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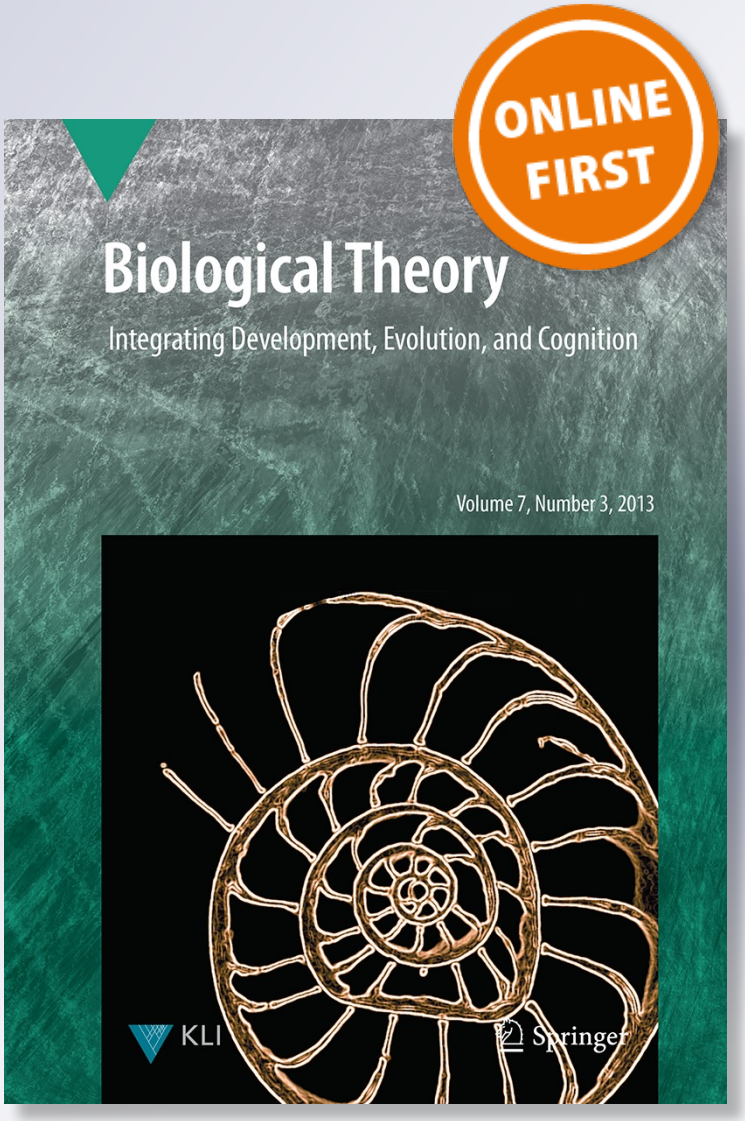

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LONG ARTICLE

The Anatomy of Motivation: An Evolutionary-Ecological Approach

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Abstract There have been few attempts to bring evolutionary theory to the study of human motivation. From this perspective motives can be considered psychological mechanisms to produce behavior that solves evolutionarily important tasks in the human niche. From the dimensions of the human niche we deduce eight human *needs*: optimize the number and survival of gene copies; maintain bodily integrity; avoid external threats; optimize sexual, environmental, and social capital; and acquire reproductive and survival skills. These needs then serve as the foundation for a necessary and sufficient list of 15 human motives, which we label: lust, hunger, comfort, fear, disgust, attract, love, nurture, create, hoard, affiliate, status, justice, curiosity, and play. We show that these motives are consistent with evidence from the current literature. This approach provides us with a precise vocabulary for talking about motivation, the lack of which has hampered progress in behavioral science. Developing testable theories about the structure and function of motives is essential to the project of understanding the organization of animal cognition and learning, as well as for the applied behavioral sciences.

Keywords Evolutionary ecology · Human · Motivation · Motives · Needs · Niche

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The study of motivation has a long and checkered history in psychology. While most psychologists agree that humans and other animals engage in motivated behavior, there is little agreement as to how much, or how little of human behavior can be described as motivated, or how many motives there are. Indeed some scholars deny that distinct motives exist at all. (Barrett and Russell 1999; Russell 2003). At times the topic of motivation covered much of the psychology of behavioral causation; at other times it became just one of its component parts; most recently it has almost vanished (Reeve 2005; Heckhausen 2008).

Early philosophers and psychologists took a biological approach to motivation. Bentham (1983) catalogued various "springs to action." For William James (1890), motives were genetically programmed "instincts" that maintained or varied behavior in the face of changing circumstances. McDougall (1908) attributed all human behavior to motivational dispositions ("instincts"). Hull (1943) criticized the idea of fixed instincts as being too mechanistic and replaced it with the idea of needs and drives. Drives were related to the satisfaction of needs, which were an internal sense that some resource was lacking (see also Murray 1938). Drives were thought to cause the rectification of deficits in internal systems, ignoring other cues in the process (Hull 1943; McClelland et al. 1953). Current cognitive approaches to motivation emphasize the conscious control of behavior—for example, in expectancy value theory (Fishbein and Ajzen 1975), self-regulation theory (Carver and Scheier 1981, 1998; Oettingen et al. 2004), or volitional phase models (Schwarzer 1992). However, such cognitive approaches have been challenged by recent experimental work demonstrating that a good deal of motivation is implicit or non-conscious (Bargh and Chartrand 1999; Wilson 2004). More

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than a century after James, attention is reverting to the evolved biological causes of motivated behavior (Bernard et al. 2005; Kenrick et al. 2002).

All of these schools of thought agree that motivation has distinguishable component constructs (hypothesized mental mechanisms that cannot be directly observed), which they have variously labeled "motives," "needs," "values," or "instincts." (one author attempted to evade the nomenclature controversy by coining a new word—the "erg"; Cattell 1957). The number and choice of constructs has varied widely, from 44 "needs" (Starch 1923) to Ryan's three "intrinsic motivations" (Deci and Ryan 2000). Online Resource 1 catalogues 20 of the best-known efforts to categorize human motivations, showing that there is still an astonishing lack of consensus (Pittman and Zeigler 2006): only five motivational constructs (affiliation, curiosity, self-assertion, sex, and nurture) are common to a majority, while about a third of the constructs are cited by only one author each.

