Genetic, Social, and General Psychology Monographs, 2005, *131*(2), *129–184*

An Evolutionary Theory of Human Motivation

LARRY C. BERNARD
MICHAEL MILLS
LELAND SWENSON
R. PATRICIA WALSH
Department of Psychology
Loyola Marymount University

ABSTRACT. The authors review psychology's historical, competing perspectives on human motivation and propose a new comprehensive theory. The new theory is based on evolutionary principles as proposed by C. Darwin (1859) and modified by W. D. Hamilton (1964, 1996), R. L. Trivers (1971, 1972), and R. Dawkins (1989). The theory unifies biological, behavioral, and cognitive approaches to motivation. The theory is neuropsychological and addresses conscious and nonconscious processes that underlie motivation, emotion, and self-control. The theory predicts a hierarchical structure of motives that are measurable as individual differences in human behavior. These motives are related to social problem domains (D. B. Bugental, 2000; D. T. Kenrick, N. P. Li, & J. Butner, 2003), and each is hypothesized to solve a particular problem of human inclusive fitness.

Key words: evolutionary psychology, motivation, motives

WE PROPOSE AN EVOLUTIONARY THEORY of human motivation, wherein *motivation* is defined as purposeful behavior that is ultimately directed toward the fundamental goal of inclusive fitness. We also propose that motivation may be measured in terms of individual differences in covarying categories of behaviors and interests. These categories covary because they are guided and directed by putative cognitive structures called *motives*. Motives are hypothesized to guide behaviors and interests within one of five social domains related to ever larger systems: (a) the self-protection domain of the single system; (b) the mating domain of the dyadic system; (c) the relationship maintenance and parental care domain of the small, kin system; (d) the coalition domain of the large,

---

The authors thank Aaron Lukasewski for his assistance in the development of this theory.

Address correspondence to Larry C. Bernard, Department of Psychology, Loyola Marymount University, 1 LMU Drive, Los Angeles, CA 90045; lbernard@lmu.edu (e-mail).

nonkin system; and (e) the "memetic" domain of the large, symbolic, cultural system. Motive-guided behaviors can increase inclusive fitness by solving problems that arise within a social domain. They may be measurable as the strength of interest, desire, or concern with behaviors related to solving problems in a particular social domain.

Motives, emotions, and self-control are emergent properties of *trans*conscious processes served by widely dispersed modular brain systems that developed in response to selection pressures in the Environments of Evolutionary Adaptedness ("adaptive mental mechanisms"). Stable conscious motivational processes depend on a large neocortex that coevolved with the social domains and the size of social systems. Some motives are hypothesized to be very old and arise in nonconscious processes, some motives are hypothesized to be intermediate "exaptations" of older motives, and some motives are hypothesized to be more recent exaptations that are more influenced by social learning and culture. (An *exaptation* is an adaptation that originally evolved for one use and later evolved for a new purpose—e.g., the bones of the inner ear.) All motives, old or recent, are hypothesized to express as phenotypes in a historical and presently recurring interaction between genotype and the physical–social–cultural environment. Emotions are hypothesized to guide purposeful behavior toward inclusive fitness goals by assisting "if–then" searches among motives. Self-control is hypothesized to delay behavior, permitting more thorough if–then emotion-referenced searches and increasing the probability that behavioral responses are adaptive in the local environment. Self-control may also be measurable as an individual differences variable.

We present the theory in four parts. Part 1—Competing Perspectives of Motivation provides an introduction to the major historical influences in the field of motivation and offers a rationale for attempting to unify them. In Part 2—Ultimate Causality: Toward a New Theory of Human Motivation, we introduce evolutionary theory as a basis for unifying the historically competing perspectives of motivation. We present the "why" behind the existence of motivated human behavior, the processes that may have shaped the evolution of the human brain and its organization. In Part 3—Proximate Causality: Neuropsychological Structures in Human Motivation, Emotion, and Self-Control, we present the "how." We provide a description of some of the motivational mechanisms that operate in the brains of *homo sapiens* today as a result of evolution. In Part 4—Individual Differences in Adaptive Mental Motive Mechanisms, we define some putative motives that may be related to social domains.

PART 1—COMPETING PERSPECTIVES OF MOTIVATION

Motivation has been a robust and fertile area of theory and research throughout the history of psychology. Courses in motivation and emotion were once a staple in many undergraduate college curricula. As recently as 1975, motivation was ranked 22nd among the most frequently listed undergraduate psychology courses. However, by 1997, it had dropped to 31st (Perlman & McCann, 1999). Furthermore, those who track such data believe that the number of departments offering motivation will continue to decline in the near future (B. Perlman, personal communication, April 22, 2003).

What can account for this apparent withering of interest in the topic of motivation? First, these data do not necessarily support the conclusion that interest in motivation has declined in general, because topics historically treated within "motivation" may have been subsumed by newer research areas such as neuroscience and cognition. However, the assumption of motivation by other areas, and the commensurate reduction of courses in motivation and emotion in the undergraduate curriculum, may reflect the lack of a general theory of motivation, one that has the ability to unify the field and catalyze future research.

One reason for the lack of a general, integrative theory may be that, like many areas of psychology, motivation has been characterized by competing perspectives. Competition among perspectives can be worthwhile when it encourages proponents of different viewpoints to develop, test, and strengthen their theories. However, competition can be stifling when it becomes overly reductionistic and discourages integration that can lead to broader theoretical attempts at understanding a phenomenon. In this section, we outline a brief history of motivation from three apparently mutually exclusive perspectives within psychology—biological, behavioral, and cognitive—and end with a proposal that an evolutionary perspective might bring some unity to this topic.

The biological perspective is represented by James (1890), who introduced the concept of instincts to mainstream psychology. In his *Principles of Psychology*, which became one of psychology's classic texts (American Psychological Society, 2003), *instincts* are defined as a function of genetics, hardwired into the brain's structure, and the basis for motivation. Thus, genes have a causal role in motivation. Early researchers described instincts as "purposive strivings" (McDougall, as cited in Boring, 1950) or "needs" and "drives" (Hull, 1943). Their work was heuristic but not without critics (e.g., Holt, 1931). Instinct theories were viewed as mechanistic, tending to give short shrift to the influence of conscious processes on motivation. Biological theories do not require a rational or conscious agent. Behavior is determined more by unconscious biological instincts, needs, or drives. This approach is of limited utility because it deals better with animal behavior in general than it does with human behavior and its greater potential to be informed by conscious processes.

The behavioral perspective is represented by Thorndike (1911), and it changed the focus of motivation from the internal to the external. Thorndike demonstrated that the behavior of animals is not strictly the result of instincts but is modified by environmental consequences. His "Law of Effect" specified that behavior followed by a satisfying state or reward is more likely to be repeated, whereas behavior that is followed by an unsatisfying state or punishment is less likely to be repeated. Thus, the environment has a causal role in motivation.

Thorndike (1911) believed that he could infer the workings of the animal mind from behavioral experiments, but J. B. Watson (1913), who also represents the behavioral perspective, took issue with Thorndike's inferences about mind. Arguing that mental events and consciousness can never be observed or measured directly, Watson wished to limit psychology to the study of observable behavior. Watson took Thorndike's rather "mentally tolerant" behaviorism in a "radical" direction and, like Skinner (1938, 1971) after him, banished mental processes as explanations of behavior. Skinner (1971) even labeled mental processes "superstition and magic" (p. 201).

Behaviorists demonstrated the general principles by which the environment shapes and directs behavior, even instinctual behavior. According to behavioral theory, motivation is an automatic and reflexive process, satisfying basic organismic requirements and shaped by environmental consequences. Although they were successful in applying these principles to animal behavior generally, under the influence of the more radical behaviorists, rational and conscious processes were banished altogether or reinterpreted as behavior. Holt (1931) criticized this approach as descriptive rather than explanatory, and it did not satisfy the many psychologists who study conscious processes. Like the instinct theories before them, behavioral theories were also faulted as mechanistic, and the behavioral perspective on motivation was challenged by a subsequent interest in cognitive processes (Neilsen & Day, 2000; Tinbergen, 1951).

The challenge began soon after J. B. Watson (1913) promulgated his ideas. Tolman (1932) also embraced the behavioral perspective but helped to open the behavioral door to what would become the cognitive perspective with his notion of "purposive behaviorism." Although not fully accepting the existence of consciousness, he did demonstrate that rats could remain "objective" within a situation and emit novel (i.e., unlearned), purposeful behavior to obtain a desired goal. In his famous equation, $B = f(S, A)$, where B = behavior, S = the situation, A = antecedent or other causes, Tolman allowed cognitive intervening variables to reenter the behavioral equation as antecedents. Tolman's work is only one of many precursors to cognitive behaviorism. Today, cognitive behaviorism is still grounded in learning theory but accepts mental processes as an intermediary of behavior.

In the intervening years, the cognitive perspective in psychology has taken two forms: (a) "cognitive behaviorism" as introduced by Tolman (1932), Bandura (1977), and others, which has remained largely functional and focused on behavior; and (b) "cognition," which addresses mental processes themselves and is an exceptionally broad field within psychology. Cognition encompasses such areas as artificial intelligence (e.g., Ballard, 1997), rationality and decision making (e.g., Plous, 1993), and consciousness (e.g., Hameroff, Kaszniak, & Scott, 1996). Both cognitive behaviorism and cognition have influenced many aspects of recent research and theory of motivation: achievement motivation (McClelland, Atkinson, Clark, & Lowell, 1976), attention and arousal (e.g., Berlyne, 1970; Hebb, 1949), goals (e.g., Locke & Latham, 1990; Miller, Galanter, & Pribram, 1960), intrinsic–extrinsic motivation (e.g., Deci, 1975; Deci, Koestner, & Ryan, 1999; Deci & Ryan, 1987; Lepper, Greene, & Nisbett, 1973), self-awareness and self-motivation (Silvia & Duval, 2004), self-perception (Bem, 1967), and self-regulation (e.g., Carver & Scheier, 1981, 1998; Oettingen, Bulgarella, Henderson, & Gollwitzer, 2004). Even the role of "conscious will" has not been overlooked (e.g., Solomon, Pyszczynski, & Greenberg, 2004).

Taken together, this prolific research supports a view of the individual as a conscious, rational (i.e., thinking, processing) agent, able to operate less reflexively and more symbolically on the basis of expectations, plans, and goals. In the cognitive perspective, motivation is caused by a more rational and deliberative process than the biological and behavioral perspectives allow. The cognitive perspective reinserted conscious processes into the study of motivation where they could be demonstrated to be important influences on human behavior. And, just as behavioral principles apply generally across species, new models of consciousness may also apply generally across species (Baars, 2001).

However, cognitive motivational psychologists have not typically addressed other fundamental issues in motivation. These issues include the origin of conscious processes, the relationship of conscious processes to the biological or behavioral perspectives, and the role of nonconscious processes in motivation. Cognitive theories suffer from the same criticism that Holt (1931) leveled at behavioral theories of motivation—they can be descriptive without being explanatory. For example, cognitive theories deal with proximate questions—*how* people think and behave. They have substantial predictive power, as evidenced by a large body of literature. But, again, if behavior is purposeful, what purpose does this *how* serve? Why does less reflexive and more conscious behavior occur at all? What is the advantage of expectancies, intrinsic motivation, goals, or self-regulation? These are the ultimate questions that evolutionary psychology seeks to answer. Cognitive theories seem best equipped to describe thoughtful processes and their outcomes and less able to provide explanations for the existence of these thoughtful processes in the first place.

It does not seem possible to develop a comprehensive theory of motivation without addressing all of these issues, including a role for nonconscious processes in both instincts and an organism's responses to reinforcement. With modern brain-imaging techniques, neither conscious nor perhaps even nonconscious processes need any longer be banished on the grounds that they are unobservable (e.g., Haier, White, & Alkire, 2003; Jeffries, Fritz, & Braun, 2003; Tyler et al., 2003). Finally, the role of culture has not been fully incorporated into motivational theory, even within the cognitive perspective. Culture, by providing an environment of shared expectations and values, imposes a certain consistency on social reinforcement and the development of cognition (Avital & Jablonka, 1994; Donald, 1997; Oyama, 1993). By understanding the role of culture, we may increase our understanding of the common variance in motives shaped by the context in which reinforcement occurs.

We propose that divisions between biological, behavioral, and cognitive perspectives have hampered development of a general theory of motivation. Perhaps competition among different perspectives in psychology has resulted in too much reductionism. Perhaps the lack of a general approach has contributed to the decline of course offerings in motivation and emotion at the undergraduate level, as well as the assumption of motivation topics by other areas of psychology and related fields. An insidious dualism within our field may be responsible for such competing divisions. Consistent with Oyama (1991), we use *dualism* as "the belief that genetic 'programs' or 'information' account for some characteristics, while the environment shapes others" (p. 29). Such beliefs may facilitate the parsing of motivation into biological influences ("genetic programs") to be researched by neuroscientists; the influences of cognition ("information") to be researched by cognitive psychologists; environmental influences, including reinforcement and learning, to be researched by behaviorists; and social and cultural factors to be researched by developmental and social psychologists.

But, these are not "parts that need rejoining," for "once the metaphor of a partitioned whole is accepted, all sorts of oddities follow" (Oyama, 1991, p. 31). Oyama argued that "causation is therefore always interactional," that biological forms are "wholes that emerge in this interaction" (p. 32). The "whole" she refers to is what evolutionary psychologists call an organism's *phenotype*. Therefore, those who wish to study motivation in its own right, rather than as a subarea of cognition, neuroscience, or learning, might benefit from a comprehensive theory that could unify these perspectives; a theory that could treat motivation as a whole. We believe that an evolutionary theory that eschews dualism (see Oyama for a discussion of dualism within evolutionary psychology itself) can provide the necessary unifying foundation for such a comprehensive theory of motivation.

PART 2—ULTIMATE CAUSALITY: TOWARD A NEW THEORY OF HUMAN MOTIVATION

Evolutionary Psychology and Motivation

Motivation refers to the *why* that causes an organism to initiate and persist in certain behaviors as opposed to others. Motivation is purposeful and includes the processes that guide the general strength and direction of an organism's activity over time. This sense of duration is important because although motivated behavior takes place only in the present, its orientation is toward the future—either in nonconscious service to inclusive fitness (survival of one's genes) or in conscious service to an individual's goals and expectancies (which may also increase the probability of one's genes surviving). So, too, is the sense of general strength and direction important because specific instances of behavior may deviate from an organism's typical pattern of behavior. But, if motivation is purposeful, what purpose does it serve? That is the ultimate question to which a theory of motivation must provide an answer. None of the extant competing perspectives seem to adequately answer this question.

Any attempt at such a comprehensive, integrative theory of motivation needs a strong unifying foundation. Evolutionary theory has played a dominant unifying role in the biological sciences and may now be poised to play a similar role in the social sciences (de Waal, 2002). Therefore, we grounded the present theory of motivation in contemporary evolutionary concepts. Evolutionary theory may serve this unifying role well for motivation because it has great explanatory power, particularly when it addresses brain and social development.

Yet, there is considerable "fear and loathing of evolutionary psychology in the social sciences" (Leger, Kamil, & French, 2001, p. ix). Some social scientists have been rather harsh in their criticism of evolutionary psychology (e.g., Fairchild, 1991; Travis & Yeager, 1991). Leger et al. suggested that this "often shrill" criticism of evolutionary psychology may be the result of basic misunderstandings of contemporary evolutionary theory.[1] Perhaps evolutionary theory was not embraced because it was confused with early, flawed instinct theories and the criticisms were more reasonable then, before evolutionary psychology had progressed. Once these misunderstandings are corrected, Leger et al. believe that "Darwinian ideas [will] have an important influence on our understanding of psychological processes, an influence that will grow dramatically in the next 25 years" (p. x).

Inclusive Fitness

James (1890) would have been familiar with the term *survival*—simply put, it is living longer than others—but not the term *inclusive fitness*—defined as the individual's reproductive genetic output plus the reproductive output of that individual's kin, who also carry the individual's genes (Hamilton, 1964, 1996). It has been suggested that the reproductive output of many species, including humans, depends on a few very specific activities: individual survival and locating, courting, copulating, and retaining a mate, as well as raising offspring that are, themselves, able to reach sexual maturity and repeat the process (Simpson, 1999).[2] We propose that motivated human behavior is a manifestation of evolved adaptive mental mechanisms that were selected because they increased inclusive fitness through the promotion of specific activities in ever larger social systems and in various ancestral environments.

Motivation—and emotion—is an interaction of genes (history) and environment (both historical and proximate) played out in the evolved genetic development and organization of neuropsychological structures:

> Genes are involved in all development. They cannot function without the proper surroundings, however, and their functioning is *regulated by those surroundings* [italics

> added]. Environments at many scales are therefore also involved in all development. The genes interact only with the microscopic milieu. At higher levels, tissues, hormones, and organs interact with each other, and the organism interacts with its environments. (Oyama, 1991, p. 32)

This may be called the *strong interaction hypothesis* because it goes beyond the concept that nature and nurture each provide some “amount” of influence (variance) in the development of a phenotype. The recent rush to clone animals provides a “real-life” illustration of the strong interaction hypothesis. It has been reported in the popular media that people who lost or were about to lose their cats recently have been able to have them cloned, but they have been surprised to discover that the cloned version is not an exact replica of their pet (Mott, 2004). In fact, the cloned offspring, with identical genetic makeup, neither look the same nor act the same as the original. Even such heavily genetically influenced factors as coat coloring and pattern differ in the clone. This is attributed to environmental influences on genetic expression. The people who cloned their cats underestimated the strength of the interaction between genes and the environment.

