

The adaptive nature of the human neurocognitive architecture: An alternative model

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ABSTRACT The model of the human neurocognitive architecture proposed by evolutionary psychologists is based on the presumption that the demands of hunter-gatherer life generated a vast array of cognitive adaptations. Here we present an alternative model. We argue that the problems inherent in the biological markets of ancestral hominids and their mammalian predecessors would have required an adaptively flexible, on-line information-processing system, and would have driven the evolution of a functionally plastic neural substrate, the neocortex, rather than a confederation of evolutionarily prespecified social cognitive adaptations. In alignment with recent neuroscientific evidence, we suggest that human cognitive processes result from the activation of constructed cortical representational networks, which reflect probabilistic relationships between sensory inputs, behavioral responses, and adaptive outcomes. The developmental construction and experiential modification of these networks are mediated by subcortical circuitries that are responsive to the life history regulatory system. As a consequence, these networks are intrinsically adaptively constrained. The theoretical and research implications of this alternative evolutionary model are discussed.

An extensive literature underscores the enormous functional plasticity of the neocortex (1–3), a distinguishing characteristic of mammals (1, 4). This evidence supports the position that cortical representational features are systematically constructed by the dynamic interaction between environmentally derived neural activity and intrinsic neural growth mechanisms (3). The information-processing capacities of the neocortex are largely constructed by the problem domains confronting the individual throughout development, and remain modifiable throughout the life history. This neurobiological constructivist account of the human neurocognitive architecture contrasts sharply with the account of evolutionary psychologists, who conceive of the mind as a confederation of information-processing adaptations, each of which evolved in response to a problem posed by *Pleistocene* selection pressures (5).

Numerous methodological problems and theoretical flaws call the validity of the evolutionary psychological paradigm into question (6). Its proponents claim that three categories of evolved mechanisms support human intelligence—domain-specific mechanisms, domain-general mechanisms, and an integrative circuitry—but their research programs have focused exclusively on generating evidence for postulated domain-specific mechanisms. The standard protocol involves assessing subjects' relative performance on tasks that vary in the degree to which they correspond to an inferred ancestral adaptive problem. Although results that align with predicted patterns of reasoning performance have been interpreted as

providing support for the hypothesized domain-specific mechanisms under investigation, the absence of a definitive analysis (i.e., a method that parses out the possible contributions of the other postulated mechanisms, specific and general), makes such conclusions, at best, speculative.

Within the theoretical framework of evolutionary psychology, the critical problem of the adaptive selection of behavior rests heavily on the integrative circuitry that is presumed to engage the appropriate domain-specific mechanism. Yet, like the postulated domain-general mechanisms, this circuitry remains theoretically unconsidered and empirically unexplored within the paradigm.

An obvious source of information that might illuminate these hypothetical mechanisms is the extensive neuroscientific literature on the biological basis of adaptive behavior in mammals. But evolutionary psychologists have suggested that analysis at the implementation level (i.e., investigation of the neural correlates of behavior) is not mandatory for the study of cognitive adaptations (7, 8). In our view, this failure to reconcile theoretical claims with neurobiological data has veiled from evolutionary analyses the functional organization of the information-processing circuitries that comprise the human neurocognitive architecture. Indeed, the alternative, neurobiologically based model we present here compels a reconceptualization of the domain-specific/domain-general/integrative circuitry constructs as they are currently employed by evolutionary behavioral scientists.

Reconceptualizing the Nature of Social Adaptive Problems and Solutions

Evolutionary psychologists have appropriately acknowledged the importance of adaptive social behavior to the inclusive fitness of hominids. Recognizing the complexity of the ancestral social environment, they propose that humans have inherited a vast array of cognitive adaptations that facilitated social negotiations. Examples include postulated domain-specific adaptations to detect “cheaters” (9); to “have an appetite to be recognized and valued for [one’s] individuality or exceptional attributes”; and to “be motivated to cultivate specialized skills, attributes, and habitual activities that increase [one’s] relative irreplaceability,” etc. (10). In contrast, we suggest that a functionally plastic neocortex was the evolutionary solution to the adaptive navigation of ancestral social environments. [In fact, other researchers have proposed that the evolutionary appearance of the neocortex in mammals was the consequence of navigating fluctuating environments (11–14)].