These authors derived their motivational constructs in a variety of ways. James (1890) based his proposals on naturalistic observations of adults, children, and animals. Murray (1938) used the results of projective, picture-based, psychological tests. Maslow (1954) derived his set of needs largely from reading the biographies of famous individuals. Personality psychologists have employed factor analysis, either surveying the existing literature for candidates (Reiss and Havercamp 1998), or collecting linguistic terms for factoring (Cattell 1957). Some authors mined the previous literature. Deci and Ryan (2000), for example, found that three "basic" needs (autonomy, competence, and relatedness) are reported as being most important in fostering an active mental state. Other authors simply choose one motive and argue that it is central to any explanation of human behavior—such as the need for achievement (McClelland et al. 1953), power (McClelland and Watson 1973; Winter 1973; Fiske and Berdahl 2007), or affiliation (Schachter 1959; Baumeister and Leary 1995; Fiske 2002). A few authors begin from theory. Bugental (2000), for example, based her approach on identifying all the basic logical forms of social relationship. Bernard et al. (2005) used evolutionary theory, arguing that a mental mechanism should be associated with each type of selection process (e.g., sexual selection, reciprocal altruism, and parental investment).

Most of these methods of identifying motivational constructs have drawbacks. Literature surveys or factor analysis using self-reported feelings may be a poor guide to motives because not all motivation may be accompanied by conscious affect (Bargh and Chartrand 1999; Wilson 2004). Lexical sources need not necessarily reflect the psychological processes responsible for individual variation in behavior (Block 1995; Westen 1996; Bandura 1999). Many lists are also subject to circular reasoning: some kind of behavior (e.g., aggression) is argued to be due to a particular need (e.g., an aggression "drive"), which is proven to exist by anyone exhibiting aggressive behavior. Some means must be found to identify motivational constructs which is not tautological, and which does not depend on linguistic data or self-report of feelings.

A number of previous lists of motives have found wide use because they have some predictive value. For example, Reiss (2008) has shown that his constructs predict variation in behavior (e.g., military officers scored higher than average on the motive "honor"). Atkinson (1964) found that achievement motivation scores increase with occupational level. These lists have hence been used for employment screening, career planning (Reiss 2008), and tests of leadership (Atkinson 1964). Developing testable theories about the nature, evolution, operation, and delineation of motives is an essential step towards understanding the functioning of animal and human minds.

Since motives are based in brains that evolved to produce adaptive behavior (Hebb 1949; Churchland and Sejnowski 1992; Freeman 1999; Llinas 2002; Swanson 2003), the best place to start in anatomizing human motives must be with the evolutionary function and history of brains. We assume that motives are specific adaptations that evolved to bias behavior towards actions that assisted our ancestors to survive and reproduce in the niches in which they evolved. However, since there are huge numbers of potentially adaptive behaviors, we need some means to separate out classes of behavior driven by discrete motives. We do this in three steps: (1) We present a principled definition of *motivated behavior* that separates it from that which is caused by other kinds of mental mechanisms. (2) We then use principles of evolutionary theory to deduce a necessary and complete list of *needs*. This process leads us to the conclusion that social animals have only eight discrete needs and that humans have 15 corresponding motives, most of which we share with other mammals. (3) We compare our proposal to existing evidence from neurobiology, psychiatry, evolutionary biology, and the previous history of investigation into discrete motivational constructs. Finally, we discuss the implications of taking this approach to motivation.

Deducing Motives

How then can we produce a complete list of human motives? If the brain was designed by evolution as an organ for producing adaptive behavior, we should expect that regularly encountered problems should have produced regularities in the brain for solving them. Separate motives are therefore present in the human psyche as a result of the

evolutionary requirement to meet specific ecological needs, as defined by the niche within which our species lives (Tooby and Cosmides 1992; Godfrey-Smith 1996; Barton 2008). Evolutionary theory allows us to define these recurrent problems and, hence, to hypothesize about the constructs that are used to solve them. Our strategy will be to identify what humans need to do in order to maximize their biological fitness, examine the ecology within which this process occurs, specify the ways in which fitness can be maximized within that ecology, and deduce the mental mechanisms needed to negotiate a way through these various threats and opportunities.

Evolutionary theory suggests that behavior is produced by brains that have been designed by a long history of pressures to produce adaptive responses to situations important to natural selection (Tooby and Cosmides 1992; Cziko 2000). These tasks are defined by evolutionarily significant aspects of an animal's niche. For example, some animals reproduce by fissioning (which only requires sufficient internal resources) while others must seek out mates to exchange genetic material when reproducing sexually. Further, because all humans occupy the same niche, needs should be universal across cultural groups. (However, tactics used to satisfy those needs can vary, depending on the availability of cultural aids such as tools; Baumeister and Leary 1995; Deci and Ryan 2000; Doyal and Gough 1991; Tooby and Cosmides 1992.) Given this perspective, a *need* can be defined as *a mechanism to carry out a task related to an evolutionarily significant aspect of an animal's ecological niche, which requires goal-directed behavior*.

Needs need not appear, either implicitly or explicitly, in an animal's mind. A need reflects the existence of a relationship (recognized by selection pressure) between an animal's way of life and its niche (e.g., to have sex, and so reproduce; or to eat fruit and thereby acquire nutrients).

Constraining Motivation

Since we cannot discuss motives without agreement as to which behaviors are, and are not, motivated, we will begin with some definitions. We call *motivation* an aroused state of goal pursuit, and individual *motives* psychological mechanisms designed by evolution to cause animals to seek to meet a need through behavior.

Three distinct kinds of mechanisms have evolved in brains to produce and control behavior in human evolutionary history. The earliest forms of behavior were reactive: an automatic response to a cue from the environment, or to an internal bodily system. For example, a large, rapidly approaching object will cause an individual to duck, while a bad taste will cause a gagging reflex. These responses are pre-mammalian in origin and are not motivated, by our definition, because they do not involve the meeting of evolutionarily important needs. (Although such behaviors assist the individual in surviving, the response is automatic rather than requiring the formation of a mental representation of a goal.) At the other extreme is complex, often conscious, executive behavior (Koechlin and Summerfield 2007; Wiecki and Frank 2011). Planning by the executive cortex allows humans to use foresight to achieve long-term objectives such as getting a driving license, losing weight, or saving for retirement. These objectives are achieved through consciously constructing and following a succession of steps. For example, saving for retirement might involve setting up a pension fund, investing in a portfolio of stocks, and adjusting investments throughout one's life. Forming such plans depends on an ability to evaluate them for their likely success in helping to meet various needs.