Modern Adaptationism

The strong interaction hypothesis may also be seen in the development of mental adaptations. A behavioral trait is a phenotypic manifestation of mental adaptations present today because they conveyed fitness benefits in the past. *Mental adaptations* are underlying neuropsychological structures that reliably develop in most humans. An adaptation’s function is the benefit that led to its evolution. However, not all traits seen today are adaptations. Some traits may have evolved as “side effects” or byproducts of other traits that were adaptations (see Gangestad, 2001, for a more thorough discussion of adaptive design). In humans and other species, there is a wide range of behaviors linked to reproductive activities, only some of which may be adaptations. This range of behaviors results from variance introduced by individual differences and differences in local physical and cultural environments in the past and present. This variance-induced “diffusion of behavior” may make it difficult for an observer, or the behaving individual, to readily appreciate the link between a specific behavioral adaptation and inclusive fitness.

However, human beings should be viewed more as adaptation executors than as fitness maximizers (Symons, 1992; Tooby & Cosmides, 1992). They, and other organisms, execute a set of complex computational mechanisms that result from adaptive demands in the past—adaptations that were calibrated to increase the inclusive fitness of humans in the ancestral environment. In our modern technological environment, these adaptations may or may not increase inclusive fitness. For example, human beings are motivated to copulate; however, today, because of the availability of birth control (the use of which may be the result of other motives), copulation may or may not increase fitness through reproduction.

Furthermore, these complex computational mechanisms are represented in widely distributed neural circuits that operate more or less independently because they evolved more or less independently as the result of different adaptive pressures at different times and in different environments. This reflects current thinking in evolutionary psychology, which proposes that the brain's general organization was selected to increase inclusive fitness, although this is realized in separately evolving adaptive circuits that serve subgoals in pursuit of the general fitness goal (Gangestad, 2001).

Overall, then, motivation is what animates us, what prompts our initiation, choice, and persistence in particular behaviors in particular environments. In the ancestral environment, humans evolved a set of motivations that generally increased their inclusive fitness. This required locating, courting, copulating, and retaining a mate; raising offspring; and ensuring their offspring's success. But, early instinct theories missed that motivation promotes behavior that develops interpersonal and group ties because these can also increase inclusive fitness (Hamilton, 1964, 1996). The probability of reproductive success for individuals and their offspring increases with increasing support from kin and nonkin alike. Therefore, purely selfish behavior may be a successful strategy for individual survival, but prosocial behavior that develops interpersonal and group ties may also help increase inclusive fitness. Although a few researchers (e.g., Sober & Wilson, 1998) have argued that in rare situations group selection can occur and select such prosocial behavior, we are not arguing for strict group selection. Instead, we are basing the evolution of prosocial behavior (particularly altruism) on a relatively new, and perhaps controversial, proposal of a predisposition to cooperate with others, termed *strong reciprocity*, which may evolve under certain conditions (Bowles & Gintis, 2003; Gintis, Bowles, Boyd, & Fehr, 2003). As a result of the success of these strategies for both survival and prosocial behavior, over time the human brain has evolved mental mechanisms that support their accomplishment (Daly & Wilson, 2001).

PART 3—PROXIMATE CAUSALITY: NEUROPSYCHOLOGICAL STRUCTURES IN HUMAN MOTIVATION, EMOTION, AND SELF-CONTROL

Transconscious Processes in Human Motivation

In this section, we switch our analysis from an ultimate (or "why") level to a proximate (or "how") level as we explore the functioning of the evolved brain and its implications for motivated behavior. We must now identify the specific motivational adaptations in the brain that may have been selected as a result of evolutionary pressures. The role of evolutionary pressures in brain development is supported by several types of research. Brain volume is a strongly inherited trait, with genes accounting for 90% of the variation between people in the brain's total volume (Baaré et al., 2001). In addition, MZ and DZ twin studies have revealed a strong hereditary influence on the patterns of sulci and gyri in the human brain (Bartley, Jones, & Weinberger, 1997). Interestingly, these studies have also shown some variation in smaller sulci resulting from proximal environmental influences, such as experience and learning, supporting the strong interaction hypothesis.

The human brain is about three times larger than the brains of great apes and has a proportionally larger frontal lobe (Semendeferi & Damasio, 2000; Semendeferi, Lu, Schenker, & Damasio, 2002). This is important for the present theory because, although some motives arise in older brain structures, many more recent motives may depend on the development of neocortex and stable conscious processes carried on in large frontal lobes. The evolution of the proportionally larger frontal lobe is believed to have taken place after the great ape and human split from other anthropoid primates around 20 to 25 million years ago. The human frontal lobe has probably not changed in the past 500,000 years (Bookstein et al., 1999).

What follows is a description of genetically initiated but "environment-guided neural circuit building" (Quartz & Sejnowski, 1997, p. 537) that we will attempt to apply to motivation. Such cortical circuit building evolved to allow increased representational flexibility, hence adaptation, variation, and differentiation in motivation. We first describe a tripartite hierarchical neuropsychological structure of nonconscious and conscious processes (as depicted in Figure 1) that is dependent on a variety of adaptations in brain structure. This structure would have emerged during different stages of brain evolution (Panksepp, 1998). Similar tripartite models of consciousness have also been proposed by others (e.g., Damasio, 1999; Kihlstrom, 1987).

Nonconscious Processes

Nonconscious motivation probably arises in the oldest brain structures, those identified as the hind brain or midbrain (brain-stem nuclei and the hypothalamus). Damasio (1999) proposed that consciousness emerges from a hierarchical brain structure rooted in what Kihlstrom (1987) called "truly unconscious mental processes" (p. 1445) and Panksepp (1998) called "primal" or "primary-process consciousness" (p. 309). One such structure, the rostral ventral medulla, mediates cardiovascular control, respiration, pain and analgesia, and "facilitates adaptive responses to urgent environmental events" without access to consciousness (Van Bockstaele & Aston-Jones, 1995, p. 153). Another structure, the periaqueductal gray, which surrounds the midbrain aqueduct, plays an important role in autonomic regulation and analgesia (Bandler & Shipley, 1994). There is a convergence of emotional information (panic, fear, rage, sex and nurturance, and seeking) in the periaqueductal gray and a convergence of somatic information (hearing, touch, vision, as well as a locomotor region) in the superior colliculus (Panksepp). These adjacent midbrain structures maintain the status of the organism's internal physi-

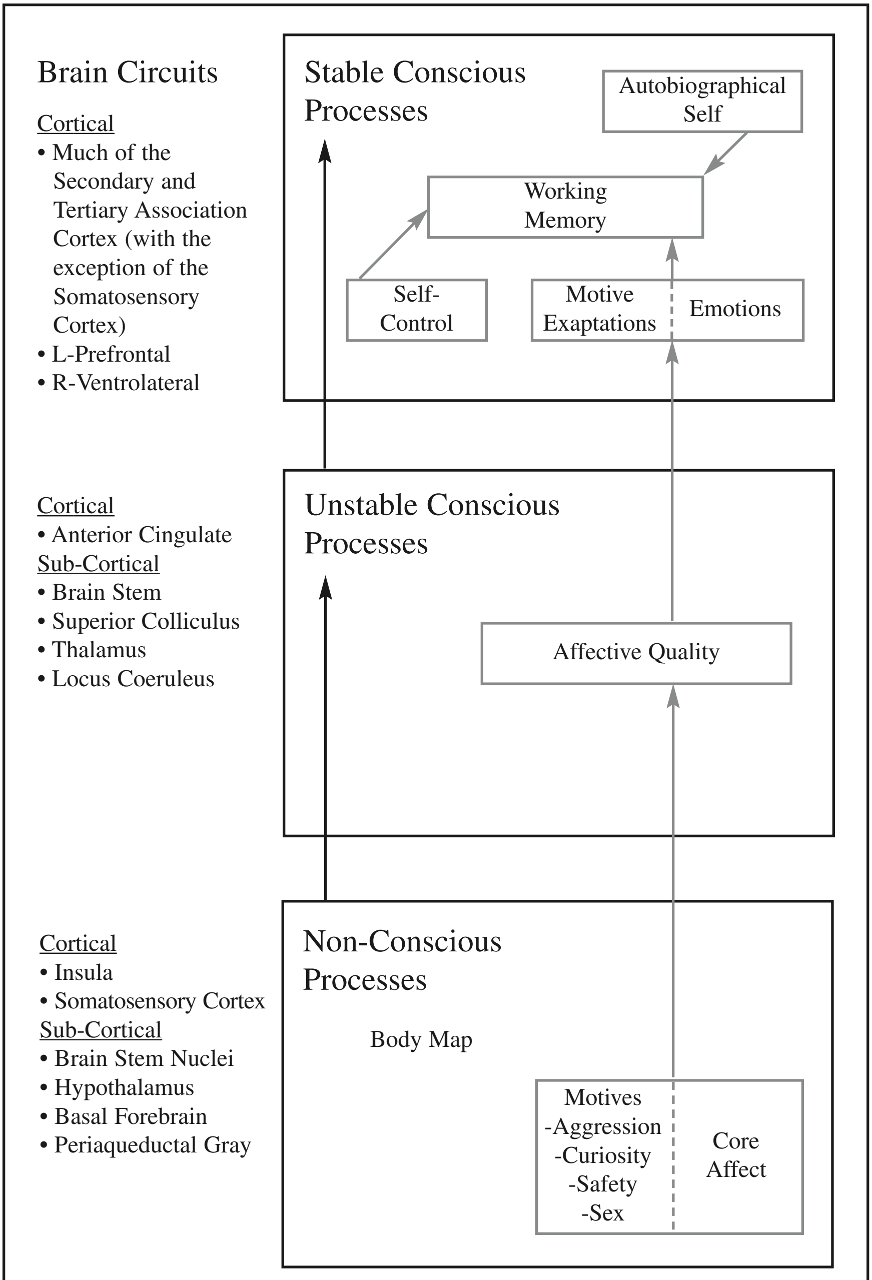

FIGURE 1. Transconscious processes in human motivation.

ology and subserve the hedonic principle (Damasio). These structures also project to the anterior cingulate cortex, which encodes perceived unpleasantness without primary somatosensory cortical activation (Rainville, Duncan, Price, Carrier, & Bushnell, 1997) and could play a role in generating hedonic tone.

These structures serve nonconscious processes consisting of the simple, repetitive patterns, reflexes, and basic metabolic regulation necessary for survival. They are the basis for what Damasio (1999) labeled "proto-self . . . a collection of neural patterns which map, moment by moment, the state of the physical structure of the organism" (p. 154) and regulate its life state. This may be referred to simply as the *body map*. Panksepp (1998) also described an innate, nonconscious brain-stem representation of the body that links body and self. He called it "primary-process consciousness" or "primordial SELF": "rooted in (these) fairly low-level brain circuits that first represented the body as an intrinsic and coherent whole . . . ancient in brain evolution and hence situated near the core of the brain . . ." (p. 310). He reasoned that, because observations of split-brain human patients and animals decorticated early in life reveal strong levels of behavioral coherence in affect and intentional motor conduct, despite what would appear to be extreme neocortical disabilities, some "low-level" nonconscious representation of "self" within the brain must exist. Recent evidence that a substantial amount of brain activity and behavior can take place without conscious control or awareness supports this argument (Rees, Kreiman, & Koch, 2002). For example, reptiles lack an extensive cortex, yet they are capable of purposeful behaviors such as those involved in self-protection and mating.

Unstable Conscious Processes

Unstable conscious processes are an intermediate level of consciousness and are probably served by brain structures that also developed early in evolutionary history. Some of these structures are located in the brain stem and diencephalon (including the thalamus and hypothalamus). One potentially important structure in unstable consciousness is the locus coeruleus, which has been a focus of attention for some time because of its projections throughout the central nervous system (Aston-Jones, Ennis, Pieribone, Nickell, & Shipley, 1986). Limited pathways appear to carry highly processed sensory information to the locus coeruleus from the medulla, which could provide sensory preprocessing at the level of the nonconscious body map. The locus coeruleus does not appear to be engaged in complex processing of these inputs, but rather "weigh[s] activity in inputs . . . and widely distribute[s] a uniform message over its divergent efferents" to many cortical areas (Aston-Jones et al., p. 737). The locus coeruleus may thus help modulate forebrain areas such as those that subserve memory and learning. This would place it between nonconscious and stable conscious processes in the hierarchy.

However, the locus coeruleus is just one among several structures that may be involved in unstable conscious processes. For example, Strehler (1991) believed the superior colliculus of the tectum, a midbrain structure that lies behind the thalamus, is the seat of consciousness, which is a more definitive and central role for this structure in consciousness than others allow (e.g., Damasio, 1999). However, the superior colliculus does appear to have a central integrating role that may allow it to synthesize representations of the self versus environment (Strehler).

James (1890) distinguished between the self as “I” and the self as “me”: the *I* as knower and the *me* as the known. This is also referred to as *self-recognition*, *self-awareness*, or a *sense of self as distinct from* (“*vs.*”) *environment*. Environment, as used here, encompasses both internal and external stimuli, and the amygdala may serve as the point of higher order associations between internal and external sensory data (Nahm, Tranel, Damasio, & Damasio, 1993). At this intermediate level, one probably has a fleeting awareness of hedonic tone, pleasure and pain, as happening to me. The level of unstable conscious processes is the likely mediator of basic self-awareness, that is, self-awareness unencumbered by past and future (“autobiographical self”). Experiments have demonstrated that humans typically manifest self-awareness by 18 months of age after some period of brain development (Lewis & Brooks-Gunn, 1979). This is consistent with the fact that the neocortex matures later than do hind or midbrain structures. Other researchers have shown that self-recognition appears to involve the right frontal lobe in particular (Keenan, Nelson, O’Connor, & Pascual-Leone, 2001). Two other species, chimpanzees and orangutans, also demonstrate self-awareness; however, it does not emerge in these species until they are 6 to 8 years of age, reflecting, perhaps, the need for a much more extensive period of brain development or experience (Povinelli et al., 1997).

Unstable conscious processes, even self-awareness, do not have access to working memory or the language centers of the brain. They may depend on constantly generated pulses of subjective awareness, hence the term *unstable* (Damasio, 1999). Lacking access to working memory, unstable conscious processes cannot hold images over time. The sense of self they provide, although conscious, is fleeting because it is constantly regenerated. Any change in the status of nonconscious processes in response to a stimulus will trigger a change in unstable conscious processes.

Stable Conscious Processes

What is meant by *consciousness*? Roser and Gazzaniga (2004) characterized it as a sense of unity, an apparent cohesiveness that, at its highest level, is a constructed personal narrative that helps one make sense of the brain’s own behavior. Certainly, consciousness depends on alertness, and there is a role for hind and midbrain structures, particularly the reticular activating system, in maintaining cortical alertness (Munk, Roelfsema, König, Engel, & Singer, 1996; Steriade, 1996). But alertness is not sufficient for full, stable consciousness or a personal narrative. Perhaps because of the apparent unity of conscious processes, some researchers have argued for a central role of one or another single structure in full consciousness. This role should be accorded to the central lateral and paracentral nuclei of the intralaminar group, a part of the thalamus (Bogen, 1995). This region receives projections from the visual cortex, medulla, pons, superior colliculi, the pretectal region, and other areas of the thalamus. Because it receives inputs from so many sensory modalities and regions involved in the body map and unstable conscious processes, it could have an important integrating role in consciousness. However, the structures that serve stable consciousness are probably more widely dispersed and absolutely dependent on working memory (e.g., Roser & Gazzaniga; Tononi & Edelman, 1998; Tononi, Sporns, & Edelman, 1992).

Even the structures that make up working memory appear to be widely dispersed. Baddeley (1992) provided a detailed description of working memory as a system that allows temporary storage and manipulation of information. It consists of three components: (a) a "central executive," which controls attention; (b) a "visuospatial sketch pad," for the manipulation of visual images and "imaginative" processes; and (c) a "phonological loop" where speech-based information is stored and rehearsed. (This is the first point at which linguistic functions necessary for an internal dialogue may be incorporated in transconscious processes.) In a series of experiments, Smith, Jonides, and Koeppe (1996) demonstrated the neural basis of working memory using positron-emission tomography (PET). Their results suggested a clear laterality in left hemisphere activation for verbal tasks (the phonological loop) and right hemisphere activation for spatial tasks (the visuospatial sketch pad). The verbal and spatial working memory buffers appear to be distinct and have separate neural circuits to implement storage and rehearsal functions. The left hemisphere structures implicated in verbal working memory are the parietal cortex (Broadmann area 40), Broca's region, the pre- and supplementary motor region (area 6), and the prefrontal cortex. The right-hemisphere structures implicated in spatial working memory are the ventrolateral frontal cortex, occipital cortex, and parietal cortex.

Information about the self and experience does not reside in working memory but, rather, in a latent or covert form dispersed in the brain as dispositions (Damasio, 1999). Dispositions could be used by working memory to regenerate images and actions without external stimuli. Dispositions may be stored in what has been called an *association cortex* (or *convergence zones*) located in the temporal and frontal regions and subcortical nuclei, such as the amygdala (Damasio; Nahm et al., 1993). Perhaps these sites are activated by thalamic nuclei and the dispositions then regenerate as information that is held and processed in working memory in the prefrontal cortices (Bogen, 1995).

The concept that there are separate widely dispersed brain regions that subserve stable conscious processes, storage of dispositions, and working memory is consistent with the concept of the brain as comprising multiple, independent systems. These multiple systems have also been referred to as the brain's "distributed society of specialists" (Baars, 1988, p. 42) and "a coalition or bundle of semi-independent agencies" (Dennett, 1991, p. 260; attributed to the work of Michael Gazzaniga). Dennett went so far as to suggest that such multiple systems are the very basis of human consciousness, with each independent system acting as a "virtual machine" that is implemented on the brain's parallel hardware.