In game theoretic models of biological market dynamics, various classes of traders exchange commodities to their mutual benefit (15–17). Biological market models are characterized by competition within trader classes by contest or

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Abbreviation: VUMmx1, ventral unpaired median cell of maxillary neuromere 1 (in the honeybee).

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outbidding, conflicts over the exchange value of commodities, and preference for partners offering the highest value (16, 17). They have significantly greater correspondence to most social exchange phenomena than earlier game theoretic conceptualizations, but these models only begin to suggest the multi-dimensional, dynamic character of hominid biological markets.

An individual can be engaged in numerous cooperative and competitive relationships simultaneously, with one or more other individuals who are themselves concurrently engaged in various cooperative and competitive constellations within the same group. Cooperative alliances between individuals can be based on one or more of any number of different commodities or services, and a cooperator for the attainment of one goal can be a competitor for another. The intrinsically fluctuating nature of critical market variables further increases the complexity of problem-solving in the market environment. The value of an individual as a cooperative partner can change directly as a function of age, injury, pregnancy, the formation of new alliances, and/or changing cooperative task priorities, and it can change indirectly as a function of shifting alliances, power centers, and numerous other perturbations in the greater market. In the relatively closed biological markets of ancestral hominid populations, a single social behavioral output, the product of a moment's cognitive processing, could have profound long-term (even dire) consequences for the individuals involved in the interaction, and produce reverberating changes in the market that would impact on subsequent social exchange decisions.

The temporally dynamic, individually specific cost-benefit analyses that any given social behavioral decision entails renders each information-processing problem an essentially novel and ephemeral construction, not an evolutionarily static social adaptive problem that might be captured by selection processes. The critical issue for evolutionary behavioral scientists, then, concerns the nature of the neural information-processing substrate capable of solving social survival and reproductive problems given the extent of fluctuation in the biological market environment and one's immediate position within it. The neuroscientific literature suggests that the plastic properties of the neocortex provided the requisite substrate: a matrix for the construction of representational networks.

The critical adaptive feature of cortical representational networks is that they allow for the functional linkage of information derived from the external environment and the internal milieu, with the predicted utility—for an individual—of a given behavior in a particular environment. The construction, modification, and ultimate utilization of representational networks is described in detail in the subsequent section of this paper. Here, we will simply note that they inform, and are informed by, subcortical structures that select and sequence behaviors, facilitating, on line, the adaptive guidance of the behavior of an individual, in a specific environmental situation, and in a specific internal state.

Cortical representational networks are modified on the basis of experience as a function of the newly estimated adaptive utility to the individual of an existing inferential circuit. They automatically reconfigure information that is directly relevant to a problem-solving task. Representational networks have associative properties. Consequently, representations that might have been established as components of circuits used in one domain can be accessed and influenced by circuitries that support problem-solving in other domains. Moreover, they form metarepresentational hierarchies that can support abstract inferential processes, and complex, temporally ordered networks that can support historical records. In brief, cortical representational networks constitute the type of information database/processing circuitry that is required for the adaptive guidance of behavior in changing environments.

Mammalian Behavioral Intelligence in Phylogenetic and Systematic Perspective

The *sine qua non* of behavioral intelligence systems is the capacity to predict the future—to model likely behavioral outcomes in the service of inclusive fitness. This logic is already evident, in a primitive sense, in *Escherichia coli*: information transduced by environmental sensors directs behavioral responses in a manner that increases the probability of the attainment of bioenergetic resources in the next moment (18, 19).

