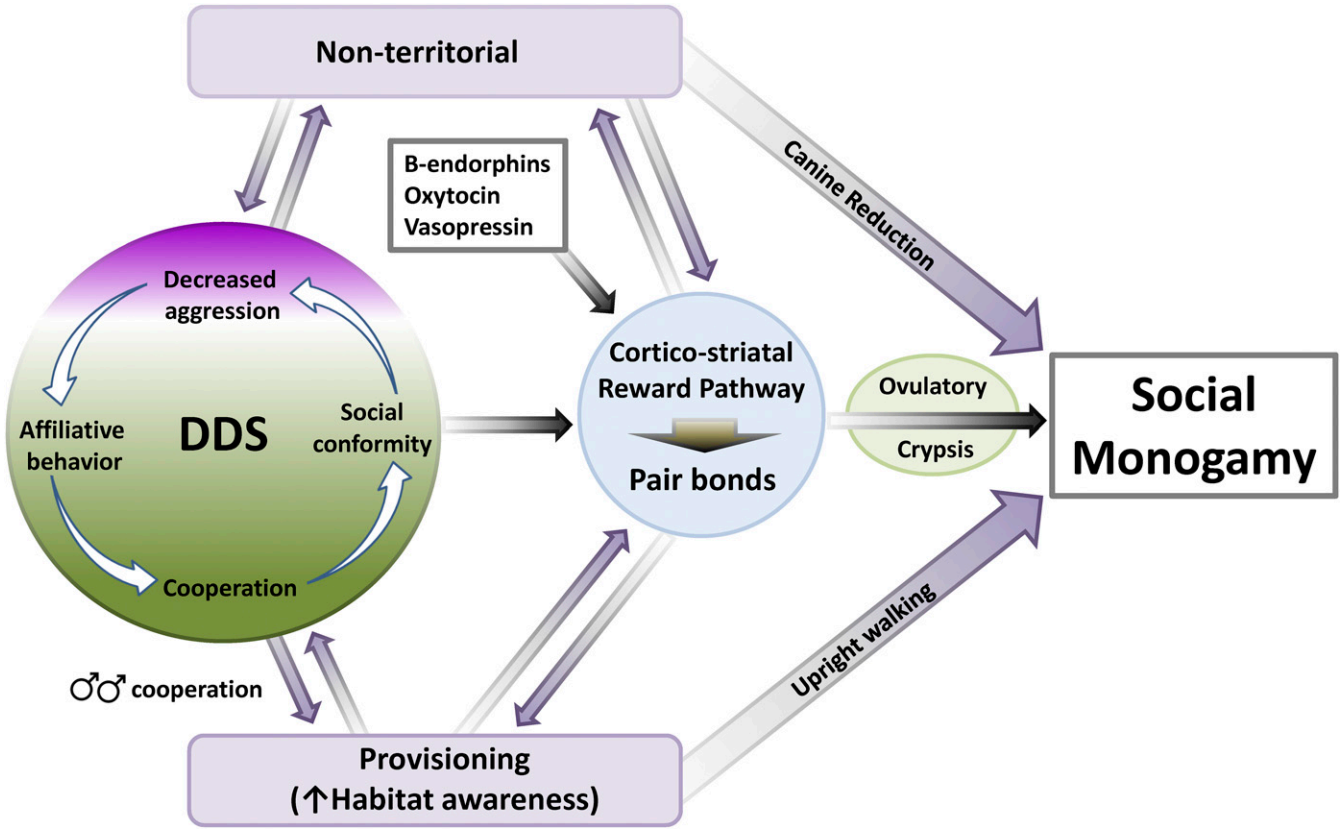

Fig. 4. Extraordinary characters in earliest known hominids. *Ardipithecus* displays evidence of the simultaneous elimination of the sectorial canine complex and adoption of upright walking. Its likely descendant, *Australopithecus*, exhibits unusual demographic success (15). As outlined here, each of these is strikingly consistent with pivotal changes in the cortico-striatal reward pathway and striatum (Fig. 3). Although our knowledge is still incomplete, some elements of the human reward pathway are similar to those of primates that pair-bond, and such primates are typically territorial. However, early hominids were omnivores relying substantially on lower canopy/terrestrial resources. Territoriality like that either of chimpanzees (ripe fruit frugivores defending upper canopy patches) or gorillas (relying on continuously distributed terrestrial herbaceous vegetation) would have been strategically unsustainable for hominids. Terrestrial collection sectors would have been too large for aggressive defense because of their requisite search-intensive food strategy, and broad searches would have been hazardous for females with dependent offspring. However, habitual male copulations with individual females in exchange for collected protein-rich food items (provisioning), as occasionally seen in extant chimpanzees, could have dramatically increased male paternity and enhanced subadult and female survivorship. The changes in basal ganglia neurochemistry shown here would have allowed multiple pair-bonds to coexist within a single social group. Other aspects of a DDS personality type would have increased habitat awareness, which is critical for food location and predator evasion. Under such conditions, selection would have favored male choice of females whose ovulatory status remained cryptic, especially if it included a simulation of lactational amenorrhea (noncyclicly enlarged mammary glands). The breakthrough adaptation of early hominids was therefore likely dependent upon multiple modifications in the basal ganglia that could promote social (nonterritorial) monogamy.

structure—social monogamy—that is, a cohesive collection of cooperating pair-bonded dyads. Critical to this is the decreased striatal ACh that reduces aggression. Dramatic reduction in interpersonal aggression within such a group, coupled with those other social consequences known to characterize a DDS personality style, could have introduced dramatic communal power to early hominids, all of which would have been likely to elevate survivorship and cooperatively repel predation. Selection on individual males and females to comply with such an organization would have been direct and intense (12, 13, 17).