Baars (1988) suggested that working memory, in addition to holding and processing information, also simultaneously broadcasts to the multiple brain systems. Working memory is where all of the parallel, but independent, activity of multiple brain systems is pulled together into consciousness. Several psychologists who have studied consciousness have proposed similar ideas (e.g., Jaynes, 1976; Ramachandran, 1991; Rozin, 1976). Ramachandran observed that multiple systems better fit the noise (and chaos) of the real world. Dennett (1991) used this colorful analogy of human consciousness and its multiple systems: "[I]t is a bit like two drunks; neither of them can walk unsupported but by leaning on each other they manage to stagger towards their goal" (p. 260).

Stable consciousness, although dependent on self-awareness as input from unstable conscious processes, permits an emergent sense of an *endurable identity*: the sense of self as extended across time, with a history of past experiences and a projected future. That sense of self is what being fully conscious means or, in other terms, how the full extent of stable conscious processes are experienced. Stable consciousness is the outcome of an interactive process of a stimulus or thing observed, the individual as observer, and the awareness of being the individual in the act of observing, which Damasio (1999) called the "autobiographical self" (p. 199) and Panksepp (1998) called "awareness of awareness" (p. 35):

> Indeed, it may well be that specific higher brain areas are specialized to help elaborate the cognitive contents of different types of affective (and motivational) processes. . . . Thus, one general way to view many higher cortical functions is as providing ever more flexible ways for animals to deal with basic survival issues. One of the most important of these functions is the ability to utilize past experiences to inform future plans. (Panksepp, p. 316)

At the level of stable conscious processes, basic self-awareness can be informed by past experiences and future plans. Therefore, motivation in species with extensive neocortex and stable conscious processes can become more elaborated. In addition to the motivated self-protection and mating behaviors of reptiles, for example, humans can display motivated behaviors that are more diverse and prosocial. Stable conscious processes allow the comparison of self versus social standards (culture), which has been hypothesized to lead to motivation to act consistently with values, attitudes, and beliefs (Duval & Wicklund, 1972).

Schemas, semantic networks, and nodes of parallel distributed processing (PDP). At this point, two questions about the nature of stable conscious processes arise: What is the structure of the distributed dispositions that are used to construct autobiographical memory? How might motive adaptations be represented in consciousness? Cognitive psychologists have, for some time, been aware of several well-established principles of memory storage of factual information: (a) clustering—there is a tendency to remember similar, related facts together; (b) conceptual hierarchies—related facts are organized into multiple hierarchical levels (e.g., Bower & Clark, 1969); (c) schemas—organized sets of facts concerning a specific event, situation, or object develop from experience into clusters or schemas and tend to be recalled together; and (d) semantic networks—individual facts called nodes are widely distributed in the brain but are linked by neural pathways to form the foundations of schemas (Collins & Loftus, 1975).

Together, these principles suggest how knowledge is organized and stored by the brain. Individual concepts, such as "rose," "red," and "flower," need be stored only once but can be linked and relinked structurally (by neural pathways or perhaps specific changes in individual neurons) many times over to other concepts and each other. "Flower," after more varied experiences, may also become linked to "iris," which may itself be linked to "blue." Then, in attempting to remember "flower," one could ultimately get to the concept "blue" from "rose." One word of caution is in order. These principles were developed with respect to factual (i.e., semantic) memory only. It may well be that the storage of other types of experiences—visual, olfactory, kinesthetic, or auditory—may follow different principles.

More recently, cognitive psychologists have proposed a "connectionist" model—compatible with the four principles of memory storage—to describe how the neural pathways that create semantic networks are organized to handle information processing. It is known as the *parallel distributed processing* (*PDP*) *model* (McClelland, 2000; McClelland & Rumelhart, 1985; Smolensky, 1995). The PDP model assumes that (a) information is stored in neural networks of nodes consistent with semantic networks, (b) these networks are highly interconnected, and (c) cognitive processing depends on patterns of activation in the networks. Specific memories are represented in specific patterns of neural activation, not specific locations. These patterns are facilitated by *long-term potentiation*, the strengthening of synaptic connections from repeated exposure (learning; Beggs et al., 1999). The patterned representation of memories is not unlike Pribram's (1977) proposal of a "nonhomogeneous" brain in which storage and processing take place in hologram-like wave patterns.

Applying this to motivation, different motives would be mediated by different brain structures (as described by Damasio, 1999)—Baars's (1988) "distributed society of specialists"—each with different (competing?) patterns of neural activation. For example, researchers have suggested that medial temporal structures (rhinal cortex, amygdala, and hippocampus) may be involved in storage of memories (Corkin, Amaral, Gonzalez, Johnson, & Hyman, 1997; Wheeler, Petersen, & Buckner, 2000), while the left frontal lobe may be involved in encoding them, and the right frontal lobe may be involved in retrieving them (Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). Another region, the orbitofrontal cortex, appears to be involved in both coding the reward values of different outcomes and in processing emotional responses to situations (Bechara, Damasio, &

Damasio, 2000). These different brain regions all appear to share a single working memory that is primarily dependent on frontal lobe functioning (Goldman-Rakic, Scalaidhe, & Chafee, 2000).

Recent neuroscience research supports the PDP view of the brain. One example is the discovery that the hippocampus encodes spatial relationships with two separate but complementary mapping systems (Jacobs & Schenk, 2003). A "sketch" map is constructed in the hippocampus itself, while a "bearing" map is independently constructed in the dentate gyrus. These parallel mappings are then integrated to produce a functional map. The hippocampus is also strongly implicated in the storage of declarative memories (e.g., Fell, Klaver, Elger, & Fernandez, 2002). Paller (2004) investigated "declarative memory," which is fundamental to autobiographical self. Declarative memory is a "vast but imperfect storehouse of information, and a basis for our own life story" (Paller, p. 49). Consistent with the present model, declarative memories do not seem to be stored in a single brain region but are distributed throughout many cortical networks in a lengthy process (that may extend over years) called *cross-cortical storage*, with prefrontal cortex figuring prominently in retrieval and remembering of the "life story."

These principles do provide a testable model to describe how the factual and semantic knowledge about motives may be organized within cognitive structures that make up autobiographical memory and stable consciousness. For example, perhaps "Rolls Royce" is part of a semantic network that also links "expensive," "impressive," "status symbol," and "the envy of others." Such a network should be interrelated (e.g., linked by neural pathways) as a social status motive related to mating that we term *material*. The material motive would help solve the evolutionary problem of attracting a mate by facilitating behavior toward acquiring resources that demonstrate the ability to support their potential offspring.

We propose that individual motive structures, or adaptive mental mechanisms, such as these are linked to yet another cognitive structure existing in PDP nodes, the *self-schema*. As proposed by Markus (1977), the self-schema links beliefs, experiences, and memories and could well function as autobiographical self. Research by Craik et al. (1999) and Kelley et al. (2002) supports the existence of a self-schema, with both PET and functional magnetic resonance imaging (fMRI) studies indicating the midline of the frontal lobes may be integral to its functioning. Self- and motive schemas may be closely integrated, shaping the general direction of behavior toward increasing inclusive fitness.

Issues in Consciousness Studies

Our description of transconscious processes provides the neuropsychological foundation for the present theory of motivation, yet we are aware that raising the subject of consciousness has introduced complex philosophical issues and disagreements into psychology for decades. Among contemporary learning theorists, Blumberg and colleagues (Blumberg & Sokoloff, 2003; Blumberg &

Wasserman, 1995) have been particularly strong advocates for a nonmentalist psychology. For example, Blumberg and Wasserman would banish from psychology all "mentalist" explanations, such as mind, awareness, intention, understanding, or conscious thought. Consistent with this, Blumberg and Sokoloff also maintained that emotions (a topic we will take up in the next section) are merely "fictional causes" of behavior.

Despite these criticisms, a growing literature supports the empirical investigation of consciousness. Barriers to the study of mental processes are breaking down within the neurosciences, affecting both psychology and biology alike (Kandel & Squire, 2000). Examples of this literature include Vogeley and Fink's (2003) review of the neural correlates of human self-consciousness; Clément and Malerstein's (2003) reanalysis of Piaget's theories; Sun's (1997) neural network model, CLARION, that may explain implicit learning; Jeannerod's (1994) review suggesting that schema exist for the representation of motor imagery and intention; and Lloyd's (2002) reanalysis of fMRI datasets supporting a "neurophenomenology," in which past and future brain states may be embedded in present brain states. This literature generally supports conscious motivation, particularly the neurophenomenology of past and future brain states, which is a necessary foundation for a personal narrative and autobiographical self. Given our description of motivation as a purposeful general behavioral direction over time, such a neurophenomenology would be necessary for the very existence of conscious motivation.

Comparative psychology's contributions to the evolutionary study of consciousness also tend to support an evolutionary theory of consciousness. For example, Barber (1996) concluded from his research that many bird species "are far more anthropomorphic and mentalistic than the percepts of Blumberg and Wasserman (1995) can possibly encompass" (p. 59). Consistent with this, Gärdenfors (1996) reviewed comparative studies of many species and concluded that "there is convincing evidence that the behaviorists are wrong and that animals have not only cued representations but also detached ones" (p. 272). *Detached representations*—images that arise independently of stimuli—are necessary for an inner mental environment and self-consciousness. In reviewing these studies, we wonder why varying degrees of evolved consciousness in animals should be a surprise. Evolutionary theory would predict that instances of self-awareness and consciousness might be found in other animals. Conscious processes of varying degrees probably occur in many animals, whereas conscious self-awareness is probably more rare (Bekoff, 2002).

We do not believe that emerging theory and research on the nature of consciousness and self-awareness can be ignored in an evolutionary theory of motivation, just as we cannot conceive of explaining human motivation from an evolutionary perspective without incorporating genetics, the structure of the brain, and mechanisms of learning. This is consistent with other basic research models that attempt to bring learning and consciousness together (e.g., Salzen, 1998;

Sun, 1997). We hope this raises and ultimately answers some interesting questions. For example, a self-aware organism would be aware of and reflect on the very fact that it is receiving reward and punishment, which suggests that the organism has a representation of itself and of being itself in relation to the reinforcement it is receiving (see Gärdenfors, 1996; also Paller, 2004; and Roser & Gazzaniga, 2004). Presumably, the development of such a level of representation aids adaptation and inclusive fitness.

Transconscious Processes in Human Emotion

In the preceding section, we described how motivation may be organized within a three-part hierarchical neuropsychological structure of transconscious processes. We use the same hierarchical structure (depicted in Figure 1) to describe how emotions may arise and what their function may be in motivation. Plutchik (2003) described *emotions* as feeling states that are activated when issues of survival are raised in fact or by implication and disturb the organism's homeostasis. Thus, he implied a connection between inclusive fitness, motivation, and emotion, which we seek to make more explicit in the present theory. Russell (2003) recently advanced a new theoretical framework of emotion, and we use his terminology here: *Emotions* are the consciously constructed (labeled) experience, and *affect* is the raw, nonconscious aspect of the prelabeling process. *Emotion* can also be used as a general term, as in the title of this section.

Nonconscious Processes

Panksepp (1998) has observed that the line between nonconscious emotional processes and consciously experienced emotions is not yet known. We are not even certain whether there is such a line; therefore, we again use *transconscious processes* to emphasize the presumably parallel nature of emotional processes. There are, however, some brain systems that are specifically implicated in emotional experience at a nonconscious level. Consistent with evolutionary theory, these nonconscious emotional processes originated prior to emotional processes in unstable and stable consciousness (Winkielman & Berridge, 2004). Affect may be mediated by a small number of different brain systems consistent with Baars's (1988) distributed society of specialists. These brain systems are older, largely subcortical, and are integrated with nonconscious processes in general. They include the periaqueductal gray region, as well as hypothalamus and amygdala (J. F. Bernard & Bandler, 1998). The midbrain periaqueductal gray, which was previously described as implicated in nonconscious autonomic regulation, the body map, and analgesia, also may have a role in coordinating potentially emotional reaction strategies to stress, threat, and pain (Bandler & Shipley, 1994). Evidence suggests that the amygdala responds nonconsciously to, and encodes, positive and negative emotional experiences (Mather et al., 2004). These systems are genetically prewired, respond to challenging environmental experiences, and organize behavior toward the overarching goal of inclusive fitness (Panksepp). The motive–emotion relationship is based on links (neural pathways) between these brain systems, which are subcortical, as well as cortical cognitive structures (schemas) that are part of stable consciousness.

The aforementioned structures could serve a basic, ongoing neurophysiological state of "core affect" (Russell, 2003). Core affect is presumed to be nonconscious, yet guides cognitive processing. There is considerable evidence that many of the brain's emotional circuits are nonconscious. As such, they are prewired, subject to modification through conditioning, and interact with conscious cognitive processes such as appraisal and decision making (Panksepp, 1998). Core affect may arise within reverberatory neural patterns at the level of the body map. Moods can facilitate the experiencing of certain motives in stable consciousness. Different inputs could provoke different types of moods. If the reverberatory patterns are strong enough, they affect stable conscious processes and cause "full-blown" emotional states; otherwise, they remain core affect (Panksepp). However, although emotions may facilitate the experience of motives, individuals need not always be aware of specific affective states when engaging in motivated behavior (Panksepp). In the absence of significant disruption of homeostasis, "well-worn" adaptive mental motive mechanisms can probably direct routine behavior without much conscious awareness of an attending affective state (Damasio, 1999). For example, this may be seen much in the same way that one's thirst, in less extreme cases, motivates the replenishment of fluids without much conscious thought or experience of discomfort.

Affect arises when the organism experiences a change in body state (homeostasis is disrupted), and affect releases a response pattern that changes the very environment in which cognitive processing is taking place (Damasio, 1999). This change in cognitive processing, although nonconscious, alters unstable conscious processes and opens the door to the recognition of an emotion at the next level of unstable consciousness. Affect cannot be separated from reward or punishment, pleasure or pain, approach or avoidance, and personal advantage or disadvantage (Damasio). However, there is evidence that the brain mechanisms that mediate general hedonic tone (pain and pleasure) may be distinct from those that mediate affect (Rainville, Carrier, Hofbauer, Bushnell, & Duncan, 1999; Rainville et al., 1997).

Unstable Conscious Processes

We previously mentioned several midbrain structures that could produce unstable consciousness and probably provide a basic awareness of self versus environment. For example, the amygdala may serve as the point of higher order associations between internal and external sensory data (Nahm et al., 1993) and possibly provides a fleeting awareness of hedonic tone, pleasure and pain, and, we now suggest, emotions. The amygdala also appears to have the central role in emotional learning, and, as a relatively early evolving brain structure, it is most important in analyzing threats and danger (LeDoux, 1996). Some emotional states, in particular distress, fear, and anger, are also related to the activation of sympathetic pathways in the autonomic nervous system, which is under the control of the hypothalamus (Levenson, Ekman, Heider, & Friesen, 1992). However, the relationship between sympathetic activation and emotions is so close that particular emotional states cannot be distinguished on the basis of sympathetic activation alone (Cacioppo, Klein, Berntson, & Hartfield, 1993). Finally, circuits of the periaqueductal gray are linked to the major genetically coded emotional systems identified by Panksepp (1998), and they are especially closely linked to the regions of frontal cortex that participate in stable conscious processes and working memory. The destruction of the periaqueductal gray seriously compromises stable conscious processes, but its circuits are more likely an intermediary between nonconscious and stable conscious processes, hence the implication that they serve unstable conscious processes.

It is in unstable conscious processes that core affect may first be perceived. It is important to appreciate that the perception of an affective state is a representation, not a direct experience, of core affect. The perception of an affective state takes place simultaneously with "'affective quality' . . . a property of the (real or imagined) stimulus: [*sic*] its capacity to change core affect. Perception of affective quality is a process that estimates this property" (Russell, 2003, p. 149). Russell maintained that this process affects all stimuli, can be done independently of general knowledge, and is not the same as appraisal. Therefore, it does not depend on stable conscious processes or access to autobiographical knowledge. However, perception implies some level of conscious awareness, and it seems reasonable that this estimation process could begin in unstable conscious processes.

One can say one is feeling tense or feeling fine only because there is some change in a quality that one can sense (Damasio, 2004). The change is in the moment-to-moment status of the body as represented in nonconscious processes and perceived in unstable consciousness. Changes in unstable conscious processes in turn become stimuli to be perceived by stable conscious processes.

Stable Conscious Processes

As noted previously, widely dispersed regions in the frontal and temporal cortices, as well as association cortex, participate in stable conscious processes. In particular, the orbitofrontal cortex has a general role in the processing of emotional cues (Bechara et al., 2000), but there is also asymmetry of frontal activation and emotional processing (Davidson, 2000a, 2000b). There is greater activation of the left prefrontal cortex with positive affect and greater activation of the right prefrontal cortex and right amygdala with negative affect. Activation of the left prefrontal cortex is also associated with the overall general level of motivation, increased confidence, and effort, whereas the reverse is true with activation of the right frontal cortex.

In the present theory, affect may arise due to either a deprivation stimulus or satisfaction stimulus. In addition, emotions may arise in the absence of a tangible stimulus from the conscious imaging of a deprivation stimulus or a satisfaction stimulus, that is, without input from nonconscious processes. For example, the awareness of an absence of affection may be accompanied by a consciously experienced state of displeasure, which would likely be labeled “sadness” by English speakers, whereas achieving an affectionate relationship may be accompanied by a consciously experienced state of pleasure, which would likely be labeled “joy” by English speakers. Also, the simple act of constructing mental representations (imagining) of either of these situations could evoke similar states of displeasure and pleasure.

When either core affect, as passed through unstable consciousness, or conscious imagining alters stable conscious processes, they become experienced (Damasio, 1999). Both core affect and conscious imagining would then be subject to an attribution process. *Attribution* is the process whereby the labeling of emotions, sometimes with “folk” terms, takes place. Attribution allows individual and cultural differences to affect emotional experience (Russell, 2003). This could only occur at the level of stable consciousness and draws from changes in somatosensory status (homeostasis), core affect, behavior, cognition, and appraised objects.