Centralized nervous systems are characterized by numerous design features that enhance predictive capacity. An adaptation found in even the simplest centralized nervous system is a region of highly plastic tissue specialized for the purpose of instantiating representations (i.e., neural activation vectors that convey information). This substrate, acting in concert with the integrated system in which it is situated, allows for the retention of essential information about the probabilistic relationships between specific sensory inputs, behavioral responses, and the adaptive value of the outcomes of these behaviors as established by homeostatic/life history regulatory system components.

Recent work exploring mechanisms of associative learning in bees is illustrative (20–23). During foraging, bees associate the location, shape, symmetry, color, and odor of flowers with “rewards” (feedback to homeostatic regulatory centers) (22, 24, 25). In the standard classical conditioning paradigm, when arbitrary stimuli with no intrinsic reward values are repeatedly associated in time with rewarding objects (unconditioned stimuli), they then function as rewarding stimuli. After this association has developed, the previously neutral stimuli (now the conditioned stimuli) elicit a conditioned response. For example, bees develop a proboscis-extension response as a conditioned response to an odor (i.e., the scent of a flower) after a single pairing of the odor (conditioned stimulus) with a biologically salient sucrose reward (unconditioned stimulus), the nectar in a flower.

Foraging patches represent a fluctuating environment (different species of flowers come and go, various environmental factors determine which type of flowers currently yield the most concentrated nectar, etc.). The adaptive problem of meeting nutritional needs in an uncertain environment did not drive the evolution of an array of discrete stimulus-specific neural adaptations for nectar foraging in the honeybee. Rather, it promoted the evolution of a system that could construct an environmentally appropriate behavioral guidance subsystem for foraging. The key components are a core instinctual mechanism that captured the evolutionarily stable regularities of the organism-environment foraging problem, a functionally plastic central nervous system substrate, and a neural mechanism that mediates the construction and modification of adaptive representational networks in the plastic substrate.

In the honeybee, the latter function is served by the ventral unpaired median cell of maxillary neuromere 1 (VUMmx1), an interneuron in the suboesophageal ganglion (a homeostatic regulatory system component) (22, 24). VUMmx1 (an octopaminergic neuron) projects widely to associatively plastic brain regions involved in odor processing (notably, the mushroom bodies and the lateral protocerebral lobe). In addition to mediating the instinctual proboscis-extension response (the adaptive behavior) to nectar (the fitness resource assessed by the homeostatic regulatory component), VUMmx1 mediates the acquisition of the conditioned response to the adaptively relevant novel stimulus features of the environment. It does so by constructing a network connection between the representation of the novel stimulus and the representation that is instinctually linked to the adaptive behavior. The strength of this neural link is subsequently increased or decreased (man-

ifested as synaptic changes in the representational network) on the basis of the bee's experience of resource acquisition (as registered by the homeostatic component) after network activation.

In a model of this system, Montague *et al.* (26) have used a predictive form of Hebbian learning to elucidate VUMmx1 octopaminergic modulation of the representational networks that regulate optimal foraging behavior in the honeybee. The VUMmx1-based model is expressed as a computer simulation of a bee foraging for nectar in a novel environment of blue and yellow flowers. The mean return from blue and yellow patches in the environment is equivalent, but the variability of nectar concentration differs; color is the only predictor of nectar delivery. The bee, which has a cone of vision that senses changes in the percentages of flowers, computes a trajectory through the environment in a manner that optimizes its nectar harvest. The model, based on the neural substrate and tested in a simulation of bee flight, accounts for a wide range of experimental results from studies of bee learning during foraging. The findings illustrate how the VUMmx1 neuron provides the bee with a representational inferential circuit for the prediction of reward that is updated in real time. By instantiating changes in the synapses of relevant representational networks in the mushroom bodies and lateral protocerebral lobe—driven by adaptive outcomes—VUMmx1 has constructed, on line, an inferential circuit that promotes fitness-enhancing behavior in uncertain environments.