The relatively enormous early taxonomic and demographic success of hominids is a strong testament to their likely adoption of some form of such an adaptive complex, and Fig. 4 summarizes some of its potential effects. Social conformity and decreased aggression associated with the DDS style would have increased affiliative behavior. Reduction in the *Ardipithecus* upper canine as well as the tooth's transformation into a nonaggressive shape must have altered its role in social communication (85). The nearly ubiquitous primate "threat grin" was likely inverted into the novel act of "smiling"—a new mechanism that could assure group members of an absence of aggression. Under this scenario, males who pair-bonded to females lacking external signs of ovulation (i.e., an absence of ano-genital swellings as seen in chimpanzees) would have been more likely to avoid cuckoldry. A further advantage would be selection of females with noncyclic mammary inflation that discourages interest by other males and can be achieved by simply increasing the gland's tendency to accumulate inert fat (12, 13, 17). It is worth noting that in domesticated animals bred for an affiliative ("friendly") disposition, females more frequently engage in extraovulatory copulations (92, 93). These could have further cemented "public" male–female bonds. Conversion of penis structure from "complex" (i.e., with keratinous mechanoreceptors) to "simple" (elimination of such structures) would have provided further social signaling of the pair bond by extending the duration of copulatory bouts between habituated mates within the bounds of the social group (109, 110).

The DDS personality style would have encouraged cooperative food search and perhaps even simple collective hunting. Provisioned females would have enjoyed increased fat stores, elevated infant survivorship, reduced exposure to predation, and more rapid reentry into the ovulatory cycle. Increased awareness of habitat, also characteristic of a DDS personality style, would have been of

great benefit in food searches by males. Alloparenting may have become more prevalent and would have also improved female survivorship (15).

Almost all of the traits described above have previously been posited to have appeared in concert with the emergence of the greatly enlarged cortex of the genus *Homo*. Our argument here, however, is that a shift toward a DDS personality style is more likely to have encouraged our clade to progress into human-type socialization much earlier in its evolutionary emergence. This early shift would have contributed, via a positive feedback loop with factors such as social intelligence, to the exceptional affiliative and prosocial characteristics that are part of the human self-domestication hypothesis (3). Perhaps most importantly, such a scenario directly comports with a uniquely powerful selective mechanism–pair bonding enjoined to provisioning—a relationship by which individual reproductive success encourages ever more successful socialization as it simultaneously escalates both male and female fitness. That is, those reproductive dyads that were most dietarily and socially successful were also likely to have experienced the highest procreative rates. This scenario also provides an immediate and powerful selective force in favor of upright walking—a causal factor long sought after but always lacking sufficient selective power to justify such a radical shift in anatomical structure away from that favoring quadrumanual clambering (14, 16). But what are the prospects of testing such a hypothesis?

The two species of *Pan* (chimpanzees and bonobos) differ substantially in those same behavioral and physiological characters that we have posited to have been pivotal in earliest human evolution (reviewed in ref. 111). Compared with bonobos, chimpanzees are more aggressive, more territorial, and less likely to share food. In addition, their copulatory windows are much more restricted within the ovulatory cycle than are those of bonobos, which are, in contrast, more affiliative, more willing to share food, and more socially tolerant (112–114). Bonobos also exhibit a longer period of subadult dependency and outperform chimpanzees in cooperative tasks; behaviors that we posit were uniquely favored by a shift to a DDS personality style.

It is of special note that the feeding ecologies of these two species also differ in ways that parallel those that would have isolated *Ardipithecus* from its most contemporary ape relatives. Whereas extant chimpanzees rely heavily on seasonally available ripe fruit, bonobos also forage on more ubiquitous and less defensible forest floor terrestrial herbaceous vegetation (115–117), although neither ape species shows evidence of the more generalized search-intensive omnivory that likely characterized *Ardipithecus* and its immediate descendants.

Although we do not yet have data for the bonobo striatum equivalent to those that we are reporting here for chimpanzees, we do have indications of a neural divergence between these two species that parallels these differences in social behavior. Bonobos exhibit greater leftward striatal asymmetry and have less putamen volume than do chimpanzees (118). Further, they also possess more gray matter and connectivity in brain regions involved in social behaviors, including the amygdala (part of the emotional system that is connected with the ventral striatum) and anterior insula (119). A twofold increase of 5HT has been documented for their amygdala relative to that of the chimpanzee (120). Future studies using extant primates with divergent social behaviors, such as the bonobo versus chimpanzee, will provide further resolution to these hypotheses.

In conclusion, we have argued here that once established, selection would have favored further amplification of the DDS personality style in the descendants of *Ardipithecus* and that greater sensitivity to social cues would eventually have facilitated even more intensive conformity behaviors and altruism. Both would have enhanced parenting, further decreasing interbirth intervals and especially reducing offspring mortality (15). Positive feedback from the increased social competence that it would have provided would have also increased cognitive and behavioral flexibility as well as fostered facial expressions as mechanisms of communication. Eventually, these would have been followed by adoption of language, a factor that also requires exquisite sensitivity to social cues, and is supported by increased striatal DA innervation. The DDS personality style could have initiated most everything that defines humanness, thus accelerating the advanced behavior that would later become manifested in early *Homo*.

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