Labeling Emotions

Russell (2003; Russell & Barrett, 1999) proposed that nonconscious core affect can be represented by two perpendicular dimensions. One dimension, the horizontal, is the *valence*, the degree of pleasure–displeasure, and ranges from ecstasy through a homeostatic neutral point (adaptation level) to agony. The notion of hedonic tone is based on pleasure–pain (or approach–withdrawal) responses along this continuum and is observed in many species. *Hedonic tone* is the general, ongoing pleasure–pain balance. It is largely mediated by the hypothalamus—and other structures involved in nonconscious processes—but the frontal and temporal lobes may become involved as well (see Mook, 1996, for a discussion). Hedonic tone is motivational, but motivation cannot be explained by hedonic tone alone. On the vertical dimension, Russell proposes a continuum of activation–deactivation, which ranges from excitement through various stages to sleep. There is evidence that combinations of these two dimensions are neurophysiologically distinct: positive (pleasurable) activation is associated with an increase in dopamine, whereas negative (displeasurable) activation is associated with an increase in norepinephrine (D. Watson, Wiese, Vaidya, & Tellegen, 1999).

However, Russell's (2003; Russell & Barrett, 1999) two-dimensional affective framework stands in contrast to more innate views of emotions as discrete, universal experiences that can be categorized and described with labels such as anger, fear, or joy (e.g., Izard, 1991; Lewis, 1995; Plutchik, 2003; Plutchik & Kellerman, 1974). Discrete affective processes (which have been given labels such as anger or joy) are believed to arise from intrinsic brain systems (Panksepp, 1998). In this view, emotional experiences are "prepackaged," that is, hardwired, at the level of nonconscious processes. Instead, Russell views such categorical descriptions as part of the attributional process, which takes place in stable consciousness. This is consistent with Bem's (1967) theory of self-perception. Bem maintained that people are seldom directly aware of their emotions, so they infer them from their own behavior and the surrounding environment.

With the belief that "every approach has something to offer" in this complex area (Panksepp, 1998, p. 45), for heuristic purposes, we will take an eclectic view. Some specific experiences of core affect are prewired, that is, reflexive and hence categorical. However, we recognize that the labels used for the presumed discrete affective processes may be part of an attribution process based on subsequent learning. For example, research suggests the self-conscious emotions, such as envy, empathy, embarrassment, pride, shame, and guilt, develop between 2 and 3 years of age and parallel the development of stable conscious processes (Lewis, 1995). These emotions, then, should be particularly subject to the attributional processes.

In summary, what is commonly referred to as an emotion may be the conscious awareness (perception) of either a hedonic response (an emotional valence attached) to (a) external stimuli (in a strictly behavioral sense), (b) a conscious imaging, or (c) an alteration in internal homeostasis. It is *knowing* a feeling (Damasio, 1999). However circular this may seem, it is explained by the notion that affect arises in nonconscious processes as a result of neurally mapped changes in homeostasis or in response to external stimuli and is neither conscious nor felt. The fleeting feeling of knowing the affective quality only emerges in unstable consciousness when the change in the body map is experienced as an object in relation to the self. This is the immediate experience expressed in the sense that "something is happening to *me*." The full knowledge that we have emotions, their labeling and processing, takes place in stable consciousness and becomes part of autobiographical self. As we propose in the next section, knowing what emotions we have may provide tremendous advantage in guiding purposeful behavior in a large brain with an extensive autobiographical record.

Emotions and the Search for Motivated Direction

How could emotions work with motivations to provide the fundamental direction or purposefulness to which behavior is generally directed? One answer might be found in the "search hypothesis of emotion." Based on Simon's

(1955) work on artificial intelligence, the search hypothesis provides an explanation for the adaptive role emotions may have in extended consciousness. The "search problem" arises in cognitive science when attempting to explain how human memory is searched. If declarative memories (and, as we maintain, motive dispositions) are stored in widely dispersed, "multiple representational fragments" (Paller, 2004, p. 49), how then does the hypothesized prefrontal search coordinator find those that are relevant? Borrowing from artificial intelligence models, Evans (2002) proposed that emotions may focus the search by preventing us from "getting lost in endless explorations of potentially infinite search spaces" (p. 503).

If–Then Searching

In the present theory, we propose a memory-focusing role of emotions in the service of motivated behavior. Working memory forms the basis of stable conscious processes and has access to the potentially vast space of all stored memory and experience—all the possible imaginings of human consciousness. Despite evidence that verbal and spatial working memories may be implemented by different neural structures (Smith et al., 1996), the unitary nature of conscious experience suggests that the brain's many parallel distributed processing systems are integrated (Roser & Gazzaniga, 2004), and this most likely takes place through working memory.

Working memory is where various and potentially competing motivated behaviors may be informed by autobiographical self and considered rationally. However, searching such a potentially vast space for an optimum behavioral solution could delay a response beyond the time frame in which it is optimally adaptive or paralyze action altogether. This situation may be avoided by searching dispositions with if–then images (Evans, 2002; Salzen, 1998). These images may be conscious to some degree, and the searches are probably sequential, although it may be possible for several to be done simultaneously. These if–then images may consist of varieties of possible behavioral strategies for each motive. Each strategy is tried out mentally (imagined) and, as memory is searched, each triggers an emotional response in stable consciousness. These emotional responses are experienced as "gut feelings" (the affective quality occurring within unstable and stable conscious processes). The emotional responses are automated and focus attention on potentially positive and negative (pleasure–pain) outcomes of the if–then search scenarios (Damasio, 1994, 2004). These emotional responses provide ready-made estimates of likely behavioral consequences, consistent with the goals of inclusive fitness for that organism.

Experimental evidence has suggested that induced emotional states do have selective effects on executive search functions in working memory (Gray, 2001). Neural activity related to such emotionally mediated cognitive control appears to take place in the prefrontal cortex (Gray, Braver, & Raichle, 2002). Gray (2004) suggested that emotion and cognitive control are integrated and emotional states may help set priorities among competing motivated behaviors.

As an example of an if–then search, consider a married man whose sexual interest has been triggered by proximity to a new, attractive female coworker. As he imagines the *if*, sex with her, he anticipates the *then*, a strong emotion of pleasure resulting from the anticipation that sex and curiosity motives will be satisfied (these motives will be described in Part 4). Perhaps he next imagines another *if*, sex with his wife, which would also be related to the sex motive, and he anticipates another *then*, possibly lesser pleasure due to lack of simultaneously satisfying the curiosity motive. Finally, he imagines one more *if*, his wife's reaction to his infidelity, and he anticipates one more *then*, her anger and, perhaps, his own guilt for not acting in accord with the conscience motive. Individuals will persist or stop at different points in this if–then search process.

One may stop after only the first search, whereas another may proceed through several more. Where a search stops probably depends on the strength of the emotion encountered. The strength of any emotion is probably jointly influenced by individual differences in physiology as well as learning. Furthermore, this is only one out of many possible if–then search orders. The order of searches may be determined by which stimulus occurs first and what other (conceptual) stimuli are linked to the first stimulus through prior experience. The most probable outcome of any if–then search among motives is predicted by the relative strength of self-control, which would extend the number of searches (more on self-control in the next section) and the relative strength of the various imagined emotional responses.

A search may be neither fully logical nor exhaustive; rather, it may typically cease when the first projected pleasing (or less displeasing) emotional outcome is found (Evans, 2002). The imagined if–then behavior responsible for the first pleasing (or less displeasing) emotional response is then more likely to be engaged than is any other previously searched behavior with a hypothetically less pleasing or more displeasing emotional outcome. Thus, "gut feelings" help us avoid the paralysis that could result from becoming overwhelmed and unable to act or acting inopportunely as a result of having to consider too many behavioral alternatives without any method to value them. In fact, studies of brain-damaged patients have indicated that emotion is integral to the process of reasoning and decision making (Bechara, Damasio, Damasio, & Anderson, 1994; Bechara, Tranel, Damasio, & Damasio, 1996). One experiment has demonstrated that some behavior may be guided by nonconscious emotional processes even before conscious knowledge (Bechara, Damasio, Tranel, & Damasio, 1997). And, at the level of stable consciousness, other researchers have suggested that emotions serve an adaptive, heuristic purpose, allowing quicker decision making (Slovic, Finucane, Peters, & MacGregor, 2002).

Searching by if–then images provides a fuzzy method for motives and emotions to prioritize behavior. It is fuzzy because it does not ensure the most adaptive response but, rather, an efficient (as in timely) response that may be relatively more adaptive (and result in more pleasurable consequences) than the others that had been considered up to that point. This may explain why not all behavior an individual engages in appears linked to a motive and why individuals may engage in some behavior that does not appear to further inclusive fitness.

Motivation and Emotion

The relationship between consciousness, motivation, and emotion may now be discussed in more detail. *Core affect* signals a change in homeostasis or hedonic tone at the level of the nonconscious sensory inputs of the body map. Core affect first has an opportunity to become sensed at the level of unstable conscious processes. Most core affect never reaches conscious awareness. It remains at a "low grade," but sometimes quite intense level, providing the background tone to our being (Damasio, 1999, p. 286). At the nonconscious level, core affect and motives are probably closely linked and may be mediated by some of the same brain systems. However, some core affect is felt in stable conscious processes, where it is experienced (labeled) as "*my* feelings" but not necessarily as "*my* motives" because the motive is not the felt aspect. The processing and expression of nonconscious core affect and conscious emotion, although related, may also function in an independent, parallel manner (Winkielman & Berridge, 2004).

Stable conscious processes offer access to working memory and extensive autobiographical data from which causal attributions for emotions could be made (see Weiner, 1989). Consciousness itself may actually depend on the affect that reaches it (Damasio, 1999). It is at this level of stable conscious processes that emotions fully interact with cognitions. In his two-factor theory of emotion, Schachter (1971; Schachter & Singer, 1962) viewed emotion as both a physiological response and a cognitive interpretation. The cognitive interpretation results in the labeling of the physiological response as joy, sadness, anger, and so on.

Izard (1991) identified seven emotional states that are universally present at birth: joy, anger, interest, disgust, surprise, sadness, and fear. (Pride, shame, and guilt—the "social emotions"—supposedly develop later.) These are similar to those identified by Plutchik (2003) in his extensive attempts to distinguish among emotional states. Plutchik and Kellerman (1974) developed the Emotions Profile Index (EPI) as a measure of both emotions and personality. Plutchik's efforts have spawned many studies of different languages that have corroborated his English-language results. He identified the emotions considered primary or basic by most evolutionary psychologists—fear, anger, sadness, joy, love, and surprise—among a comprehensive taxonomy that expands to 32 "secondary" emotional states. These are not too far from a list of emotions measured in relation to their behavioral and physiological markers in eight countries (Wallbott & Scherer, 1989): joy, anger, disgust, sadness, fear, shame, and guilt.

However, as reliable as these lists of emotional labels appear to be, other research results suggest that there is no common or universal set of emotional experiences that can be labeled quite so discretely (Russell, 2003). Russell (1991) demonstrated that words for even such apparently simple and universal experiences as the English "fear" and "anger" are not found in all languages. There appear to be no emotional labels that are universal in all language groups (Wierzbicka, 1992, 1999). In fact, even the English word "emotion" is not found in all languages (Russell, 1991). This suggests that the specific label given to a conscious experience of core affect may vary by language and culture. However, the specific emotional labels used are not as important to the present theory as the nonconscious processes that underlie the conscious experience of emotion. The role of affective quality in guiding if–then searches is more important than is any potential labeling process. Russell's (2003) two-factor pleasure–displeasure, activation–deactivation framework may be sufficient to inform if–then searches, regardless of what labels are ultimately attributed to gut feelings.

In stable conscious processes, motives and affect can interact with all manner of other cognitions. If cognitions, motives, and emotions arise from distributed brain modules, then there is the possibility of some initial degree of anarchy in these interactions—conflict among and between cognitions, motives, and emotions. This anarchy may provide additional adaptive advantages because it allows for some degree of "slippage," of flexibility or unpredictability, in behavior. (There should be less conflict, and more predictable responding, in species without stable conscious processes.) Nevertheless, in this anarchic environment, inclusive fitness may provide the overarching evolutionary direction or purposefulness to which behavior is generally directed. When affect becomes conscious, there is the possibility for motivation—the general purposefulness of the person's behavioral direction—to interact with all of the contents of consciousness—autobiographical self—and far more complex planning and choice may be brought to bear on behavior. Emotions furnish information about stimuli, goals, and future behaviors, helping people to prepare for action (Frijda, 1994). As Zajonc (1980) observed, affective responses are automatic evaluations (*valuations* might be more appropriate in this meaning) that affect decision making, memory, behavior, and, we would add, motivation. Finally, once motives are considered in extended consciousness, self-control can be exerted, delaying more reflexive behavior with a lower probability of success in local circumstances and allowing it to be replaced with more carefully considered behavior that has a higher probability of success.

Self-Control of Motivated Behavior

Defining Self-Control

A comprehensive theory of motivation should address not only mechanisms that motivate (i.e., activate) goal-directed behavior but also mechanisms that delay, alter, deactivate, and rechannel all manners of goal-directed behavior. Therefore, we address self-control, which is not anticipated in any of the concepts described so far. *Impulsivity* is used to describe the opposite of self-control in the psychological literature. Although an imprecise construct, impulsivity is often characterized by irrationality (Monterosso & Ainslie, 1999). We are not suggesting that motivated behavior is irrational and that self-control forces rationality on motivation. That would not make sense because motivation is purposeful and inclusive fitness must be rational from an evolutionary perspective. However, *irrationality* is defined in very specific terms in the literature: In animals, irrationality is defined as failure to maximize overall reward. In humans, irrationality may more accurately be defined as failure to follow one's own recognized best interest. Therefore, irrational behavior may still be motivated behavior, but without the benefit of self-control (e.g., without the delay and alteration of behavior necessary to maximize inclusive fitness).

Another term for self-control is *delay of gratification*, which is defined as resisting more immediate rewards in favor of achieving longer term goals. Individual differences in the ability to delay gratification in childhood predict later academic success (Mischel, Shoda, & Rodriguez, 1989). Competing neural circuits may be involved in successful strategies for delaying gratification (Metcalfe & Mischel, 1999). Metcalfe and Mischel have proposed that an amygdala-based cognitive system processes the rewarding or pleasurable characteristics of stimuli, and a hippocampus-based cognitive system processes the conceptual or symbolic characteristics of stimuli. The hippocampus is more involved with plans and goals and, therefore, allows more self-control. Presumably, differences in the relative activation of the amygdala and hippocampus would reflect the ability to delay gratification.

Another related term is *self-regulation*, which again involves delay of gratification and self-control. Self-regulation has been described as a resource or strength that varies among individuals (Baumeister & Heatherton, 1996). There is only so much self-regulation at an individual's disposal: It can be depleted by situational demands, and it can be renewed by practice. It should also respond to reinforcement. There is no substantive distinction between any of these terms or concepts as far as they are used here. Therefore, we shall define *self-control* as the ability to delay gratification of the hedonic principle—to delay reflexive behavioral and emotional responses—to carry out more extensive if–then searches for behavioral strategies that are anticipated to result in pleasurable hedonic tone in a particular context.

Self-Control as an Additional Cognitive Mechanism

We propose that self-control is realized in a cognitive mechanism—another node of parallel distributed processing—that is part of extended consciousness and mediates motivated behavior. Differences in the relative activation of the amygdala and hippocampus hypothesized to play a role in delay of gratification are likely components of this mechanism. However, the prefrontal cortex should have a central role in coordinating it, reflecting its well-documented general inhibitory role in behavior.

Clinical and objective observations of the neuropsychological condition known as “frontal lobe syndrome” (FLS) relate to this role. Patients with FLS have damage to the prefrontal cortex and occasionally the anterior temporal lobes. The results are both cognitive and personality dysfunction (Filskov & Boll, 1981). Lezak (1995) observed that patients with FLS “cease to be in adequate *control* of themselves or their *destinies* [italics added]: the greater the defect, the more socially dependent and socially dysfunctional they become” (p. 188). Note that FLS patients are described as no longer able to control their destiny, their purpose, or direction. One of us (L. B.) has evaluated several patients with prefrontal lesions and FLS. All had a striking lack of personality, affect, and motivation. They initiated no behavior other than what is automatic or reflexive, that for which Damasio (1999) maintains only core consciousness is necessary. When these patients were directed or encouraged to take a particular course of action, they perseverated in it. They were unable either to change an unproductive course of behavior or to conform behavior to serve a different goal of their own. What is more, they had no affect about what would be viewed objectively as a frustrating and useless activity.

FLS in humans and its implications for self-control are based on molar-level observation and analysis of people with brain dysfunction and damage. Schall and his associates focused on the neuronal level in animals (e.g., Schall, Hanes, & Taylor, 1999; Schall & Thompson, 1999) and suggested that a region of the anterior cingulate cortex may be responsible for monitoring and controlling intentional behavior (Schall, 2001) and that it appears to do so “by monitoring the *consequences* [italics added] of such (intentional) actions, not the actions themselves” (Schall, as cited in Salisbury, 2003, p. 1). Furthermore, there is a time lag in the response of anterior cingulate neurons previously shown to signal success or error relative to other frontal lobe neurons. The delay is not presumed to allow correction of actions as they take place but, rather, to consider consequences. This suggests that delay of gratification allows more extensive if–then searches of consequences (e.g., of anticipated emotional outcomes of projected consequences).

Libet (1985) reviewed another line of research on electrophysiological “readiness potentials” in the brains of human subjects that is consistent with the results of Schall and his associates (e.g., Schall, 2001; Schall et al., 1999; Schall & Thompson, 1999) and with the present theory of motivation and self-control. Libet reported that “the initiation of a spontaneous voluntary act begins unconsciously. However, it was found that the final decision to act could still be consciously controlled during the 150 ms or so remaining after the specific conscious intention appears” (p. 529). He concluded that the “conscious will” is permissive, it does not initiate specific voluntary acts, but rather permits or prevents the motor implementation of what arises unconsciously. The functions Libet attributed to conscious will we would ascribe to the self-control circuits of extended consciousness.