A large body of evidence suggests that the same general plan characterizes the mammalian behavioral intelligence system. A direct analog exists between the VUMmx1 octopaminergically modulated construction of adaptive inferential circuits in the mushroom bodies and protocerebral lobes of bees, and dopaminergically modulated construction of inferential circuits in the cortex of mammals. A notable difference is that, whereas the bee system relies on an invariant instinctual mechanism to establish the adaptive utility of a representational “inferential”

circuit, the mammalian system we describe below ultimately arrives at these assessments by correspondence with homeostatic/life history regulatory systems and functionally related subcortical structures. It is important to note that humans and other mammals do have instinctual mechanisms that, in the earliest stages of postnatal development, invariably generate behavior (e.g., sucking and grasping reflexes); but, concomitant with the massive increase in cortical volume that begins in the immediate postnatal period, instinctual behavior is quickly supplanted by adaptively learned behavior.

Adaptive learning requires that relevant sensory and motor representations of the world be established, and that they then be combined to form fitness-enhancing sequences of behavior (27). In mammals, including humans, these coordinated functions are centrally supported by the basal ganglia (described below), in communication with the hypothalamus (the complex of nuclei that constitutes the core of the homeostatic/life history regulatory system), the thalamus (the major sensory ‘relay’ center of the brain), and the cortex (see Fig. 1).

The basal ganglia, unlike most components of the motor system, have no direct connections with the spinal cord; rather, their primary input is from widespread areas of the cortex, and their output is directed back to the premotor and prefrontal cortices by way of the thalamus. Three pathways originating in the basal ganglia—the mesolimbic, nigrostriatal, and mesocortical dopamine systems—are implicated for critical roles in the construction, modification, and activation of cortical representations that adaptively guide behavior. The nuclei that give rise to these pathways (the ventral tegmental area, and the substantia nigra pars compacta) are in direct correspondence with the hypothalamus.

A 40-year research literature supports the role of the mesolimbic dopamine system in “reinforcing” behaviors that lead to motivational state changes (28, 29). In the past decade, an increasing body of research has clarified a more comprehensive role of diffuse dopaminergic systems in adaptive