Motivated behavior lies between reflexive and planned behavior (Panksepp 1998; Rolls 1999; Sloman 2001; Aunger and Curtis 2008). Its task is the meeting of regularly occurring, largely day-to-day, evolutionarily important needs. Restricting the definition of motivation to the meeting of evolved needs means that not all of human behavior can be described as motivated. So, while an automated reflexive behavior can help to meet a need, that is not its central purpose (which is to respond to some stimulus). And, while planned behavior can be subtended by a variety of motives, its purpose is to employ higher levels of control over behavior to reach consciously constructed, longer-term objectives, potentially ignoring the satisfaction of immediate needs on the way.

Making this tripartite distinction between the reflexive, motivated, and planned control of behavior is our first step in anatomizing motivation. Motives are thus produced by a motivational system that is separate from both reflexes, which are automatic responses, and from executive control, which is associated with the prefrontal cortex and consciousness. Feelings are conscious, and therefore associated with planned behavior. Motives, on the other hand, are goal-directed, but need neither be conscious, nor reflexive, as reflexes are at a more primitive level of mental processing (not requiring goal pursuit).

Hunger is a classic example of motivated behavior. In terms of our model of behavior determination, if someone hasn't eaten for a while, ghrelin (a cue of the need for food) drops below a threshold level in the bloodstream. This is registered as an input from the body and causes a goal to be formulated coupled potentially with a feeling of hunger (a psychological indicator of a body state). An episode of motivated food search behavior is implemented when the need to acquire metabolic resources outweighs other needs, objectives, or reactions at that moment, so that hunger-driven behavior is selected. Once food is consumed, the

need is ameliorated (as indicated by a reduction in the amount of ghrelin in the bloodstream), and the animal can move on to the satisfaction of other needs.

Meeting Needs

But what, then, are these needs that humans seek to meet? Biological fitness is a function of both survival and reproduction, because an organism's success in the struggle for fitness can be divided into differential mortality (survival to reproductive age) and fertility (total genetic contribution to subsequent generations) (Lande 1982). Behavior can therefore be classified (as it is in behavioral ecology) by whether it serves to promote reproduction directly (e.g., through mating effort), or through the survival and growth of the body (i.e., somatic needs), which provides the foundation from which reproduction can later be achieved (Davies et al. 2012).

Individuals can attain fitness benefits in three different ways. (1) They can directly invest in their own fitness, by improving their physiological state and by reproducing. (2) They can improve their fitness indirectly, by investing in altering their physical and social situation in the world so as to improve their and their kin's chances of survival and reproduction. (3) They can improve their fitness even more indirectly, by investing in their proficiency—by improving their mental and physical ability at solving the above problems (Aunger and Curtis 2008). Table 1 provides the simple set of eight needs that all sexually reproducing animals must have by setting the basic life history tasks of reproduction and survival against the three ways in which animals invest in achieving evolutionary benefits.

From Needs to Motives

From these eight basic mammalian needs we can now identify human motives by determining the dimensions of the human niche that are relevant to each need. Table 2 lists the eight mammalian needs and their corresponding human motives. For each motive, we set out the niche-based problem which that motive has evolved to solve (column 7). Each motive is described in detail below. Note that we have chosen a single label for each motive, using a word that comes as close as possible to describing its central function. We have sometimes had to select a "feeling" label for a motive, but the two should not be confused. So, for example, in this scheme, *disgust* is the motive that drives parasite avoidance behavior; however, it is also the name of the associated feeling (Curtis et al. 2011). *Love* is the name we give to the pair-bonding motive, but it is also a feeling. The table shows that there are many more feelings than motives.

In the final column we have also provided sample behavioral tactics that are commonly employed by humans to meet their needs. Table 2 further lists evolutionary theories and pathologies relating to each motive that will feature in the discussion. We now describe each motive and the human niche problem it evolved to solve in turn.

Lust

First, humans reproduce through sexual intercourse. Thus the motive to meet the need to maximize gene copy production is the pan-vertebral drive to engage in copulatory behavior. This requires a search for and pursuit of appropriate candidates and the consummation of sexual union.

Hunger

The need to optimize bodily functions is met by vertebrates in two ways; first, through seeking, acquiring, and consuming resources such as nutrients, water, and oxygen.

Comfort

Second, because terrestrial niches vary spatially in terms of physical conditions such as temperature, elevation, and moisture levels, maintenance of the body's physiology or *comfort* also requires behavior. Comfort produces tactics such as seeking shade when the sun is hot, covering the body with warm, dry clothes, finding shelter, removing thorns, tending wounds, consuming medicated plants, saving energy by sleeping or resting, and voiding wastes.

Fear and disgust

Humans, like most animals, face threats from biological agents that can either attack from outside (predators) or

Table 1 Evolved *needs*

Task/need type	Physiology (body)	Situation (world)	Proficiency (brain)
Reproduction	Maximize gene copy production	Optimize sexual capital	Optimize knowledge/skills
		Optimize survival/growth/reproduction of offspring/kin	
Survival	Optimize bodily functions	Optimize environmental capital	
	Minimize environmental dangers	Optimize social capital	