In the present theoretical conceptualization, self-control is not a motive because it does not initiate, activate, or propel behavior that increases inclusive fitness. Let us clarify that statement, because it is possible to conceive of an individual who desires—is *motivated*—to increase (or decrease) the amount of his or her self-control (this certainly fits with the idea of self-regulation as a resource). In such an instance, we propose that the effort to modify self-control is not the motive. Instead, the motive would be, for example, to reduce self-control to allow more playfulness (*play* being a motive) or to increase self-control to acquire more material resources through disciplined labor and thereby increase one's attractiveness to a potential mate. Although self-control is not a motive, we believe the cognitive structures that allow it are as much an adaptation as any motive.

Our concept of self-control as an adaptive delay of gratification to allow more extensive if–then searches does not differ much from the notion of cognitive control as proposed by Braver, Cohen, and Barch (2002) and Gray (2004). In the conceptualization of cognitive control, emotion and cognitive control are integrated functions, with emotions modulating cognitive processes to help facilitate prioritizing of actions and resolution of dilemmas. In the present theory, self-control is limited to delay of gratification or latency of action, and cognitive control would appear to be subsumed in our notion of the search hypothesis of emotions. This may just reflect a different parsing of control functions.

In conclusion, self-control is dependent on autobiographical self and includes cognitions about the social appropriateness of behavior. Self-control's inhibitory effect on motivation permits increased conscious rehearsal of if–then search scenarios and the resulting conscious realization of emotions that help the individual search for what might be more socially successful strategies of homeostatic regulation and inclusive fitness. According to Bermond (2001), "the emotional experience derives its fitness function from the fact that it can inhibit the stimulus-bound emotional behaviour so that, by using imagination and information from the past and future, more adaptive behavioural responses can be imagined, planned and later executed" (p. S59).

We posit that self-control can intervene to channel motivated behaviors into prosocial behaviors that more directly serve the fitness of kin, coalition, and larger systems but only indirectly serve the individual's own survival (through the increased probability that kin will survive). This evolutionary trade-off between what is best for the individual and what is best for kin, coalition, and larger systems promotes inclusive fitness and arises out of the genetic potential for human beings to socialize and be socialized. This genetic potential to socialize and be socialized is subject to varying degrees of development, social learning, and transmission of memes (described in the next section), all of which produce potentially vast individual differences in self-control.

PART 4—INDIVIDUAL DIFFERENCES IN ADAPTIVE MENTAL MOTIVE MECHANISMS

Defining Human Motives in Evolutionary Terms

If motivation is mediated by adaptive mental mechanisms that reliably guide surface-level behavior and interests, then motivation should be measurable as individual differences in behavior and interests. We propose that individual differences in motivation will appear in categories of purposeful behavior, which covary due to brain structures that responded to inclusive fitness selection pressures in the ancestral environment. We call these categories of hypothesized reliable individual differences *motives*. A motive (i.e., a category of purposeful behaviors) should be identifiable by its logical relationship to inclusive fitness. The motives are hierarchical in terms of their evolutionary development. Some arose early and are mediated by old brain structures, and some arose later when a large neocortex could support more consciously integrated adaptive mental mechanisms.

However, a word of caution is in order. We do not mean to reify motives, as if there were a "motive" for curiosity that is entirely genetically programmed. To do so would ignore the strong interaction hypothesis, the environment's role in producing phenotype. Also, we do not claim that any and all of an organism's apparently exploratory movements in and about an environment would be motivated exclusively by a curiosity motive. We use terms such as "curiosity" for motives only because they conveniently represent and communicate a construct about a category of behavior familiar in human experience. We also realize that some motives are not adaptations but rather exaptations. Again, an *exaptation* is an adaptation (in this case, an adaptive mental mechanism) that arises for one use and becomes co-opted for a new purpose (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1995). Buss et al. maintained that exaptations may be more important than adaptations for evolutionary psychology, and that may be borne out particularly well in motivation. The remaining challenge is to determine how many motives there may be and how to operationalize the nature of their logical relationships to inclusive fitness.

Human Motives and Social Domains

Bugental (2000) proposed that separate human neurohormonal systems evolved to solve adaptive problems in different social domains and described five social domains related to these proposed neurohormonal systems: attachment, coalitional group, mating, reciprocity, and hierarchical power. These neurohormonal systems are consistent with the adaptive mental motive mechanisms of the present theory, and the social domains suggest a logical framework in which motives may operate. Kenrick et al. (2003) modified Bugental's framework somewhat, hypothesizing six domains of social interaction: coalition formation, status, self-protection, mate choice, relationship maintenance, and parental care. They also attempted to unify evolutionary psychology and dynamical systems theory and to associate each of these domains with a fundamental evolutionary goal and principle.

We propose that motives developed to promote and guide behavior necessary to solve problems of inclusive fitness encountered within simultaneously evolving social domains, similar to those described by Bugental (2000) and Kenrick et al. (2003). The motive adaptations stem from new selection pressures in the growing complexity of the social environment—specifically, the increasing size of human social systems—and the new and different possibilities and demands such complexity introduces for inclusive fitness. Dunbar (1993) developed data that suggest a coevolution of the size of the human neocortex, the size of social groups in which humans interact, and the development of language, and concluded, "In evolutionary terms, the size of a species' neocortex is set by the range of group size required by the habitat(s) in which it typically lives . . . in proximate terms . . . current neocortex size sets a limit on the number of relationships that it can maintain through time, and hence limits the maximum size of its group" (p. 682).

We propose that neocortex size, transconscious processes, social domains, and motives coevolved. Different motives evolved to increase inclusive fitness in response to the pressures of ever larger social systems and, as the brain and motives evolved, they permitted ever larger social systems to develop. Figure 2 depicts this process of coevolution.[3]

Because one important goal of the present theory is to provide a basis for meaningful measurement of human motives, we slightly modified the categories created by Bugental (2000) and Kenrick et al. (2003): *Relationship maintenance* and *parental care* were combined into a single domain because they involve similar-sized systems and may involve similar motives. *Mate choice* was changed to *mating*, to focus on what an individual does to attract a mate rather than what an individual is looking for in a mate. Consistent with that, *status* was subsumed in the mating domain, because we hypothesized that human status motives developed resulting from mate attraction and selection pressures in more complex social environments. We also subdivided status into four intermediate, quasi-independent categories of behavior. Finally, we added a social domain called *memetic* (Dawkins, 1989) to capture the broad cultural influences in very large social systems.

This scheme yields five social domains. As indicated in Figure 2, the social domains are linked in a hierarchical manner to the increasing size of the system to which each social domain pertains: *self-protection* is at the single-system level; *mating* involves a two-person (dyadic) system; *relationship maintenance and parental care* takes place at the small-system level comprising kin; *coalition formation* involves potentially large systems of nonkin; and the *memetic* system is symbolic and involves potentially very large, idealistic systems.

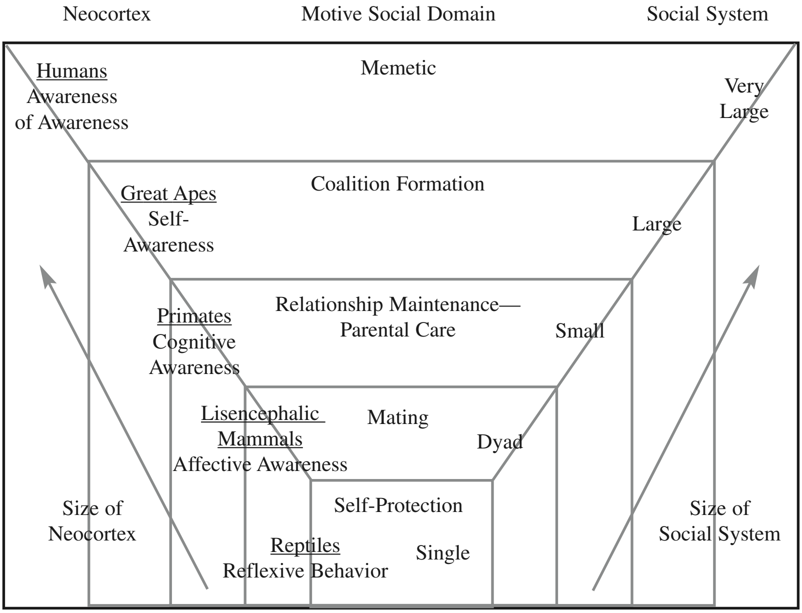

FIGURE 2. Coevolution of neocortex, motive social domains, and social system size. Left side adapted from *Affective Neuroscience: The Foundations of Human and Animal Emotions,* p. 35 by J. Panksepp, 1998. New York: Oxford University Press.

Human motives may have developed in response to different pressures from different environments and different social systems. Therefore, they may act independently; yet, because all are either adaptations or exaptations that increased inclusive fitness in ancestors, they also direct the individual's "stagger" toward inclusive fitness, to borrow Dennett's (1991) term. Given such multiple overlapping systems, it would be possible for an individual's behavior to be motivated by several different, and perhaps even conflicting, motives simultaneously. Therefore, our model of human motivation is multidimensional.

Identifying Human Motives

Most evolutionary biologists define an *adaptation* as the end product of a historical process of evolution (Williams, 1966). As such, it should be evident that an adaptation has been "designed" (i.e., selected) for the purpose of increasing fitness. If an adaptation increases fitness, it should confer a survival and reproductive advantage on the organism and its offspring (Tooby & Cosmides, 1992). Most evolutionary psychologists do not model the human brain as a single adaptation that is designed to accomplish all tasks relating to fitness. Instead, they hold a view consistent with that expressed herein, that the brain consists of quasi-independent, function-specific modules (Gallistel, 1990; Hirshfeld & Gelman, 1994). Evolutionary psychologists expect an adaptation to be (a) universal (present in all people), (b) interactive (develop with exposure to certain environments), (c) complex (because evolution is "messy" and an adaptation may have been based in previous adaptations), and (d) economical (develop in a manner that does not waste energy; Schmitt & Pilcher, 2004).

We propose that human motives, whether adaptations or exaptations, are measurable as individual differences (variance) in the strength, desire, or concern about particular behavioral goals that solve fitness problems within the five social domains. In a lengthy deliberative process, we linked each of the domains to a "classic idea" in evolutionary theory (Mills, 2004) and used three criteria to identify putative motives and place each within the social domain where, we propose, it first developed. These criteria state that a motive should (a) be related to one of the five social domains, (b) represent a cluster of behaviors that solve problems of inclusive fitness within that specific domain, and (c) be measurable as individual differences in terms of strength of interest, desire, or concern with behaviors related to that motive. The following is the result of our deliberations, which are summarized in Table 1.

Self-protection. The first motives to develop were for self-protection and to promote the survival of the individual. Darwin (1859) proposed the concept of "natural selection" (or "survival selection") in which adaptations (in the present theory, motives) help the organism survive in a particular ecology. These motives depend on older structures located in the brain stem and diencephalon. We identified these motives as aggression, curiosity, and safety.4 Aggression is a method of obtaining power, and it can bring rewards and freedom (Keltner, Gruenfeld, & Anderson, 2003), both of which may increase survivability. Curiosity, as mentioned, facilitates exploration of the physical environment. Safety involves avoiding harm, submission, or, in less social species, simply withdrawing or recoiling.

Play is an exaptation of curiosity that directs behavior toward learning about the social environment, rules, reciprocity, and how people react and interact through mock aggressive situations. Therefore, play should provide an additional advantage in larger systems than should curiosity alone. *Health* is an exaptation of safety and promotes it by directing behavior toward goals supportive of organismic vitality and integrity, such as exercising, maintaining healthy nutrition, and obtaining appropriate medical care. The behaviors identified with the health motive are more adaptive on the larger system level (e.g., attending an exercise class or joining and effectively using a health maintenance organization) than those identified with safety.

Mating. Motives involved in the mating domain operate primarily on the dyadic system level. Darwin (1859) also proposed “sexual selection.” Sexual selection allows physical and mental traits to develop to attract mates or facilitate competition for them. The sex motive itself does not require the unstable or stable conscious processes of a large brain and can be observed in the highly hormonally regulated sexual activity of many species.

Kenrick et al. (2003) also called this domain “mate choice,” emphasizing differential parental investment. We subsume Kenrick et al.’s domain of “status” in this category, but we focus on the behaviors an individual engages in to *attract* a mate. That is in keeping with our goal of producing measurable human motives. Four exaptations of the sex motive involve enhancing status by improving one’s personal appearance (e.g., getting cosmetic surgery, wearing fragrance, or buying designer clothing); physique (e.g., exercising to become thinner or add bulk); display of wealth (e.g., driving an expensive automobile); or display of knowledge, talents, or abilities (e.g., obtaining advanced educational degrees). We call these four status motives, respectively, *appearance*, *physical*, *material*, and *mental*. We anticipate sex differences in the relative strength of status motives, depending on genetic as well as social and cultural influences. Evolutionary explanations of such differences have been the subject of much study (e.g., Buss, 2004) but are beyond the scope of the current analysis.

Relationship maintenance and parental care. The motives in this domain operate from the dyadic to the small-system level. Hamilton (1964, 1996) developed the concepts of kin selection and inclusive fitness. Inclusive fitness is increased through offspring raised by individuals in stable relationships who invest mutually in the offspring’s care. Relationship maintenance and parental care depend on the development of *affection*, behaving in a warm, supportive, and tender way toward others. Affection may be an exaptation of sex in social species with lengthy parental investment in offspring. The rewarding experience of orgasm may elicit warm and tender feelings toward one’s partner and may dispose partners to exchange more such feelings, thus aiding the development of affection. Affection requires a large brain and is dependent on stable conscious processes.

Coalition formation. These motives operate in large social systems primarily made up of nonkin. Trivers (1971, 1972) proposed that membership in nonkin groups (coalitions) could increase one’s own, and one’s kin’s, survivability through greater safety and shared resources, so long as mutually beneficial, reciprocal relationships are maintained and cheating is punished (social species may even develop a cognitive adaptation for cheater detection; see Cosmides & Tooby, 1992). The development of larger social systems is correlated with increased neocortex size (Dunbar, 1993), and it would take extensive stable conscious processes and autobiographical memories to successfully operate within large coalitions. Two motives aid coalition formation, increasing the likelihood of one’s kin and offspring surviving with support from a wider nonkin group: al-

TABLE 1. Social Problem Domains, 15 Putative Motives, Operational Definitions, and Evolutionary Goals

Social problem domain/motive	Operational definition: Individual differences in the strength of interest, desire, or concern with . . .	Evolutionary goal: The motive solves problems of . . .
Self-Protection		
Aggression	Being physically dominant, combative, intimidating others	Protecting oneself, kin, and coalition members
Curiosity	Exploring new things, places and situations; finding out about things, what they have to offer, and how they work	Understanding the physical environment in order to anticipate difficulties and protect oneself, kin, and coalition members
Safety	Being safe and secure in, and vigilant about, one's person and surroundings	Securing one's person, territory, and possessions (and later kin and coalition members) against hostile forces
Play	Spontaneous or speculative activity; sportive, frivolous, mocking, or jesting behavior with others; free, unimpeded, stylish, or humorous interpersonal activity	Understanding the social environment, rules, reciprocity, and how people act, react, and interact through nonaggressive, mock situations
Health	Remaining healthy and fit; improving one's health and fitness	Protecting one's physical integrity
Mating		
Sex	Sexual activity; obtaining a desirable sexual partner	Genetic propagation
Appearance	Improving one's physical appearance, grooming, and wardrobe; cosmetic attractiveness	Increasing status and desirability as a mate by appearing physically attractive
Material	Acquiring assets; material competitiveness	Increasing status and desirability as a mate by accumulating material resources
Mental	Developing one's knowledge, skills, and talents; nonathletic competition, such as academics, games, arts, crafts, and hobbies	Increasing status and desirability as a mate by appearing smart and talented

Physical	Developing one’s physical strength or endurance; athletic competitiveness	Increasing status and desirability as a mate by appearing strong and dominant
Relationship maintenance & parental care		
Affection	Tender attachment to others	Forming and maintaining cooperative alliances, maintaining relationships, and caring for young
Coalition formation		
Altruism	Assisting others without self-benefit and possibly to one’s personal detriment	Forming and maintaining cooperative alliances
Conscience	Doing what is legally, morally, and ethically prescribed; maintaining the traditions and rules of social interaction; reciprocity	Forming and maintaining cooperative alliances and maintaining relationships
Memetic		
Legacy	The commonwealth; making a lasting contribution, a better world for the next generation; leaving something of lasting value behind	Forming and maintaining broader (even symbolic) cooperative alliances in order to produce a general social–cultural–community environment better suited to survival of kin and nonkin
Meaning	Constructing a personal philosophy, meaning, or purpose for life	Explaining (rationalizing) one’s existence and nonexistence

Note. The social problem domains were adapted from “Dynamical Evolutionary Psychology: Individual Decision Rules and Emergent Social Norms,” by D. T. Kenrick, N. P. Li, and J. Butner, 2003, *Psychological Review, 110,* p. 3. Adapted with permission of the author.

truism, assistance provided others without obvious self-benefit; and conscience, doing what is prescribed and entering into reciprocal arrangements, where cheater detection allows the development of necessary trust.

Altruism has been a much-discussed topic in evolutionary psychology, and there may be different types. Hamilton (1964) proposed "kin altruism," wherein inclusive fitness is increased through offspring raised by individuals in stable relationships who invest mutually in the offspring's care. In the present theory, kin altruism is incorporated in the previously described affection motive within the relationship maintenance–parental care domain. More recently, Bowles and Gintis (2003) and Gintis et al. (2003) have proposed an altruism based on "strong reciprocity," which goes beyond Trivers' (1971) "reciprocal altruism." *Strong reciprocity* is a supposed predisposition to cooperate with others, obey norms, and punish those who violate them, even when it has a personal cost. They support their proposal with evidence from a series of behavioral experiments (see Gintis et al. for a review) and suggest that "the same behaviors are regularly described in everyday life, for example, in wage setting by firms, tax compliance, and cooperation in the protection of local environmental public goods" (Gintis et al., p. 153).