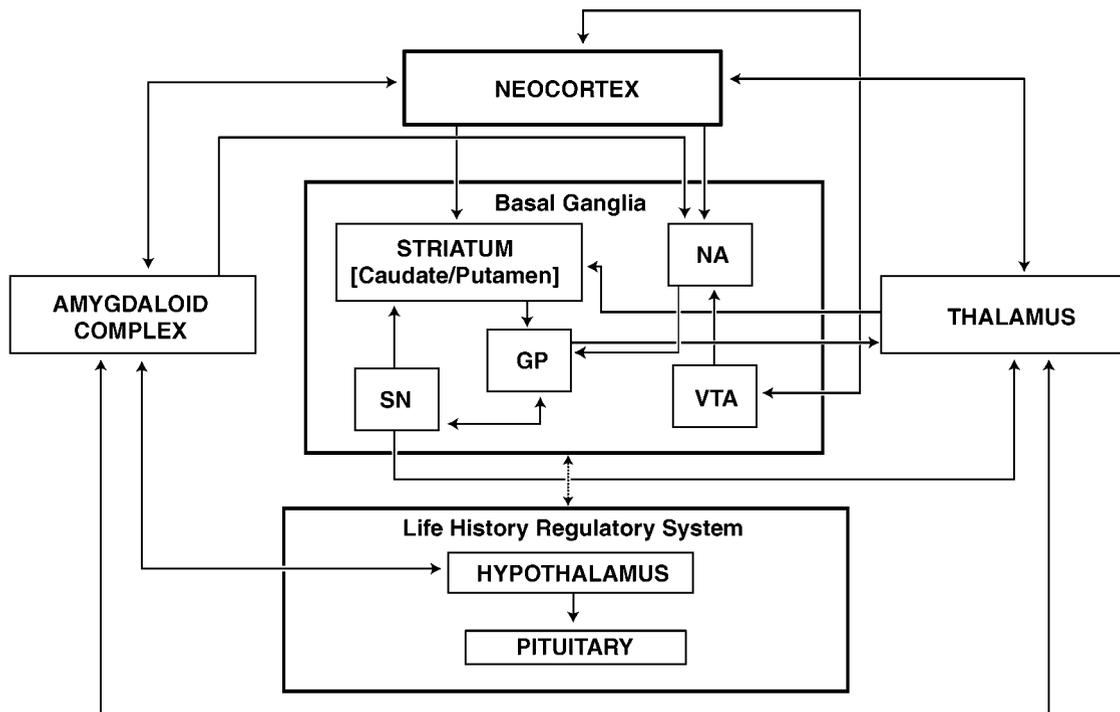


FIG. 1. Schematic representation of the principal brain regions comprising the neurocognitive architecture described in text. In the alternative evolutionary model we propose, basal ganglial circuitries, in correspondence with the life history regulatory system, support the developmental construction, and subsequent experiential modification of cortical representational networks. The neural correlates of cognitive and behavioral processes are activation patterns in specific representational networks. The basal ganglia play a central role in the selection and sequencing of behavior and cognitive activity. VTA, ventral tegmental area; NA, nucleus accumbens; SN, substantia nigra; GP, globus pallidus.

behavioral guidance (27, 30, 31). Recent findings suggest that the marking of stimuli that serve as predictors of reward is mediated by activity in substantia nigra neurons (the cell bodies of the nigrostriatal pathway) (32), and that the tracking of behavioral progress toward the attainment of a reward is mediated by activity in ventral striatal neurons (33). A recently developed theoretical framework, based on physiological findings and supported by a neurocomputational model of choice behavior, suggests how dopamine systems might be correcting predictions of reward via signals sent to their cortical and subcortical targets (34).

In mammals, including humans, the formation of fitness-enhancing sequences of behavior is facilitated by a neural circuitry that begins with nigrostriatal dopaminergic inputs to the caudate-putamen (the striatum). This circuit continues through an output nucleus (the globus pallidus pars internalis) to the thalamus, and then on to cortical action and planning areas. As noted above, striatal components of the basal ganglia receive inputs from almost the entire cortex (i.e., sensory, motor, and association representational areas), including massive projections from the prefrontal cortex (planning and action areas). These findings suggest that the basal ganglia play an important role in planning and cognition. Moreover, there is convergence in neuron number from the input stage of the basal ganglia (i.e., the striatum) to the output stage (i.e., the globus pallidus pars internalis) further suggesting that the basal ganglia integrate various types of information to either plan or select an action from many competing possibilities represented in cortex. A functional neurocomputational model provides strong support for this contention (27). Additional findings now suggest that mesocortical dopamine neurons, which project to prefrontal cortical planning areas, facilitate the attentional processes required for adaptive learning by sustaining activation in representations corresponding to novel and adaptively relevant conditioned stimuli (30).

The model we have presented is preliminary. We have focused on circuitries that we believe to be critically important in the construction, modification, and utilization of adaptive cortical representations, but have omitted other important components for the sake of brevity (e.g., the hippocampus and limbic loop of the basal ganglia). One final system that requires inclusion is the amygdaloid complex, which mediates the acquisition of conditioned emotional responses.

The amygdaloid complex is composed of multiple individual nuclei. Most these project to various cortical areas and subcortical regions involved in the processing of affective information; one (the central nucleus) projects to the hypothalamus and brain stem to initiate endocrine and autonomic nervous systems responses. Cognitive and behavioral responses are mediated via projections from the basolateral nucleus to the ventral striatum and the prefrontal cortex. These areas are thought to be involved in the circuits that interface between the processing of emotionally salient stimuli and planned behavior (35); indeed, reciprocal connections between the basolateral nucleus and prefrontal cortical areas have been implicated in the assignment of affective markers that inform choice behavior (36).