Table 2 Human motives

Type	Task	Need	Motive	Label	Feelings[a]	Niche feature	Example tactics	Theoretical problem	Pathology
Physiological (body)	Reproduction	Maximize gene copy production	Mate	Lust	Lust (satisfaction)	Sexual reproduction	Select/court mate, copulate	Mate selection	Sex addiction, pedophilia
	Survival	Optimize bodily functions	Acquire metabolic resources	Hunger	Hunger, thirst, (satiation)	Ecological resources	Eat, drink, forage/hunt	Optimal foraging	Compulsive overeating, bulimia, anorexia
			Maintain body	Comfort	Discomfort, pain (relief)	Ecological variation	Seek air/sun, relocate to dry/warm conditions, COBS, wear clothes, tend wound, self-medicate, sick-role behavior, rest/sleep, excrete	Pain avoidance	Somatoform disorders
		Minimize environmental damage	Avoid hurt-from-without threats (predation)	Fear	Fear (safety)	Predators	Aggregate in large group, stay close to kin, stay far from predator habitats, freeze/flight/fight, avoid accidents	Predation/accident avoidance	Anxiety disorders
			Avoid hurt-from-within threats (parasitization)	Disgust	Disgust (purity)	Parasites	Avoid parasites, infected others, animal vectors, and contaminated environments	Parasite avoidance	Obsessive compulsive disorder (cleaning)
Situational (world)	Reproduction	Optimize sexual capital	Acquire high quality sexual relationships	Attract	Ornamentation (attractive)	Mate competition	Adorn, self-groom, body-building/modification, acquire high-quality territory, make high-quality nest	Sexual selection	Body dysmorphic disorder, Narcissistic personality disorder
			Maintain high quality sexual relationships	(Pair-bond) Love	Romantic love, jealousy, dependency (domesticity)	Very dependent offspring	Maintain/defend pair-bond, (e.g., guard), elicit investment (e.g., cry)	Paternal investment	Avoidant personality disorder
		Optimize fitness of gene copies	Rear offspring/aid dependent kin	Nurture	Parental love, kin love	Altricial live birth	Give resources, protect from dangers, provide opportunities for play, transmit status, nepotism	Kin selection/Inclusive fitness	Münchausen syndrome by proxy, parent–child abuse disorder
	Survival	Optimize environmental capital	Accumulate/defend surplus consumable resources	Hoard	Acquire, envy (satisfaction, vengeance, loss)	Social resource competition	Acquire territory, cultivate, threaten/coerce/forcibly take resources of others, exchange, contract, collaborate in resource production; guard surplus resources	Resource acquisition/defense	Obsessive–compulsive disorder (hoarding), Hoarding disorder, Kleptomania
			Improve habitat	Create	Desire to make/mend/clean/order, aesthetics	Ecological degradation	Migrate, build, improve/order/clean habitat/territory; remove/destroy predator habitats, remove cliffs/holes; remove/destroy pathogen habitat; make/repair artifacts	Niche construction	Obsessive–compulsive disorder (perfectionism)
		Optimize social capital	Affiliate with groups	Affiliate	Sympathy, anxiety, loneliness/panic (grief, gratitude, elevation)	Group-produced resources	Cooperate, conform, participate in group activities, display panic, display intent to cooperate/reciprocate, share knowledge (e.g., gossip), seek alliances	Direct reciprocity (reciprocal altruism)	Separation anxiety, dependent personality disorder; social phobia, sociopathy
			Invest in status improvement	Status	Ambition, envy (pride, power, embarrassment)	Social hierarchies	Derogate competitors, submit to/flatter superiors, form coalitions, accumulate tradable resources, display awareness of social error/cultural taste/confidence/superiority, seek recognition	Indirect reciprocity (reputation management)	Antisocial personality disorder, depression, chronic stress
			Maintain functioning of large non-kin groups	Justice	Unfairness, moral disgust, contempt (shame, guilt)	Ultrasocial society	Punish/shun free-riders/cheaters, engage in/reward selfless behavior, preserve environment for future	'Strong' reciprocity	Intermittent explosive disorder

Table 2 continued

Type	Task	Need	Motive	Label	Feelings[a]	Niche feature	Example tactics	Theoretical problem	Pathology
Proficiency (brain)	Repro-duction and survival	Optimize knowledge/ skills	Acquire knowledge about the world	Curiosity	Sensation- seeking, confusion, uncertainty (awe, security)	Memory	Wander, roam, observe, seek to understand/ explain, manipulate (novel) objects, consume symbolic information (e.g., read)	Uncertainty reduction	Schizophrenia
			Acquire/increase/ hone skills	Play	Boredom (mastery/ effectance)	Learning	Invest in practice behavior/skills (e.g., sport, poetry, music, conversation), observe/ imitate	Skill acquisition	Attention deficit hyperactive disorder

[a] Feelings experienced after goal achievement, or failure, are in parentheses

sneak inside (parasites). Two motives organize behavior that meets the need to minimize bodily damage from these threats. First, *fear* drives behavior that avoids hurt-from-without threats, including predators, but also aggressive conspecifics and accidents (Ohman and Mineka 2003). Tactics include aggregating in a group, fleeing, hiding, and avoiding environmental dangers such as fires and floods. Second, the *disgust* motive drives the avoidance of hurt-from-within threats. Its task is to cause the avoidance of sick others, "off" foods, disease vectors, and pathogen contamination (Curtis et al. 2004).

While the five aforementioned motives deal with the three physiological needs, the motives that follow involve changing the state of the world so as to better survive and reproduce.

Attract

In any sexually reproducing species there is competition for high-quality mates. *Attract* drives investment in the means to secure one-time copulations or long-term pair-bonds. It causes humans to produce displays of sexual attractiveness through body adornment, painting, or modification; or through activities that display mate quality such as sport and dancing, which might secure a pair-bond. This can involve demonstrating the ability to overcome a self-imposed handicap, such as scarification (Ludvico and Kurland 1995) or risk taking (Wilson and Daly 1985).

Love

Love causes individuals to seek to build and defend a pair-bond to meet the mammalian need for joint investment in offspring with a long period of dependence on parents (Quinlan and Quinlan 2007). Mothers need to keep partners around to share the burden of rearing offspring (Fox 1984). Love causes human males and females to invest in the pair-bond with tactics that include making costly gifts, offering tokens of commitment, and the jealous driving away of rivals.

Nurture

Mammalian offspring are born highly dependent, requiring provisioning, protection, and education. Parental care is therefore another important aspect of the human way of life. *Nurture* is the motive to rear offspring and aid other kin. This is most likely to be directed at immature relatives, but may target other kin, with the degree of investment reflecting the likelihood of gene copies being present in that individual (Hamilton 1964). Nurture encourages maternal and paternal feeding, cleaning, and protective behavior, as well as the provision of opportunities for play learning, and attempts to influence the social world in favor of kin (Geary and Flinn 2001).