Memetic. These motives operate on the level of systems that are very large indeed, to the extent that some of these systems may exist only symbolically, as in all the perceived members of one's ethnic, linguistic, or religious group. Individual members could not possibly be acquainted with all other members of such large groups, but they share a symbolic, abstract sense of mutual affiliation. Memes may allow such large systems to develop, which is why we called this social domain *memetic*.

Dawkins (1989) suggested that genes are not the only replicators. *Memes*—the mental representations of ideas, concepts, frames of reference, and perspectives—can also replicate by "infecting" the brains of people who are in contact. He proposed that memes are also subject to evolutionary change according to many of the same principles that apply to genes. Blackmore (1999) is one of the strongest proponents of the gene–meme analogy, going so far as to claim that memes drive the evolution of the brain-mind. There is, however, a difference of opinion over just how far this analogy can be taken (Aunger, 2000). Gil-White (2004) assumed a more balanced perspective, arguing that the concept of the replicating "selfish meme" is wrong and unnecessary but that memes are still subject to Darwinian analysis.

We propose that stable conscious processes allow human beings to share internalized representations of very large systems or "symbolic" groups. Shared representations may be necessary for a sense of affiliation among nonkin to develop. Memetic motives are dependent on the cultural transmission of memes to minds that have adapted—developed a facility—for them (Gil-White, 2004). The memetic motive category is highly speculative at this point, and it is difficult to determine whether there are none, one, two, or possibly more. For heuristic purposes, we have defined two: *legacy* and *meaning*.

Legacy motivates behavior in directions that promote survival of the broader group or culture. A culture is maintained through dissemination of memes that invest individual minds with shared notions of membership in a kinship broader than one's own genes would allow. The concept of patriotism and the notion of "honor" that motivates dying for one's god, country, or cause would be examples of legacy. Presumably, the relative strength of both safety and legacy motives is involved in such an action. Another example of legacy would be donating money to a university. The university might be viewed as an institution (a very large system) that perpetuates values with which the donor agrees. There is no direct benefit to the donor (or his or her kin) of educating the offspring of others (i.e., increasing *their* mental status), yet people can be persuaded to donate resources that might otherwise go to their own kin to assist the education of others' kin, "for the greater good" of society.

Meaning is engaging in behavior as an attempt to construct meaning in or for one's life, and we speculate it would be an outcome of awareness of mortality. Although it has been argued that chimpanzees have a "theory of mind" akin to self-awareness (Gallup, 1979), it is by no means established (Heyes, 1998). However, even if one or more other species do have a theory of mind, awareness of mortality may be unique to human beings. In fact, awareness of mortality may absolutely depend on the development of a large brain with extensive working memory, autobiographical conscious processes, and the ability to project a future (in this case, the end of one's future or the construct of an afterlife). In such a brain, a motive to construct meaning may serve as an adaptive antidote to despair in the face of certain knowledge of personal mortality. Meaning may keep stable conscious processes going when they contain the knowledge of their own termination.

Meaning-motivated behavior might be evident in sacrificing for others (such as a physician volunteering for Doctors Without Borders—altruism?) or producing a lasting creative product (such as an architect who designs an impressive building or an author who writes best-selling or prize-honored works—legacy?). However, we propose a specific motive of meaning to include situations in which activities are motivated primarily by a desire to give one's finite existence meaning. This would also capture activities that are not closely related to existing motives. Such other meaning-motivated activities may include the belief in or practice of religion (in fact, all religions, as repositories and broadcasters of cultural concepts, may be conceived of as specific-meaning memes—they provide "prepackaged" answers to seekers of meaning). Others may engage in meaning-motivated knowledge, seeking activities of a more secular nature, such as a scientist who tries to understand the foundational principles of the universe. The meaning motive is intended to capture the strength of interest, desire, or concern with the business of finding or creating meaning for one's life within a very large, symbolic system.

A recent example of how the deaths of soldier heroes are treated may tell us something about our culture's legacy and meaning motives (and the memes that shape them). On April 23, 2004, U.S. Army soldier Pat Tillman was killed in action in Afghanistan. His death drew much attention in Arizona, where he played football for the Cardinals before giving up a 3-year, multimillion-dollar contract 7 months after the September 11, 2001, attacks to join the U.S. Army Rangers. The *Arizona Republic* devoted many column inches to the story and ran an excerpt from U.S. Senator John McCain's (2004) book *Why Courage Matters: The Way to a Braver Life*. The reporter said Tillman "felt a sense of duty, of obligation—qualities so rare that it was difficult for many people at the time to fully grasp that they were in fact his real reasons" (MacEachern, 2004, p. V2). Tillman was compared to a hero of the Vietnam War, Special Forces Master Sergeant Roy Benavidez, who struggled with multiple life-threatening injuries for 6 hr to save his fellow soldiers in 1968. Certain common traits were ascribed to both these heroes: modesty, bravery, self-sacrifice, and patriotism. We do not mean to diminish their true acts of bravery but, rather, to study how these acts are construed and replicated as motives for subsequent generations. Perhaps these are legends in the making, and a legend is a meme. As far as meaning is concerned, these words suggest Tillman's sacrifice was almost a religious act: "[S]ome heroes . . . might have led less than admirable lives. . . . The stories cherished most by all *sinners* [italics added] whose consciences are not permanently mute concern the *life-redeeming* [italics added] act of courage" (MacEachern, p. V2). Tillman was posthumously awarded the Silver Star for fighting to rescue his comrades "without regard for his personal safety" (MacEachern, p. V2), which also sounds like altruism. This reflects the culture's meme of what altruism is, helps reinforce it through modeling (i.e., social recognition and reward), and suggests it as a potential path to meaning.

The Role of Learning

Whatever the selection pressures on these putative motive adaptations (and exaptations), they may be modified from the outset—even at the cellular level (Oyama, 1991)—through interaction with the organism's present environment. Therefore, motives should be subject to modification through the principles of classical and operant conditioning, and learning should increase variance (individual differences) in motives. Also, in keeping with our emphasis on transconscious processes, we note that learning can take place at all levels of consciousness, including nonconscious processes. Empirical evidence demonstrates covert or nonconscious learning in humans (Morris, Öhman, & Dolan, 1998), and, in at least one case, learning has occurred without the participation of cortical or limbic structures, that is, without the involvement of some of the structures necessary for unstable or stable consciousness (Tranel & Damasio, 1993). In their review of studies of the nonconscious acquisition of information, Lewicki, Hill, and Czyzewska (1992) concluded, "Most of the 'real work,' both in the acquisition of cognitive procedures and skills and in the execution of cognitive operations, such as encoding and interpretation of stimuli, is being done at the level to which our consciousness has no access" (p. 800).

Relationships Between Motives and Goals

We set out to identify 15 human motives using specific evolutionary criteria. In our deliberations, we attempted to restrict the motives to the fewest number that could serve each social domain. Chulef, Read, and Walsh (2001) used a different approach to identify a taxonomy of human goals. They defined *goals* as "stable, higher-order entities that function as abstract, organizing structures . . . [that] remain fairly stable over time . . . and play a crucial role in . . . predicting behavior" (p. 192). This definition of goals appears very similar to our concept of motives as guiding purposeful behavior, although Chulef et al. did not link goals or goal development to any explanatory theory such as natural selection and inclusive fitness.

Chulef et al. (2001) combed the psychological literature and used a deliberative process to identify 135 specific human goals. They then had three samples of research participants sort the goals objectively, "leaving their own values aside" and sorting "on the basis of how similar the goals are to one another" (p. 205). A series of cluster analytic solutions was obtained, with the best solution for the combined samples yielding a 30-cluster solution of the 135 initial items. The researchers then generated labels for the clusters based on a logical face analysis of the items in the category. These goal clusters are strikingly similar to the motives in the present theory. Table 2 presents the specific goals and cluster labels that appear on their face to be related to the hypothesized motives. Twenty-three of the 30 goal clusters appear closely related to 14 of the proposed motives. The only motive for which we could identify no related goals was aggression, which is perhaps the most socially undesirable of the motives.

One of the clusters of human goals found by Chulef et al. (2001) appears to us not to be goals at all but rather to capture what we are calling self-control. Identified as "Self-sufficiency & Self-determination" (p. 207), this cluster comprises "being logical, being practical, being reflective, being disciplined, being self-sufficient, and [having] own guidelines." Although these might be described as goals to which some people strive, they also appear to reflect our notion of adaptive delay of gratification.

The lexical approach to trait taxonomic research used by Chulef et al. (2001) has a long and fruitful history in psychology (John, Angleitner, & Ostendorf, 1988). However, before we ascribe too much importance to the convergence of these goals and the present motives, we must recognize that there is a tautology here. Language and culture constrain both the goals used in the lexical cluster analysis and the deliberative process we used to identify the

TABLE 2. Comparison of Related Human Motives and Goals

Social problem domain/motive	Goal cluster label	Specific goal
Self-Protection		
Aggression		[No goals appeared to match this motive]
Curiosity	Creativity	Being curious; novel ideas; being creative
	Flexibility, openness, & excitement	Taking risks; flexibility; being unique; being able to fantasize; being passionate; being innovative; exploring; (having) different experiences; (having an) exciting life; being spontaneous
Safety	Stability & safety	(Having an) easy life; feeling safe; being conventional; (having) stability; (overcoming) life's limitations; overcoming failure; being private
Play	Entertainment	Hobbies; being carefree; being playful
Health	Physical health	Looking fit; (having good) nutrition; exercising; physical fitness; physical ability
Mating		
Sex	Sex & romance	Feeling meshed; attracting (others) sexually; (having an) erotic relationship; (having) sexual experience; being in love; (having) romantic experiences; (having) mature romantic (experiences)
Appearance	Physical appearance	Looking distinguished; looking young; being good looking; (being) fashion(able)
Material	Finances	Descendants; (paying) bills; (having) money; buying things
Mental	Intellect & education	(Having) intellectual conversations; thinking intellectually; being intelligent; (having) educational degree(s); (having an) education
	Aesthetics	(Appreciating) world beauty; learning art; (appreciating) arts

Physical	Physical health	Looking fit; (having good) nutrition; exercising; physical fitness; physical ability
Relationship maintenance & parental care		
Affection	Marriage	(Having a) good marriage; (having a) close spouse
	Family	Providing (for) family; (being a) good parent; (having) close children; (having a) stable family life; (receiving) help from family; living close to family; feeling close to family; taking care of family
	Friendship	Sharing feelings; having friends; being affectionate
	Receiving from others	(Being or feeling) cared for; (having a) mentor; (having) others to rely (on); (receiving) support from others
Coalition formation		
Altruism	Social awareness	(Giving to) charity; (making a) contribution; (giving to a good) cause; seeking equality; seeking justice; seeking fairness
Conscience	Defense versus rejection	Avoiding rejection; defense versus criticism
	Positive social qualities	Being respected; (having) others' trust; being honest
	Ethics & idealism	(Being) ethical; (having) firm values; pursuing ideas
Memetic		
Legacy	Teaching & helping others	Setting examples; helping others; teaching (others); (having) control of (the) environment
Meaning	Religion	Achieving salvation; (having or respecting) religious traditions; pleasing God; (having) religious faith
	Higher meaning	Finding higher meaning
	Personal growth	(Having) mental health; (having) peace of mind; (having) self-esteem; (being) content with myself; knowing myself; (having) wisdom; (having a) mature understanding

Note. Specific goals from, “A hierarchical taxonomy of human goals,” by A. S. Chulef, S. J. Read, and D. A. Walsh, 2001, *Motivation and Emotion, 25,* p. 191; words in parentheses were added for readability. Adapted with permission of the author.

motives. Therefore, there can be no claim of construct validity. Nevertheless, the high degree of convergence suggests that the motives we identified on the basis of evolutionary theory are also recognizable as everyday goals by samples of nonpsychologists.

Relationships Between Motives and Emotion

Core affect should be closely related to four motives purported to arise on the nonconscious level: aggression, curiosity, safety, and sex. Although Russell (2003) preferred the two-dimensional (pleasure–displeasure and activation–deactivation) description, other researchers (e.g., Izard, 1991; Plutchik, 2003) have used the categorical approach of assigning specific labels for emotional experiences. In reviewing categorical theories, we noted there may be face-valid relationships between three of the four motives we have associated with nonconscious processes and seven emotions that are present by 6 months of age (Lewis, 1995), well before any significant conscious cognitive development, including self-awareness. These relationships include (a) surprise, interest, and joy with curiosity; (b) anger and sadness with aggression; and (c) fear and disgust with safety. The fourth motive arising at the level of nonconscious processes, sex, may require the complex interaction of later hormonal processes of puberty to mature fully; therefore, it does not make sense to try to link sex to emotions at 6 months of age.

There may be other face-valid relationships between the same three motives and Panksepp's (1998) major genetically coded emotional systems, including (a) the fear system, with safety; (b) the seeking system, with curiosity; and (c) the rage system, with aggression. Again, no claim can be made for the construct validity of these motives based on these apparent relationships, but they are intriguing to consider for future research.

CONCLUSION

Biological (instinct) and behavioral theories of motivation were available very early in the history of psychology and were heuristic in their time. More recently, cognitive theories of motivation have been proposed. These theories have also encouraged prolific research activity (e.g., Bem, 1967; Carver & Scheier, 1981, 1998; Deci, 1975; Deci et al., 1999; Deci & Ryan, 1987; Hebb, 1949; McClelland et al., 1976; Oettingen et al., 2004; Silvia & Duval, 2004). However, none of these theories takes a multidimensional approach to human motivation, nor does any attempt to explain the basis for the existence of motivated human behavior in the first place.

In this article, we have proposed an evolutionary—hence adaptational—basis for human motivation. We have laid out the rationale for proposing an evolutionary theory of human motivation and described some of the neuropsychological bases for motivational and emotional processes that may have resulted from selection pressures. We have proposed that these processes reside in adaptive mental mechanisms that have arisen to guide human behavior toward the general goal of inclusive fitness. We also proposed that individual differences in human motives would be measurable as individual differences in the strength, desire, or concern about particular goals that solve fitness problems within five social domains.

We are not the first to propose a multidimensional model of human motivation. Decades ago, Cattell and his colleagues (Cattell, 1957; Cattell, Horn, Sweney, & Radcliffe, 1964; Cattell, Radcliffe, & Sweney, 1963) proposed a multidimensional model that was developed empirically through factor analysis. However, that model was not informed by evolutionary psychology, and there are problems with the way the motives were measured (Bernard, Walsh, & Mills, 2005). A more recent multidimensional model is based on Sensitivity Theory (Reiss, 2000; Reiss & Havercamp, 1996, 1997, 1998). This model defines a "*fundamental motive* . . . as a universal end goal that accounts for psychologically significant behavior" (Reiss & Havercamp, 1998, p. 98). It incorporates 15 or 16 motives that were also identified empirically by exploratory factor analysis.

Both of these multidimensional models deal with proximal but not ultimate causality—the "how" but not the "why"—of motivated behavior. In addition, empirically derived factor analytic models have no theoretical basis for determining how many motives there are, whether motives are independent or related, and which particular adapted modules of the human brain mediate them. Chulef et al.'s (2001) empirical study of goals, as described earlier, presents the same problem of attempting to identify (discover, actually) the dimensions of behavior using empirical methods alone. Without evolutionary theory, how do we know which is a better way to parse human motivation—30 goals (Chulef et al.) or 15 to 16 basic needs (Reiss, 2000)?

In contrast, the present evolutionary theory may be used to predict how many motives there should be—15—in human behavior. It also predicts that the motives will be relatively independent of one another because each should be mediated by a separate mental module that developed to solve specific fitness problems. The theory provides operational definitions for each motive based on behaviors that solved specific fitness problems in these specific environments of evolutionary adaptedness. It links these motives to social domains and links the domains in a hierarchical manner to increasing size and complexity of social systems and the increasing size and complexity of the brain. It suggests specific brain regions that may have evolved to mediate specific motives through transconscious processes. The transconscious processes encompass the kind of proximal processes that interest cognitive motivational psychologists and neuropsychologists today. These processes are the emergent property of neuropsychological structures that result from a strong historical and proximate interaction of genes and environments. As adapted, these structures can account for culture as well (Tooby & Cosmides, 1992). These motivational adaptations are subject to modification through classical and operant conditioning. Learning should increase individual differences in the manner in which adapted motives are expressed. Although the motives should be universal, because of learning, there should be differences in the specific motivated behaviors in which individuals engage in specific social environments (and cultures). Finally, the theory incorporates a functional role for emotions and self-control, both of which are presumed to have evolved because they have increased the fitness advantages of motivated behavior.

We believe that this theory will be heuristic and that it lends itself particularly well to verification. In fact, we envision a multistage research program that could ultimately lead to acceptance of the theory. First, the operational definitions of the 15 motives presented in Table 1 can be used to develop an individual-differences measure of the motive constructs. It should be possible to demonstrate that the psychometric properties of such a measure are sound—that the 15 constructs are homogeneous, reliable, and independent, as the theory predicts. Second, confirmatory factor analysis should be used to establish the 15-motive model predicted by the theory. Third, the validity of the motives should be demonstrated in two ways: (a) the motive constructs should have convergent and discriminant validity with respect to other measures of motivation, personality, cognitive functioning, vocational preferences, values, and the like; and (b) behavioral predictions could be made and tested for each motive within its specific social domain (i.e., the material motive should correlate more highly than affection with the effort, time, etc., individuals actually expend to acquire material resources). Fourth, predictions concerning activation within certain neural circuits believed to mediate the strength of a specific motive in transconscious processes could be made and tested (e.g., individuals scoring high on a particular motive construct would be stimulated by cognitively challenging content relating to it, with increased activation of particular neural circuits, but not others, predicted and measured by PET). Once the motives are reliably and validly measured, subsequent research can explore the predicted function of self-control and emotional if–then searching. Eventually, the fruits of such a research program should permit reliable and valid predictions of future purposeful behavior based on complex multidimensional profiles of these motives, offering new opportunities to test evolutionary psychological theories in general.