DISCUSSION

In this paper, we argue that the biological marketplace was ancestrally, and is now, an environment of incessant flux. We have suggested that for social mammals, in particular for ancestral members of our species, the uncertainty inherent in the marketplace constituted a selection pressure for an adaptively plastic neural substrate, the neocortex. We have further suggested that this substrate serves as a matrix for the construction of adaptive representational networks that have intrinsic cost-benefit structure, and that can support on-line behavioral and cognitive processes.

The striato-pallido-thalamo-cortical system that drives the construction and modification of adaptive representational networks supports operant and classical conditioning processes; as such, it has been dismissed in the evolutionary psychology literature as a domain-general mechanism. It is critical to note, however, that this system is never functioning in domain-general manner: it is primarily responsive to the motivational state of the individual, as established by feedback signals to the life history regulatory system, and is concurrently responsive to evolutionarily prespecified and adaptively significant novel features of the environment. The design of this system promotes the generation of adaptive behavior without requiring *en bloc* prespecification of the range of individual and environmental variables that might constitute any given adaptive problem. Moreover, the system is configured such that the “integrative circuitry” is *intrinsic* to the “domain-specific” problem-solving mechanisms.

Evolutionary psychologists have suggested that the meta-adaptive problem of appropriate behavior selection (the so-called “frame problem”) (8) was solved by a constellation of domain-specific mechanisms that are in some way appropriately selected for by an integrative/arbitrative circuitry. We suggest that the solution to this problem is to be found in the design features of the evolved intelligence system we have presented here.

We believe that this alternative model of the human neurocognitive architecture will prove to be a fertile source of research predictions across various disciplines. We offer one example that bridges evolutionary psychology and mainstream cognitive and social psychology literatures.

Because the foundational representational features of cortex are constructed by the problem domains confronting the individual in development, we should expect that differences in the biological market constraints confronting individuals in early childhood might generate significant differences in cognitive reasoning style. The disparity in degree of competition for family resources between firstborns and laterborns provides a relevant test case. The effects of birth order on various dimensions of personality are well documented (37). For example, on average, laterborns demonstrate a greater tendency to rebel against authority than firstborns. In a recent meta-analysis of the leaders of scientific revolutions, Sulloway (37) found that laterborns are much more likely to be the leaders of radical scientific revolutions than firstborns—a difference that he attributed to a more rebellious temperament and a personality style that promotes an “openness to experience.” We suggest an alternative explanation in terms of market-driven differences in cognitive reasoning style. Confronted with stiff competition for family resources, laterborns should be prompted to assess various alternative resource options, and to make comparisons across available alternatives. We would therefore predict that, all other market variables being equal, laterborns should have a greater capacity for inductive reasoning than firstborns.

If correct, the alternative model we have proposed is likely to have far-reaching consequences for research in evolutionary psychology, and various life and social science disciplines. Although the full ramifications are beyond the scope of this paper, it is clear that the wide range of individual differences reported in various literatures dealing with cognition may no longer be dismissed as experimental “noise,” or deviation from species-typical design. Rather, the model we have outlined emphasizes individual differences as the product of an evolved self-adapting system, a neurocognitive architecture that is unique by design.