Hoard

As in all social animals, scarce resources inspire competition. However, humans are able to produce resource surpluses. *Hoard* drives behavior that involves the accumulation of resources, either directly by growing, collecting, and storing them, or more indirectly, by negotiating the rights to territory, or the fruits of group production. It may also require the guarding of resources from pilfering by envious others (Gintis 2007).

Create

Create is the label we give to the motive to improve and maintain habitat such that it is more conducive to survival and reproduction. Human tactics include building dwellings that are safe and dry, removing dangers such as predator or parasite habitat, planting, weeding and irrigating, cleaning, tidying and repairing habitat, and making artifacts such as bows and ploughs that aid the diversion of energy towards survival and reproduction.

Affiliate

Humans are highly social, territorial mammals who gain the many benefits of group life by increasing their social capital. The *affiliate* motive causes humans to participate in social activities, form alliances, conform to group norms, display their intentions to cooperate, seek to engender trust, and share resources, including knowledge about others (Baumeister and Leary 1995; Dunbar 1998; Cosmides and Tooby 2005). It also leads to a search for elevating experiences where group connectedness is reinforced (Haidt 2003).

Status

A key feature of human social groups is that they are hierarchical, giving some individuals privileged access to resources. Rank in many mammalian species is due simply to physical domination. In primates, however, preferential access to resources can be gained through alliances, deception, and other strategies (Dahl 2004; Willer 2009). *Status* drives humans to seek to optimize their social position using tactics such as flattering superiors, submitting to authority, drawing attention to one's one contributions, displaying wealth, ability, and "taste," and seeking recognition and title (Buss and Dedden 1990; Henrich and Gil-White 2001). Inappropriate or too-naked attempts to do so can lead to embarrassment and a quest to repair damage to one's social reputation (Goffman 1956; Tangney et al. 2007).

Justice

Alone among vertebrates, humans live in societies composed of large groups of cooperating non-kin (Richerson and Boyd 1998). Cooperation in ultra-social groups seems to require specific forms of punishment—in particular, so-called "third party punishment," or the costly punishment of others, even when one has not been wronged oneself (Gintis 2009). The *justice* motive causes humans to enjoy punishing those who behave anti-socially, and even to enjoy punishing those who fail to punish defectors (de Quervain et al. 2004). Probably very recently evolved are the so-called "self-conscious" feelings of shame and guilt that regulate the transgression of social norms and appropriation of unfair proportions of group resources, and provide incentives to repair social relationships damaged by overly selfish behavior (Tangney et al. 2007). These make it less likely that others will have to police social interactions in ultra-social groups, since individuals police themselves. Recent theoretical and experimental work demonstrates that ultra-social life cannot be maintained without the justice motive (Fehr and Gachter 2002; Price et al. 2002).

Curiosity

The final type of need for most animals, including humans, is to improve their own proficiency at meeting all the needs outlined above. In complex, stochastic environments, animals become out-of-date concerning environmental threats and opportunities. Ranging behavior reduces uncertainty about the amount or location of resources, or the presence of dangers or escape routes—information that is stored in memory (Inglis 2000). The function of the *curiosity* motive is to collect and codify information, thus reducing a gap in knowledge about some facet of the world (Loewenstein 1994). Curiosity results in brain structures being created or updated, such as world maps and situational expectancies (Beswick 1971; O'Keefe and Nadel 1978). Curiosity is engaged when animals have sufficient energy stores and no pressing emergencies (Nissen 1930; Panksepp 1998). In humans it drives behavior such as scientific experimentation and the trial of novel products.

Play

Play concerns the acquisition of embodied skills and knowledge of one's own physical competencies through the repeated practice of particular behavior sequences. Play behavior increases proficiency at reproductive and survival skills, both directly and indirectly (Burghardt 2005). This type of learning tends to be stored as procedural memories. (Barnes et al. 2005; Squire 2004; Tulving 1985). Play-driven behaviors involve simulating activities such as nurturing babies, fighting, hunting, or courting, without the related dangers.

The Structure of Motivation

Our 15 motives can be distinguished by their evolutionary origins and functions. Some motives serve bodily needs (e.g., hunger, comfort, lust, disgust) that can be referred to as "drives." Others serve to improve the state of the world for an individual (e.g., love, nurture, affiliation, status, create, justice); these we label "emotions." A third set of motives (curiosity, play) improve the brain, which we call "interests" (Aunger and Curtis 2008). Drives can also be distinguished from emotions by the fact that they are initiated by internal indicators, while emotions tend to be triggered by environmental stimuli. The satisfaction of drives also involves resources passing from the environment into the body (e.g., food for hunger, heat for comfort), or avoidance of internal resources being lost (e.g., to parasites through disgust or predation through fear) (Aunger and Curtis 2008).

Motives have evolved through evolutionary history. Motivation began with goal-oriented behavior, which arose in reptiles with the first primitive cortices (Streidter 2005; Swanson 2003). Reptiles in our ancestral lineage had needs for metabolic and physiological balance (hunger, comfort), the avoidance of environmental dangers (fear, disgust), and finding mates (lust), along with keeping territories clean (create) and acquiring knowledge about these surroundings (curiosity).

With the advent of mammals and the increasing complexity in their life ways came the need for new motives. Nurture arose in the primordial social grouping—a mother and her dependent offspring, pair-bond love in the nuclear family (i.e., a parental pair with highly dependent offspring), attract with the need to compete for high-quality mates, affiliation with clans (or small groups of related families), status with larger, hierarchically organized groups (characteristic of primates), hoard with the rise of a division of labor in humans, and justice with ultra-social groups (typical of modern humans; Haidt 2012). Thus novel tasks were thrown up by novel dimensions of the niche within which mammals in the human lineage came to live; and additional motives evolved to fulfill those needs.

Table 2 shows the feelings associated with each motive. The comfort drive is associated, for example, with feelings of discomfort and pain, and a sense of relief once the goal has been accomplished. The affiliation motive is accompanied by feelings of sympathy, loneliness, anxiety, and panic in an abandoned infant. When affiliation efforts are successful this gives feelings of gratitude or elevation, and when a social partner is lost this occasions grief. While feelings should not be mistaken for the motives that occasion them, feelings are associated with the mental reward system that is the common currency of all motives (Bindra 1978; Toates 1986; Berridge 2003). Rewards determine what animals do and do not learn about through associative learning, which is fundamental to animal and human intelligence (Dickinson 2012).