NOTES

1. Many psychologists, even today, were not exposed to evolutionary psychology in graduate school and may have conceived of it before Hamilton (1964, 1996) introduced inclusive fitness, which increased the explanatory power of evolutionary psychology with respect to social behavior. Leger et al. (2001) identified and addressed five misunderstandings that have contributed to the criticism of evolutionary psychology. Although too lengthy to describe here, we concur with their analysis and believe that some of the harshest criticisms of evolutionary psychology have come from a basic misperception of it.

2. Courting, retaining a mate, and investing resources in raising offspring, certainly factors in inclusive fitness of human beings, are not so for many species. However, we are

proposing a theory to account for human motivation, so, although it rests on basic cross-species evolutionary processes, the theory must necessarily include factors that apply exclusively to human beings and perhaps other primates as well.

3. Shermer (2004) recently arrived at a similar proposal for the origin and development of ethical behavior he called the "Bio-Cultural Evolutionary Pyramid." It is constructed like Maslow's (1968, 1970) hierarchy of needs. However, Shermer's pyramid has seven levels: the individual, the family, the extended family, the community, the society, the species, and the biosphere. Although not made explicit, like the present model, each level involves a larger social system. In addition, each level involves a specific evolutionary "concern," such as self-survival at the individual level and different "needs," which resemble motives but are not operationally defined.

4. The labels we have used for the motive were chosen for their ability to describe human behavior. However, many of these same motives, whatever name they are given, apply to other species as well. For example, what we are calling aggression in the behavior of human beings may be represented in a single cell organism's competitive active scouring of its local environment to acquire nutrients necessary for its own survival. Other labels could have been applied; for example, some may judge "dominance" to be a better label for the category of behaviors we have called "aggression." Therefore, we treat the labels as tentative and expect them to undergo some revision as the underlying motive constructs are better identified. In addition, we note that the behaviors represented by these constructs should be heavily influenced by the proximal environment and culture and that our initial work is bound by the culture and language in which it is done. However, the evolutionary foundation of the theory would predict that the motive constructs, as adaptive mental mechanisms, should appear cross-culturally in a species. For example, we expect the material motive to be found in diverse human groups, whereas the surface-level behavior and interests it influences, its specific expression, will vary.

REFERENCES

American Psychological Society. (2003, March). "Unforgettable" classics: Classic psychology texts stand the test of time. *Observer*, *16*, 1–26.

Aston-Jones, G., Ennis, M., Pieribone, V. A., Nickell, W. T., & Shipley, M. T. (1986). The brain nucleus locus coeruleus: Restricted afferent control of a broad efferent network. *Science*, *234*, 734–737.

Aunger, R. (2000). Introduction. In R. Aunger (Ed.), *Darwinizing culture: The status of memetics as a science* (pp. 1–24). Oxford, England: Oxford University Press.

Avital, E., & Jablonka, E. (1994). Social learning and the evolution of behaviour. *Animal Behaviour*, *48*, 1195–1199.

Baaré, W. F. C., Hulshoff Pol, H. E., Boomsma, D. I., Posthuma, D., de Geus, E. J. C., Schnack, H. G., et al. (2001). Quantitative genetic modeling of variation in human brain morphology. *Cerebral Cortex*, *11*, 816–824.

Baars, B. (1988). *A cognitive theory of consciousness*. Cambridge, England: Cambridge University Press.

Baars, B. J. (2001). There are no known differences in brain mechanisms of consciousness between humans and other mammals. *Animal Welfare*, *10*, S31–S40.

Baddeley, A. (1992). Working memory. *Science*, *255*, 556–559.

Ballard, D. H. (1997). *An introduction to natural computation*. Cambridge, MA: MIT Press.

Bandler, R., & Shipley, M. T. (1994). Columnar organization in the midbrain periaqueductal gray: Modules for emotional expression? *Trends in Neurosciences*, *17*, 379–389.

Bandura, A. (1977). *Social learning theory*. Englewood Cliffs, NJ: Prentice-Hall.

Barber, T. X. (1996). Restrictive versus open paradigms in comparative psychology [Comment]. *American Psychologist*, *51*, 58–59.

Bartley, A. J., Jones, D. W., & Weinberger, D. R. (1997). Genetic variability of human brain size and cortical gyral patterns. *Brain*, *120*, 257–269.

Baumeister, R. F., & Heatherton, T. F. (1996). Self-regulation failure: An overview. *Psychological Inquiry*, *7*, 1–15.

Bechara, A., Damasio, A. R., Damasio, H., & Anderson, S. W. (1994). Insensitivity to future consequences following damage to human prefrontal cortex. *Cognition*, *50*, 7–15.

Bechara, A., Damasio, H., & Damasio, A. R. (2000). Emotion, decision making, and the orbitofrontal cortex. *Cerebral Cortex*, *10*, 295–307.

Bechara, A., Damasio, H., Tranel, D., & Damasio, A. R. (1997). Deciding advantageously before knowing the advantageous strategy. *Science*, *275*, 1293–1295.

Bechara, A., Tranel, D., Damasio, H., & Damasio, A. R. (1996). Failure to respond autonomically to anticipated future outcomes following damage to prefrontal cortex. *Cerebral Cortex*, *6*, 215–225.

Beggs, J. M., Brown, T. H., Byrne, J. H., Crow, T., LeDoux, J. E., LeBar, K., et al. (1999). Learning and memory: Basic mechanisms. In M. J. Zigmond, F. E. Bloom, S. C. Landis, J. L. Roberts, & L. R. Squire (Eds.), *Fundamentals of neuroscience* (pp. 1411–1454). San Diego, CA: Academic Press.

Bekoff, M. (2002). Animal reflections. *Nature*, *419*, 255.

Bem, D. (1967). Self-perception: An alternative explanation of cognitive dissonance phenomena. *Psychological Review*, *74*, 183–200.

Berlyne, D. E. (1970). Novelty, complexity, and hedonic value. *Perception and Psychophysics*, *8*, 279–286.

Bermond, B. (2001). A neuropsychological and evolutionary approach to animal consciousness and animal suffering. *Animal Welfare*, *10*, S47–S62.

Bernard, J. F., & Bandler, R. (1998). Parallel circuits for emotional coping behaviour: New pieces in the puzzle. *The Journal of Comparative Neurology*, *401*, 429–436.

Bernard, L. C., Walsh, R. P., & Mills, M. (2005). *The Motivation Analysis Test: A contemporary empirical evaluation*. Manuscript submitted for publication.

Blackmore, S. (1999). *The meme machine*. Oxford: Oxford University Press.

Blumberg, M. S., & Sokoloff, G. (2003). Hard heads and open minds: A reply to Panksepp (2003) [Comment]. *Psychological Review*, *110*, 389–394.

Blumberg, M. S., & Wasserman, E. A. (1995). Animal mind and the argument from design. *American Psychologist*, *50*, 133–144.

Bogen, J. E. (1995). On the neurophysiology of consciousness: I. An overview. *Consciousness and Cognition*, *4*, 52–62.

Bookstein, F., Schäefer, K., Prossinger, H., Seidler, H., Fieder, M., Stringer, C., et al. (1999). Comparing frontal cranial profiles in archaic and modern *Homo* by morphometric analysis. *Anatomical Record* (*New Anatomist*), *257*, 217–224.

Boring, E. G. (1950). *A history of experimental psychology* (2nd ed.). Englewood Cliffs, NJ: Prentice-Hall.

Bower, G. H., & Clark, M. C. (1969). Narrative stories as mediators of serial learning. *Psychonomic Science*, *14*, 181–182.

Bowles, S., & Gintis, H. (2003). Explaining altruistic behavior in humans. *Evolution and Human Behavior*, *24*, 153–172.

Braver, T. S., Cohen, J. D., & Barch, D. M. (2002). The role of the prefrontal cortex in normal and disordered cognitive control: A cognitive neuroscience perspective. In D. T. Stuss & R. T. Knight (Eds.), *Principles of frontal lobe function* (pp. 428–448). Oxford, England: Oxford University Press.

Bugental, D. B. (2000). Acquisition of the algorithms of social life: A domain-based approach. *Psychological Bulletin*, *126*, 187–219.

Buss, D. (2004, May). Dyadic antagonistic coevolution: Reciprocal evolutionary changes within a single species between the sexes. In H. L. Roediger III (Chair), *The new biological bases of behavior*. Symposium conducted at the meeting of the American Psychological Society, Chicago, IL.

Buss, D. M., Haselton, M. G., Shackelford, T. K., Bleske, A. L., & Wakefield, J. C. (1995). Adaptations, exaptations, and spandrels. *American Psychologist*, *53*, 533–548.

Cacioppo, J. T., Klein, D. J., Berntson, G. C., & Hartfield, E. (1993). The psychophysiology of emotion. In M. Lewis & J. M. Haviland (Eds.), *Handbook of emotions* (pp. 119–142). New York: Guilford Press.

Carver, C. S., & Scheier, M. F. (1981). *Attention and self-regulation: A control theory approach to human behavior*. New York: Springer-Verlag.

Carver, C. S., & Scheier, M. F. (1998). *On the self-regulation of behavior*. New York: Cambridge University Press.

Cattell, R. B. (1957). *Personality and motivation structure and measurement*. New York: Harcourt Brace Jovanovich.

Cattell, R. B., Horn, J. L., Sweney, A. B., & Radcliffe, J. A. (1964). *Handbook for the Motivation Analysis Test*. Champaign, IL: Institute for Personality and Ability Testing.

Cattell, R. B., Radcliffe, J. A., & Sweney, A. B. (1963). The nature and measurement of components of motivation. *Genetic Psychological Monographs*, *68*, 49–211.

Chulef, A. S., Read, S. J., & Walsh, D. A. (2001). A hierarchical taxonomy of human goals. *Motivation and Emotion*, *25*, 191–230.

Clément, F., & Malerstein, A. J. (2003). What is it like to be conscious? The ontogenesis of consciousness. *Philosophical Psychology*, *16*, 67–85.

Collins, A. M., & Loftus, E. F. (1975). A spreading activation theory of semantic processing. *Psychological Review*, *82*, 407–428.

Corkin, S., Amaral, D. G., Gonzalez, R. G., Johnson, K. A., & Hyman, B. T. (1997). H. M.'s medial temporal lobe lesion: Findings from magnetic resonance imaging. *Journal of Neuroscience*, *17*, 3664–3979.

Cosmides, L., & Tooby, J. (1992). Beyond intuition and instinct blindness: Toward an evolutionarily rigorous cognitive science. *Cognition*, *50*, 41–77.

Craik, F. I. M., Moroz, T. M., Moscovitch, M., Stuss, D. T., Winocur, G., Tulving, E., et al. (1999). In search of the self: A positron emission tomography study. *Psychological Science*, *10*, 26–34.

Daly, M., & Wilson, M. (2001). Risk-taking, intrasexual competition, and homicide. In J. A. French, A. C. Kamil, & D. W. Leger (Eds.), *Nebraska Symposium on Motivation: Vol. 47. Evolutionary psychology and motivation* (pp. 1–36). Lincoln: University of Nebraska Press.

Damasio, A. (1994). *Descartes' error*. New York: Avon Books.

Damasio, A. (1999). *The feeling of what happens: Body and mind in the making of consciousness*. San Diego, CA: Harcourt.

Damasio, A. (2001, October 25). Fundamental feelings. *Nature*, 781.

Damasio, A. (2004, May). Antonio Damasio's theory of thinking faster and faster: Are the brain's emotional circuits hardwired for speed? *Discover*, *24*, 44–49.

Darwin, C. (1859). *On the origin of species*. London: J. Murray.

Davidson, R. J. (2000a). Affective style, psychopathology, and resilience: Brain mechanisms and plasticity. *American Psychologist*, *55*, 1196–1214.

Davidson, R. J. (2000b). The functional neuroanatomy of affective style. In R. D. Lane & L. Nadel (Eds.), *Cognitive neuroscience of emotion* (pp. 371–388). New York: Oxford University Press.

Dawkins, R. (1989). *The selfish gene*. Oxford, England: Oxford University Press.

Deci, E. (1975). *Intrinsic motivation*. New York: Plenum.

Deci, E., Koestner, R., & Ryan, R. (1999). A meta-analytic review of experiments examining the effects of extrinsic rewards on intrinsic motivation. *Psychological Bulletin*, *125*, 627–668.

Deci, E., & Ryan, R. (1987). The support of autonomy and the control of behavior. *Journal of Personality and Social Psychology*, *53*, 1024–1037.

Dennett, D. C. (1991). *Consciousness explained*. Boston: Little, Brown.

de Waal, F. B. M. (2002). Evolutionary psychology: The wheat and the chaff. *Current Directions in Psychological Science*, *11*, 187–191.

Donald, M. (1997). Precis of origins of the modern mind: Three stages in the evolution of culture and cognition. *Behavioral and Brain Sciences*, *16*, 737–791.

Dunbar, R. I. M. (1993). Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences*, *16*, 681–735.

Duval, S., & Wicklund, R. A. (1972). *A theory of objective self-awareness*. Oxford, England: Academic Press.

Evans, D. (2002). The search hypothesis of emotion. *British Journal of the Philosophy of Science*, *53*, 497–509.

Fairchild, H. H. (1991). Scientific racism: The cloak of objectivity. *Journal of Social Issues*, *47*, 101–115.

Fell, J., Klaver, P., Elger, C. E., & Fernandez, G. (2002). The interaction of rhinal cortex and hippocampus in human declarative memory formation. *Reviews in the Neurosciences*, *13*, 299–312.

Filskov, S. B., & Boll, T. J. (1981). *Handbook of clinical neuropsychology*. New York: Wiley-Interscience.

Frijda, N. H. (1994). Emotions are functional, most of the time. In P. Ekman & R. J. Davidson (Eds.), *The nature of emotion: Fundamental questions. Series in affective science* (pp. 112–122). New York: Oxford University Press.

Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.

Gallup, G. G. (1979). Self-awareness in primates. *American Scientist*, *67*, 417–421.

Gangestad, S. W. (2001). Adaptive design, selective history, and women's sexual motivations. In J. A. French, A. C. Kamil, & D. W. Leger (Eds.), *Nebraska Symposium on Motivation: Vol. 47. Evolutionary psychology and motivation* (pp. 37–74). Lincoln: University of Nebraska Press.

Gärdenfors, P. (1996). Cued and detached representations in animal cognition. *Behavioural Processes*, *35*, 263–273.

Gil-White, F. J. (2004). Common misunderstandings of memes (and genes): The promise and the limits of the genetic analogy to cultural transmission processes. *Behavioral and Brain Sciences*. Retrieved March 10, 2004, from http://www.bbsonline.org/documents/a/00/00/12/44/bbs00001244-00/Memes2.htm

Gintis, H., Bowles, S., Boyd, R., & Fehr, E. (2003). Explaining altruistic behavior in humans. *Evolution and Human Behavior*, *24*, 153–172.

Goldman-Rakic, P. S., Scalaidhe, S., & Chafee, M. (2000). Domain specificity in cognitive systems. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (pp. 733–742). Cambridge, MA: MIT Press.

Gray, J. R. (2001). Emotional modulation of cognitive control: Approach–withdrawal states double-dissociate spatial from verbal two-back task performance. *Journal of Experimental Psychology: General*, *130*, 436–452.

Gray, J. R. (2004). Integration of emotion and cognitive control. *Current Directions in Psychological Science*, *13*, 46–48.

Gray, J. R., Braver, T. S., & Raichle, M. E. (2002). Integration of emotion and cognition in the lateral prefrontal cortex. *Proceedings of the National Academy of Sciences, USA*, *99*, 4115–4120.

Haier, R. J., White, N. S., & Alkire, M. T. (2003). Individual differences in general intelligence correlate with brain function during nonreasoning tasks. *Intelligence*, *31*, 429–441.

Hameroff, S. R., Kaszniak, A. W., & Scott, A. C. (Eds.). (1996). *Towards a science of consciousness: The first Tucson discussions and debates*. Cambridge, MA: MIT Press.

Hamilton, W. D. (1964). The genetical evolution of social behavior. *Journal of Theoretical Biology*, *7*, 1–52.

Hamilton, W. D. (1996). *Narrow roads of gene land: Vol. 1. Evolution of social behavior*. Oxford, England: W. H. Freeman.

Hebb, D. O. (1949). *The organization of behavior: A neuropsychological theory*. New York: Wiley.

Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, *21*, 101–134.

Hirshfeld, L. W., & Gelman, S. A. (1994). *Mapping the mind: Domain specificity in cognition and culture*. New York: Cambridge University Press.

Holt, E. B. (1931). *Animal drive and the learning process*. New York: Holt.

Hull, C. L. (1943). *Principles of behavior*. New York: Appleton-Century-Crofts.

Izard, C. E. (1991). *The psychology of emotions*. New York: Plenum Press.

Jacobs, L. F., & Schenk, F. (2003). Unpacking the cognitive map: The parallel map theory of hippocampal function. *Psychological Review*, *110*, 285–315.

James, W. (1890). *Principles of psychology*. New York: Holt.

Jaynes, J. (1976). *The origins of consciousness in the breakdown of the bicameral mind*. Boston: Houghton Mifflin.

Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, *17*, 187–245.