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1. O'Leary, D. D. M. (1989) *Trends Neurosci.* **12**, 400–406.
2. Sur, M., Pallas, S. L. & Roe, A. W. (1990) *Trends Neurosci.* **13**, 227–233.
3. Quartz, S. R. & Sejnowski, T. J. (1997) *Behav. Brain Sci.* **20**, 537–596.
4. Allman, J. M. (1990) *Semin. Neurosci.* **2**, 257–262.
5. Cosmides, L., Tooby, J. & Barkow, J. H. (1992) in *The Adapted Mind*, eds. Barkow, J. H., Cosmides, L. & Tooby, J. (Oxford Univ. Press, New York), pp. 3–15.
6. Sherman, P. & Reeve, H. K. (1997) in *Human Nature*, ed. Betzig, L. (Oxford Univ. Press, New York), pp. 147–157.
7. Symons, D. (1989) *Ethol. Sociobiol.* **10**, 131–144.
8. Tooby, J. & Cosmides, L. (1992) in *The Adapted Mind*, eds. Barkow, J. H., Cosmides, L. & Tooby, J. (Oxford Univ. Press, New York), pp. 19–136.
9. Cosmides, L. & Tooby, J. (1992) in *The Adapted Mind*, eds. Barkow, J. H., Cosmides, L. & Tooby, J. (Oxford Univ. Press, New York), pp. 163–228.
10. Tooby, J. & Cosmides, L. (1996) *Proc. Br. Acad.* **88**, 119–143.
11. Dunbar, R. I. M. (1995) *J. Hum. Evol.* **28**, 287–296.
12. Barton, R. A. (1996) *Proc. R. Soc. London B* **263**, 173–177.
13. Joffe, T. H. & Dunbar, R. I. M. (1997) *Proc. R. Soc. London B* **264**, 1303–1307.
14. Barton, R. A. & Dunbar, R. I. M. (1997) in *Machiavellian Intelligence II*, eds. Whiten, A. & Byrne, R. W. (Cambridge Univ. Press, Cambridge, U.K.), pp. 240–263.
15. Noë, R., van Schaik, C. P. & van Hooff, J. A. R. A. M. (1991) *Ethology* **87**, 97–118.
16. Noë, R. & Hammerstein, P. (1994) *Behav. Ecol. Sociobiol.* **35**, 1–11.
17. Noë, R. & Hammerstein, P. (1995) *Trends Ecol. Evol.* **10**, 336–339.
18. Berg, H. C. & Brown, D. A. (1972) *Nature (London)* **239**, 500–504.
19. Koshland, D. E. (1977) *Science* **196**, 1055–1063.
20. Real, L. A. (1991) *Science* **253**, 980–986.
21. Real, L. A. (1994) in *Behavioral Mechanisms in Evolutionary Ecology*, ed. Real, L. A. (Univ. of Chicago Press, Chicago), pp. 99–132.
22. Hammer, M. (1993) *Nature (London)* **366**, 59–63.
23. Hammer, M. & Menzel, R. (1995) *J. Neurosci.* **15**, 1617–1630.
24. Hammer, M. (1997) *Trends Neurosci.* **20**, 245–252.
25. Møller, A. P. (1995) *Proc. Natl. Acad. Sci. USA* **92**, 2288–2292.
26. Montague, P. R., Dayan, P., Person, C. & Sejnowski, T. J. (1995) *Nature (London)* **377**, 725–728.
27. Berns, G. S. & Sejnowski, T. J. (1996) in *Neurobiology of Decision-Making*, eds. Damasio, A. R., Damasio, H. & Christen, Y. (Springer, Berlin), pp. 101–113.
28. Robbins, T. W. & Everitt, B. J. (1992) *Semin. Neurosci.* **4**, 119–127.
29. Robbins, T. W. & Everitt, B. J. (1996) *Curr. Opin. Neurobiol.* **6**, 228–236.
30. Horvitz, J. C., Stewart, T. & Jacobs, B. L. (1997) *Brain Res.* **759**, 251–258.
31. Schultz, W., Dayan, P. & Montague, P. R. (1997) *Science* **275**, 1593–1599.
32. Schultz, W. (1997) *Curr. Opin. Neurobiol.* **7**, 191–197.
33. Shidara, M., Aigner, T. G. & Richmond, B. J. (1998) *J. Neurosci.* **18**, 2613–2625.
34. Montague, P. R., Dayan, P. & Sejnowski, T. J. (1996) *J. Neurosci.* **16**, 1936–1947.
35. Killcross, S., Robbins, T. W. & Everitt, B. J. (1997) *Nature (London)* **388**, 377–380.
36. Bechara, A., Damasio, A. R., Damasio, H. & Anderson, S. W. (1994) *Cognition* **50**, 7–15.
37. Sulloway, F. J. (1996) *Born to Rebel* (Pantheon, New York).