Our deductive approach makes motives recognizable and statistically dissociable chunks or "modules" (Tooby et al. 2008), based on the ecological tasks they evolved to serve. Though we predict that each motive should be associated with a mechanism in the brain that has unique parts, each is unlikely to be a wholly independent adaptation. Rather, it is probable that sections of the motivational system overlap, for example, if they subserve the same needs. Thus, hoard and create should be similar in terms of how they work and where they are instantiated in the brain, not only because both originated at the same period of evolutionary history, and because both are emotions, but also because both of these motives are designed to address the issue of maximizing environmental capital. Thus, we argue that while individual motives can be identified in functional terms, it is not necessarily the case that an evolved organ such as the brain will instantiate them in separate "plots" of tissue, with unique sets of inputs and outputs. Rather, the anatomy or architecture of motivation that we have identified—where certain motives share needs, and have been added piecemeal to an operative organ over time as new ecological tasks have become relevant—suggests that motives will be found to overlap with others in terms of inputs, outputs, information processing mechanisms, and location.

Motives: What's the Evidence?

We have postulated 15 motives that drive the behavior that meets the eight key human needs. How can we test whether our deductive process has, in fact, led us to the definitive list of human motives? (1) Provided that we employ rigorous constraints as to what can and cannot be motives, we should be able to find convergence in the existing literature. (2) If we are right, we would expect brain structure and neurochemistry to reflect 15 discreet and dissociable motives. (3) Each motive should reflect a unique kind of evolutionary problem and solution as identified in evolutionary theory. Finally, (4) we would expect to find specific pathologies associated with the malfunctioning of each motive.

Existing Evidence

The first means of testing whether there are 15 dissociable human motives is comparison with the existing literature on motivation. This is not straightforward because, as we have noted, existing lists use different approaches, assumptions, and definitions. Nevertheless, Online

Resource 1 shows that our list identifies those constructs as motives that have been previously mentioned most often by scholars in this area (see the final column in Online Resource 1). Our list, though theoretically derived, thus fits the set of motivational constructs derived from introspection, projective tests, or linguistic analysis.

Other constructs that have been proposed are not motives by our definition. Some are long-term objectives associated with conscious planning (such as career, leadership, legacy, salvation, and health), which produce an idiosyncratic sequence of behaviors, not a recurrent episode, and hence cannot reflect an evolved need. Other constructs refer to moods, or long-lasting affective states (e.g., sense of well-being, harmony), not associated with goal-directed behavior designed to satisfy specific needs. Yet others of these constructs are personal or political values—i.e., enduring ideals shared by the members of a cultural group, such as honesty, tradition, equality, and peace. While laudable, they are not evolved responses to evolutionarily recurrent situations. Others are tactics associated with the situational execution of motives (submission, for example, is a tactic related to the status motive); yet others are personality traits, or psychological characteristics that produce stable behavioral differences between individuals (such as shyness, modesty, or secretiveness). The final column of Online Resource 1 shows how we classify these previously proposed constructs.

Our approach helps to disentangle these multifarious motivational constructs using simple criteria. If the candidate can be expressed as a function (e.g., "optimize resources"), it is a need. If it sounds strategic—a recurrent way of solving a particular kind of ancient problem (e.g., "improve habitat")—it is a motive. If it suggests a response to a specific situation (e.g., "engage in aggression"), it is a tactic. Motives are always associated with well-defined and finite goal states that can be arrived at through a brief bout of behavior; if such a state cannot be readily identified, the candidate is probably not a motive.

Several of the motivational constructs in Online Resource 1 could be better described as *feelings* (anger, happiness, jealousy). Our definitions separate motives from feelings, as we have made clear. Feelings may accompany the engagement of a motive, or the success or failure in achieving a goal (McClelland 1987; Winter 1996; Sheldon et al. 2001). Feelings, however, are typically not the instigators, nor the promoters, of action. They rise to consciousness, and so become felt, after the fact, rather than representing the impetus to engage in sustained goal-directed behavior of a particular type (Damasio 1994). Even when feelings are consciously felt prior to action (as in the case of hunger, lust, or injustice), we argue that they are not the causes of subsequent action, which are rather motivational systems that remain subconscious.

Anger and sympathy appear frequently in the needs lists. However, in our vocabulary, these constructs are tactics that can be used in a variety of situations to achieve different goals. For example, anger is a tactic (as well as feeling) that results in the acquisition of resources (hoard), sexual combat (lust), protection of offspring from attack (nurture), or retribution for social cheating (justice). Similarly, sympathy works to repair social relationships of almost any kind. It is probably the fact that they have an identifiable feeling that makes them perennially popular in needs lists.

Three constructs appear in Online Resource 1 that can be called "super-constructs": achievement, power, and autonomy. These are popular (Mayer et al. 2007), however, we see problems in calling these motives. Achievement motivation refers to the desire to perform tasks with greater proficiency or to a higher standard (Atkinson 1964). Recent work suggests that there are, in fact, two kinds of achievement goals: a learning goal, in which individuals are concerned with gaining competence or mastering the set of knowledge or skills necessary to successfully carry out the task at hand; and a performance goal concerned with trying to find out how capable one is in achieving normative-based standards, doing better than others, or doing well without a lot of effort (Dweck 1986). These are the motives that we have labeled curiosity and play.

Power is concerned with the desire to dominate or to have an impact on others or the world at large, and is often associated with concern about social reputation, prestige, and position (Winter 1973). Findings from longitudinal studies show that power-motivated individuals attain higher occupational levels (McClelland and Franz 1992), and have more control over how resources are distributed (Depret and Fiske 1993). Individuals can perceive their power from the deference behaviors others exhibit (Ellyson and Dovidio 1985). These factors suggest that power coincides with status (Hall et al. 2013).