Jeffries, K. J., Fritz, J. B., & Braun, A. R. (2003, April). Words in melody: An H-sub2-sup1-sup-5 O PET study of brain activation during singing and speaking. *Neuroreport: For Rapid Communication of Neuroscience Research*, *14*, 749–754.

John, O. P., Angleitner, A., & Ostendorf, F. (1988). The lexical approach to personality: A historical review of trait taxonomic research. *European Journal of Personality*, *2*, 171–203.

Kandel, E. R., & Squire, L. R. (2000, November 10), Neuroscience: Breaking down scientific barriers to the study of brain and mind. *Science*, *290*, 1113–1120.

Keenan, J. P., Nelson, A., O'Connor, M., & Pascual-Leone, A. (2001). Self-recognition and the right hemisphere. *Nature*, *409*, 305.

Kelley, W. T., Macrae, C. N., Wyland, C., Caglar, S., Inati, S., & Heatherton, T. F. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience*, *14*, 785–794.

Keltner, D., Gruenfeld, D. H., & Anderson, C. (2003). Power, approach, and inhibition. *Psychological Review*, *110*, 265–284.

Kenrick, D. T., Li, N. P., & Butner, J. (2003). Dynamical evolutionary psychology: Individual decision rules and emergent social norms. *Psychological Review*, *110*, 3–28.

Kihlstrom, J. F. (1987). The cognitive unconscious. *Science*, *237*, 1445–1452.

LeDoux, J. E. (1996). *The emotional brain: The mysterious underpinnings of emotional life*. New York: Simon & Schuster.

Leger, D. W., Kamil, A. C., & French, J. A. (2001). Introduction: Fear and loathing of evolutionary psychology in the social sciences. In J. A. French, A. C. Kamil, & D. W. Leger (Eds.), *The Nebraska Symposium on Motivation, Vol. 47: Evolutionary psychology and motivation*, *(*pp. ix–xxiii). Lincoln: University of Nebraska Press.

Lepper, M. R., Greene, D., & Nisbett, R. E. (1973). Undermining children's intrinsic interest with extrinsic reward: A test of the "overjustification" hypothesis. *Journal of Personality and Social Psychology*, *28*, 129–137.

Levenson, R. W., Ekman, P., Heider, K., & Friesen, W. V. (1992). Emotion and autonomic nervous system activity in the Minangkabau of West Sumatra. *Journal of Personality and Social Psychology*, *62*, 972–988.

Lewicki, P., Hill, T., & Czyzewska, M. (1992). Nonconscious acquisition of information. *American Psychologist*, *47*, 796–801.

Lewis, M. (1995). Self-conscious emotions. *American Scientist*, *83*, 68–78.

Lewis, M., & Brooks-Gunn, J. (1979). *Social cognition and the acquisition of self*. New York: Plenum.

Lezak, M. D. (1995). *Neuropsychological assessment* (3rd ed.). New York: Oxford University Press.

Libet, B. (1985). Unconscious cerebral initiative and the role of conscious will in voluntary action. *Behavioral and Brain Sciences*, *8*, 529–566.

Lloyd, D. (2002). Functional MRI and the study of human consciousness. *Journal of Cognitive Neuroscience*, *14*, 818–831.

Locke, E. A., & Latham, G. P. (1990). *A theory of goal setting and task performance*. Englewood Cliffs, NJ: Prentice-Hall.

MacEachern, D. (2004, April 25). The essence of courage: A special man who didn't want to be anyone special. *Arizona Republic*, pp. V1–V2.

Markus, H. R. (1977). Self-schema and processing information about the self. *Journal of Personality and Social Psychology*, *35*, 63–78.

Maslow, A. (1968). *Toward a psychology of being*. New York: Van Nostrand.

Maslow, A. (1970). *Motivation and personality* (2nd ed.). New York: Harper & Row.

Mather, M., Canli, T., English, T., Whitfield, S., Wais, P., Ochsner, K., et al. (2004). Amygdala responses to emotionally valenced stimuli in older and younger adults. *Psychological Science*, *15*, 259–263.

McCain, J. (2004). *Why courage matters: The way to a braver life*. New York: Random House.

McClelland, D. C., Atkinson, J. W., Clark, R. W., & Lowell, E. L. (1976). *The achievement motive* (2nd ed.). New York: Irvington.

McClelland, J. L. (2000). Connectionist models of memory. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 583–596). New York: Oxford University Press.

McClelland, J. L., & Rumelhart, D. E. (1985). Distributed memory and the representation of general and specific information. *Journal of Experimental Psychology: General*, *114*, 159–188.

Metcalfe, J., & Mischel, W. (1999). A hot/cool-system analysis of delay of gratifications: Dynamics of willpower. *Psychological Review*, *106*, 3–19.

Miller, G. A., Galanter, E., & Pribram, K. H. (1960). *Plans and the structure of behavior*. New York: Holt.

Mills, M. (2004, April). Evolution and motivation. In L. C. Bernard (Chair), *Integrating perspectives: Toward a new theory of human motivation*. Symposium conducted at the meeting of the Western Psychological Association, Phoenix, AZ.

Mischel, W., Shoda, Y., & Rodriguez, M. L. (1989). Delay of gratification in children. *Science*, *244*, 933–938.

Monterosso, J., & Ainslie, G. (1999). Beyond discounting: Possible experimental models of impulse control. *Psychopharmacology*, *146*, 339–347.

Mook, D. G. (1996). Motivation: The organization of action. New York: W. W. Norton.

Morris, J. S., Öhman, A., & Dolan, R. J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature*, *393*, 467–470.

Mott, M. (2004, March). Cat cloning offered to pet owners. *National Geographic News*. Retrieved June 5, 2004, from http://news.nationalgeographic.com/news/2004/03/0324_040324_catclones.html

Munk, M. H. J., Roelfsema, P. R., König, P., Engel, A. K., & Singer, W. (1996). Role of reticular activation in the modulation of intracortical synchronization. *Science*, *272*, 271–274.

Nahm, F. K. D., Tranel, D., Damasio, H., & Damasio, A. R. (1993). Cross-modal associations and the human amygdala. *Neuropsychologia*, *31*, 727–744.

Neilsen, M., & Day, R. H. (2000). William James and the evolution of consciousness. *Journal of Theoretical and Philosophical Psychology*, *19*, 90–113.

Oettingen, G., Bulgarella, C., Henderson, M., & Gollwitzer, P. M. (2004). The self-regulation of goal pursuit. In R. A. Wright, J. Greenberg, & S. S. Brehm (Eds.), *Motivational analyses of social behavior: Building on Jack Brehm's contributions to psychology* (pp. 225–244). Mahwah, NJ: Erlbaum.

Oyama, S. (1991). Bodies and minds: Dualism in evolutionary theory. *Journal of Social Issues*, *47*, 27–42.

Oyama, S. (1993). How shall I name thee? The construction of natural selves. *Theory and Psychology*, *3*, 471–496.

Paller, K. A. (2004). Electrical signals of memory and of the awareness of remembering. *Current Directions in Psychological Science*, *13*, 49–55.

Panksepp, J. (1998). *Affective neuroscience: The foundations of human and animal emotions*. New York: Oxford University Press.

Perlman, B., & McCann, L. I. (1999). The most frequently listed courses in the undergraduate psychology curriculum. *Teaching of Psychology*, *26*, 177–182.

Plous, S. (1993). *The psychology of judgment and decision making*. New York: McGraw-Hill.

Plutchik, R. (2003). *Emotions and life: Perspectives from psychology, biology, and evolution*. Washington, DC: American Psychological Association.

Plutchik, R., & Kellerman, H. (1974). *Manual of the Emotions Profile Index*. Los Angeles: Western Psychological Services.

Povinelli, D. J., Gallup, G. G., Jr., Eddy, T. J., Bierschwale, D. T., Engstrom, M. C., Perilloux, H. K., et al. (1997). Chimpanzees recognize themselves in mirrors. *Animal Behavior*, *53*, 1083–1088.

Pribram, K. (1977). Human consciousness and the functions of the brain. *Somatics*, *1*, 5–7.

Quartz, S. R., & Sejnowski, T. J. (1997). The neural basis of cognitive development: A constructivist manifesto. *Behavioral and Brain Sciences*, *20*, 537–596.

Rainville, P., Carrier, B., Hofbauer, R. K., Bushnell, M. C., & Duncan, G. H. (1999). Dissociation of sensory and affective dimensions of pain using hypnotic modulation. *Pain*, *82*, 159–171.

Rainville, P., Duncan, G. H., Price, D. D., Carrier, B., & Bushnell, M. C. (1997). Pain affect encoded in human anterior cingulate but not somatosensory cortex. *Science*, *277*, 968–971.

Ramachandran, V. S. (1991). 2-D or not 2-D? That is the question. In R. L. Gregory, J. Harris, P. Heard, D. Rose, & C. Cronly-Dillon (Eds.), *The artful brain* (pp. 249–267). Oxford, England: Oxford University Press.

Rees, G., Kreiman, G., & Koch, C. (2002). Neural correlates of consciousness in humans. *Nature Reviews Neuroscience*, *3*, 261–270.

Reiss, S. (2000). *Who am I: The 16 basic desires that motivate our actions and define our personality*. New York: Tarcher/Putnam.

Reiss, S., & Havercamp, S. M. (1996). Sensitivity theory and mental retardation: Why functional analysis is not enough. *American Journal of Mental Retardation*, *101*, 553–566.

Reiss, S., & Havercamp, S. M. (1997). The sensitivity theory of motivation: Implications for psychopathology. *Behaviour Research and Therapy*, *34*, 621–632.

Reiss, S., & Havercamp, S. M. (1998). Toward a comprehensive assessment of fundamental motivation: Factor structure of the Reiss Profile. *Psychological Assessment*, *10*, 97–106.

Roser, M., & Gazzaniga, M. S. (2004). Automatic brains—Interpretive minds. *Current Directions in Psychological Science*, *13*, 56–59.

Rozin, P. (1976). The evolution of intelligence and access to the cognitive unconscious. *Progress in Psychobiology and Physiological Psychology*, *6*, 245–280.

Russell, J. A. (1991). Culture and the categorization of emotion. *Psychological Bulletin*, *110*, 426–450.

Russell, J. A. (2003). Core affect and the psychological construction of emotion. *Psychological Review*, *110*, 145–172.

Russell, J. A., & Barrett, L. F. (1999). Core affect, prototypical emotional episodes, and other things called emotion: Dissecting the elephant. *Journal of Personality and Social Psychology*, *76*, 805–819.

Salisbury, D. F. (2003, October 3). Neurons that play truth or consequences. *Evolutionary Psychology*. Retrieved October 4, 2003, from http://www.vanderbilt.edu/exploration/news/news_intentions.htm

Salzen, E. A. (1998). Emotion and self-awareness. *Applied Animal Behaviour Science*, *57*, 299–313.

Schachter, S. (1971). Some extraordinary facts about obese humans and rats. *American Psychologist*, *26*, 129–144.

Schachter, S., & Singer, J. E. (1962). Cognitive, social, and physiological determinates of emotional state. *Psychological Review*, *69*, 379–399.

Schall, J. D. (2001). Neural basis of deciding, choosing and acting. *Nature Reviews*, *2*, 33–42.

Schall, J. D., Hanes, D. P., & Taylor, T. L. (1999). Neural control of behavior: Countermanding eye movements. *Psychological Research*, *63*, 299–307.

Schall, J. D., & Thompson, K. G. (1999). Neural selection and control of visually guided eye movements. *Annual Review of Neuroscience*, *22*, 241–259.

Schmitt, D. P., & Pilcher, J. J. (2004). Evaluating evidence of psychological adaptation: How do we know one when we see one? *Psychological Science*, *15*, 643–649.

Semendeferi, K., & Damasio, H. (2000). The brain and its main anatomical subdivisions in living hominoids using magnetic resonance imaging. *Journal of Human Evolution*, *38*, 317–332.

Semendeferi, K., Lu, A., Schenker, N., & Damasio, H. (2002). Humans and great apes share a large frontal cortex. *Nature Neuroscience*, *5*, 272–276.

Shermer, M. (2004). *The science of good and evil*. New York: Times Books.

Silvia, P. J., & Duval, T. S. (2004). Self-awareness, self-motives, and self-motivation. In R. A. Wright, J. Greenberg, & S. S. Brehm (Eds.), *Motivational analyses of social behavior: Building on Jack Brehm's contributions to psychology* (pp. 57–75). Mahwah, NJ: Erlbaum.

Simon, H. (1955). A behavioral model of rational choice. *Quarterly Journal of Economics*, *69*, 99–118.

Simpson, J. A. (1999). Attachment theory in modern evolutionary perspective. In J. Cassidy & P. R. Shaver (Eds.), *Handbook of attachment* (pp. 115–161). New York: Guilford Press.

Skinner, B. F. (1938). *Behavior of organisms*. New York: Appleton-Century-Crofts.

Skinner, B. F. (1971). *Beyond freedom and dignity*. New York: Knopf.

Slovic, P., Finucane, M., Peters, E., & MacGregor, D. (2002). The affect heuristic. In T. Gilovich, D. Griffin, & D. Kahneman (Eds.), *Intuitive judgment: Heuristics and biases* (pp. 397–420). Cambridge, England: Cambridge University Press.

Smith, E. E., Jonides, J., & Koeppe, R. A. (1996). Dissociating verbal and spatial working memory using PET. *Cerebral Cortex*, *6*, 11–20.

Smolensky, P. (1995). Connectionism, constituency and the language of thought. In C. Macdonald (Ed.), *Connectionism: Debates on psychological explanation*, *2*, 164–198.

Sober, E., & Wilson, D. S. (1998). Unto others: The evolution and psychology of unselfish behavior. Cambridge, MA: Harvard University Press.

Solomon, S., Pyszczynski, T., & Greenberg, J. (2004). Willful determinism: Exploring the possibilities of freedom. In R. A. Wright, J. Greenberg, & S. S. Brehm (Eds.), *Motivational analyses of social behavior: Building on Jack Brehm's contributions to psychology* (pp. 77–96). Mahwah, NJ: Erlbaum.

Steriade, M. (1996). Arousal: Revisiting the reticular activating system. *Science*, *272*, 225–226.

Strehler, B. L. (1991). Where is the self? A neuroanatomical theory of consciousness. *Synapse*, *7*, 44–91.

Sun, R. (1997). Learning, action and consciousness: A hybrid approach toward modelling consciousness. *Neural Networks*, *10*, 1317–1331.

Symons, D. (1992). On the use and misuse of Darwinism in the study of human behavior. The psychological foundation of culture. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind* (pp. 137–159). New York: Oxford University Press.

Thorndike, E. L. (1911). *Animal intelligence*. New York: Macmillan.

Tinbergen, N. (1951). *The study of instinct*. New York: Oxford University Press.

Tolman, E. C. (1932). *Purposive behavior in animals and men*. New York: Century.

Tononi, G., & Edelman, G. M. (1998). Consciousness and complexity. *Science*, *282*, 1846–1851.

Tononi, G., Sporns, O., & Edelman, G. M. (1992). Reentry and the problem of integrating multiple cortical areas: Simulation of dynamic integration in the visual system. *Cerebral Cortex*, *2*, 310–335.

Tooby, J., & Cosmides, L. (1992). The psychological foundation of culture. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind* (pp. 19–136). New York: Oxford University Press.

Tranel, D., & Damasio, A. R. (1993). The covert learning of affective valence does not require structures in hippocampal system or amygdala. *Journal of Cognitive Neuroscience*, *5*, 79–88.

Travis, C. B., & Yeager, C. P. (1991). Sexual selection, parental investment, and sexism. *Journal of Social Issues*, *47*, 117–129.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, *46*, 35–57.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man*, *1871–1971* (pp. 136–179). Chicago: Aldine.

Tulving, E. T., Kapur, S., Craik, F. I. M., Moscovitch, M., & Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proceedings of the National Academy of Sciences*, *91*, 2016–2020.

Tyler, L. K., Bright, P., Dick, E., Tavares, P., Pilgrim, L., Fletcher, P., et al. (2003). Do semantic categories activate distinct cortical regions? Evidence for a distributed neural semantic system. *Cognitive Neuropsychology*, *20*, 541–559.

Van Bockstaele, E. J., & Aston-Jones, G. (1995). Integration in the ventral medulla and coordination of sympathetic, pain and arousal functions. *Clinical and Experimental Hypertension*, *17*, 153–165.

Vogeley, K., & Fink, G. R. (2003). Neural correlates of the first-person perspective. TRENDS. *Cognitive Sciences*, *7*, 38–42.

Wallbott, H. C., & Scherer, K. R. (1989). Assessing emotion by questionnaire. In R. Plutchik & H. Kellerman (Eds.), *Emotion: Theory, research, and experience: Vol. 4. The measurement of emotions*. New York: Academic Press.

Watson, D., Wiese, D., Vaidya, J., & Tellegen, A. (1999). The two general activation systems of affect: Structural findings, evolutionary considerations, and psychobiological evidence. *Journal of Personality and Social Psychology*, *76*, 820–838.

Watson, J. B. (1913). Psychology as the behaviorist views it. *Psychological Review*, *20*, 158–177.

Weiner, B. (1989). *Human motivation*. New York: Holt, Rinehart & Winston.

Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory's echo: Vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences*, *97*, 11125–11129.

Wierzbicka, A. (1992). Defining emotion concepts. *Cognitive Science*, *16*, 539–581.

Wierzbicka, A. (1999). *Emotions across languages and cultures*. New York: Cambridge University Press.

Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton, NJ: University Press.

Winkielman, P., & Berridge, K. C. (2004). Unconscious emotion. *Current Directions in Psychological Science*, *13*, 120–123.

Zajonc, R. B. (1980). Feeling and thinking: Preferences need no inferences. *American Psychologist*, *35*, 151–175.

Original manuscript received July 7, 2004
Final revisions accepted March 15, 2006