Self-determination theorists argue that the third "super-construct," autonomy, is essential to the full functioning and mental health of individuals (Ryan and Deci 2006). From our perspective, in which the notion of motivation is constrained to evolved goal pursuit, autonomy cannot serve as a motive because it requires self-awareness, or seeing oneself as an independent agent in the world (Anderson and Lux 2004). Autonomy or independence is rather a long-term objective, not an evolved goal. In fact all three "super-constructs" require conscious long-term planning and have been studied from that perspective in humans (e.g., in terms of career success), implying that they are not basic motives (Schultheiss 2006).

We are alone among scholars in introducing three separate sex-related motives. Very few identify attraction as an independent motive. Starch (1923) and Reiss and

Havercamp (1998) mention only romance, not the need for sex or to pair-bond, and Chulef et al. (2001) link sex and romance as a single need. Previous evolutionary scholars combine attraction and mating with mate choice (obtain a partner who will enhance one's own fitness) and relationship maintenance (maintain a mating bond with a desirable partner) as their two sexual needs (Kenrick et al. 2002; Bernard et al. 2008). So what justifies making attraction a separate motive? In humans, a number of behaviors can be considered to be investments in sexual capital, with evolutionarily significant goals. Augmenting or modifying the human body has been common since Neanderthals first used red ochre (Knight 1995). Clothing, perfume, and cosmetic surgery are major industries serving the human goal state of being attractive. Thus, attraction should be seen as distinct from lust.

Of course, in humans, given the complexity of our brains, multiple motives are likely to feed into the causation of any given behavior. For example, playing sport can primarily involve a desire to increase skill (play), but also to demonstrate prowess to the opposite sex (attract) and bond with fellow team members (affiliation). In some cases, multiple, equally strong motives will pull an individual in different directions. Long-term plans can serve to meet a variety of needs at the same time while ignoring others. However, the fact that much human behavior is complicated does not mean that we should abandon the search for its component constructs.

Motives and Evolutionary Theory

Since our approach derives from evolutionary biology, it is perhaps not surprising that each motive can be associated with a body of theory concerning the evolution of animal and human behavior (Table 2, column 8). The problems solved by the basic drives are tightly connected to biological fitness, and have been well characterized theoretically. For example, mate selection describes the problem of getting good combinations of genes from sexual intercourse. Hunger concerns the need to optimize the benefits from foraging for food (Stephens and Krebs 1987). Pain, though rarely theorized, is a proximal physiological signal of the presence of an evolutionary problem associated with discomfort (Willis 1985). Fear and disgust have evolved specific sensory "antennae" for detecting and avoiding predators or pathogens before pain becomes a problem. "Freeze, fight, or flight" is the rubric under which standard classes of predator avoidance strategies are described (Gray 1988); a more varied set of behavioral strategies are required to keep pathogens from getting into a host body (Curtis and Biran 2001; Curtis et al. 2011).

Several theories relate to the problems of family relationships. Sexual selection strategies concern attraction or the signaling of mate quality (Buss 2003). Parental investment theory describes the "love" problem of securing parental investment in altricial offspring (born physiologically immature and hence dependent on care) (Clutton-Brock 1991). Kin selection theory concerns the issue of helping genetic relatives, which is promoted via the nurture motive (Hamilton 1964).

Similarly, the three social motives can each be associated with recognized mechanisms of social cooperation. Direct reciprocity allows individuals to get the benefits from cooperation and trade among group members through affiliation. Indirect reciprocity—when individuals can learn of one another's reputations through communication as well as personal experience (Nowak and Sigmund 2005)—establishes that there are benefits associated with higher status. Finally, *strong reciprocity* is the specific form of reciprocity that involves third-party punishment of those who attempt to cheat on the social contract, and thus promotes cohesion in ultra-social groups—justice (Gintis 2009).

A new body of evolutionary theory known as niche construction theory (Odling-Smee et al. 2003) describes the ways animals gain genetic advantage indirectly, through the manipulation of their environments. Two motives drive such behavior: hoard is concerned with resource accumulation, while create is about ensuring that the local environment supports the activity required for reproduction and survival.

Finally, there are theories about uncertainty reduction (Dall et al. 2005) and skill development (Rasmussen 1983; Ash and Holding 1990; Plourde 2008) that relate to the evolutionary problems addressed by the motives of curiosity and play.

The existence of a literature for each of the functions we have identified is another, independent kind of evidence that such a set of motives arises naturally from consideration of animal life ways. However, in this context, it is interesting to note that other authors using evolutionary reasoning have come to different conclusions about motives. Kenrick et al. (2002, 2010) identify six "fundamental domains of sociality": protect oneself from social threats against resources, develop and maintain cooperative alliances, increase or maintain status, locate high-quality mates, maintain alliances with mates, and successfully raise offspring and care for other relatives. A number of Kenrick's domains we consider to be tactics rather than motives (e.g., coalition formation (associated with affiliation), mate choice (lust) and resource defense (hoard)). Kenrick's list also includes only a subset of the social motives we identify; we suggest humans are also concerned with investing in sexual attractiveness and their social proficiency.

Bugental (2000) also limits her concern to social life, suggesting that there are five social domains: attachment

(offspring-parent love), hierarchical power (status), coalition formation, reciprocity, and mating. Bugental's list does not overlap perfectly with ours (nor Kenrick's—even though they both concentrate on social life)—again, partly due to the inclusion of what we identify as tactics rather than motives (coalition formation, reciprocity), but also because of different perspectives on human mating (i.e., no mention of attraction or pair bonding).

The third scheme based in evolutionary psychology is due to Bernard et al. (2005). Their list—aggression/dominance, curiosity, safety, play, health, sex, appearance, acquisition, self-development (skills/knowledge), strength/competitiveness, affection/attachment, altruism/aid, morality/conscience, legacy (make world better place), and meaning/self-fulfillment—is partially derived from Bugental and Kenrick et al., but also based on "classic ideas" in evolutionary theory, such as natural and sexual selection, inclusive fitness (Hamilton 1964), parental investment theory (Trivers 1972), and others. This feature makes their effort the most closely allied to ours in terms of method. Where we differ is in terms of process: we first rigorously identified needs, whereas Bernard et al. went straight to a list of motives. Thus, it seems that reliance on a theoretical orientation is insufficient; one must have the same ambition (e.g., to cover just social life or to be more general), and to follow the same deductive procedures for the outcome of such an effort to be replicable.

Pathologies of Motives

If the motives we have postulated are indeed dissociable functional units in the brain, each will be subject to developmental variation. Hence, we would expect to find recognizable conditions where hyper-, hypo-, or dysfunctioning of individual motives leads to pathological behavior. Some candidates are set out in the last column of Table 2.

Closely aligned with the need for better motivational measurement is the issue of personality scales. In our view, motives should provide a more detailed and illuminating account of individual differences than is currently available from personality psychology, where the dominant "Big Five" model (Costa and McCrae 1992) was developed based on empirical factor analyses (from work by Cattell, and before him, Murray), and which has proven difficult to tie to a more fundamental theoretical foundation (Nettle and Clegg 2006; Denissen and Penke 2008). We suggest that individual differences can be more fruitfully explained by variation in the relative importance of motives than from personality dimensions as currently constructed. Being able to characterize personality accurately has major implications for the determinants of the behavior of individuals, whether in career choices, in relationships, or as consumers (Miller 2009).

Discussion

It seems that the effort to develop an all-inclusive model of motivation has been largely abandoned, except for scattered efforts by evolutionary psychologists (Bugental 2000; Kenrick et al. 2003; Bernard et al. 2005). What is the point of identifying a complete set of human motives? First of all, it is vital for behavioral science that, if motives exist, we characterize them correctly, and then agree about what to call them. No scientific endeavor can progress without some accord between scientists as to the nature and nomenclature of its elementary components. Fields such as animal cognition and human psychological science need theory-driven prediction to set the agenda for empirical research into the structure and functioning of brains.

Here we have proposed 15 distinct motives using reasoning about the evolutionary purposes of kinds of behavior, and we have given them candidate labels. Using this approach has further yielded principled definitions of words concerning behavioral causation such as motivation, motives, needs, and goals. It also suggests a way in which the long-contested terms "drives" and "emotions" could usefully be recast.

An example of how this theory-driven approach helps to reduce conceptual confusion is the distinction that we make between motives as fundamental drivers of behavior and the consciously represented feelings that sometimes, but not always, accompany them (Nesse 1990; Griffiths 1997). According to our model, feelings may variously be associated with arousal, with satisfaction, and with outcomes of motivated behavior. A feeling of thirst or hunger may accompany a search for a drink or food, a feeling of satiation may result from consumption, and a feeling of contentment may accompany the conclusion of the behavioral episode, all of which are due to the hunger motive. There are thus many more feelings than there are motives. The reverse is also true: particular feelings can be associated with a variety of motives. Anger, for example, is associated with behavior serving a wide variety of different functions. For these reasons, feelings are unreliable indicators of motives—a fact that has major implications for measurement in psychology.

Armed with principled characterizations and definitions, neurobiology and neurochemistry will be better able to test for, and tease apart, the operative components of the brain. Comparative psychologists will be able to trace the homologous evolution of motivational structures in species other than our own. Associative reward-based learning underlies much of human and animal intelligence (Dickinson 2012). We expect such learning in animals to be organized around meeting needs (those actions that meet needs being reinforced while those that do not being edited out). Hence associative learning should be organized

around the motives we have identified in humans and other mammals. And an advanced science of motivation will allow the principled characterization of neuropathologies, currently a much-contested field, offering hope for more effective chemical and behavioral therapies.

Conclusion

Our ambition here has been to devise a means to identify the necessary and sufficient set of motives that trigger any and all motivated behavior. The crucial difference between our approach and those of previous authors is the use of a theoretical foundation and a stepwise a priori deductive process out of evolutionary biology to arrive at our list of motives. Our process specifies what organisms need to do in order to maximize fitness, examines the ecology within which this process occurs, identifies the threats and opportunities relevant to fitness maximization posed by that ecology, and deduces the mental mechanisms needed to negate these threats or capitalize on opportunities. Each stage of our argument results in a further refinement of the distinctions made possible by evolutionary principles. We thus start with a theoretical position, not an optimal size for the list. Based on the history of the evolution of vertebrate brains we constrain motives to the problem of meeting only those medium-term recurring needs that are driven neither by immediate reflexes nor by long-term conscious plans. Because of this deductive process we can present our list as a suite of interrelated claims rather than a set of independent ones.

The list of motives that results is relatively small, consisting of reproductive motives (lust, attract, love, nurture), physiological motives (hunger, comfort, fear, disgust), environmental motives (hoard and create), social motives (affiliate, status, justice), and psychological motives (curiosity and play). We submit that this list is clear and complete—qualities that have been sought for motivation lists since the first efforts of William James. The evidence from neuroanatomy, psychiatric pathology, and previous work on motivation lends support to our conceptual scheme.

Our approach also suggests that it should be possible to identify 15 distinct networks or regular patterns of neural activity that can reliably be associated with each motive. Similarly, there should also be neurochemical signatures typical of motives across mammals (excluding justice, which is unique to humans). For example, the thalamus is known to be involved in affiliation, and the opioid beta-endorphin has been shown to produce social bonding (its administration reduces separation distress in mice and chicks) (Kehoe and Blass 2004; Panksepp et al. 1978).

There is evidence from neurobiology that the motives we describe here are indeed separable mechanisms. For example, fear can be dissociated from disgust in fMRI studies (Lawrence et al. 2004). More work will be needed to identify specific areas or mechanisms for all of the motives corresponding to dissociable entities in brains (for preliminary attempts, see Panksepp 1998; Schultheiss 2008). However, brain imaging studies need to take careful note of the hypothesized evolutionary purposes of each so as to be able to arouse the correct response in a scanner. Work on dissociating the basic emotions has been difficult (Hennenlotter and Schroeder 2006; Chen et al. 2009) at least in part because researchers in neuroscience have not paid attention to the different evolutionary purposes of each when devising stimulus sets. Hence, subjects in scanners have been tested with stimuli that mix motives (e.g., fear studies have used snarling dogs and disgust studies flesh wounds, stimuli which should elicit both disgust and fear), which have probably clouded the results (Phillips et al. 1997; Sprengelmeyer et al. 1998; Moll et al. 2005). Setting out the evolutionary functions of motives should also help to disentangle the complex story of the multiple functions of the many neuropeptides known to be involved in both animal and human motivation. Empirical work is, of course, now needed to test all of these claims.

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