CHAPTER

5

The Motivational Architecture of Emotions

Marco Del Giudice

Abstract

Evolutionary research on emotion is increasingly converging on the idea that emotions can be understood as superordinate coordination mechanisms. Despite its plausibility and heuristic power, the coordination approach fails to explicitly address the relations between emotions and motivation. This chapter aims to fill this conceptual gap. The author argues that the current view of emotions as coordination mechanisms should be extended—and partially revised—to include motivational systems as an additional control layer, responsible for the activation and deactivation of specific emotions in the pursuit of domain-specific goals. The extended coordination approach proposed in this chapter facilitates the analysis of folk emotion categories; helps clarify the distinction between emotions and moods; suggests new ways to think about emotion regulation; and provides a more natural interface to model the link between emotions and personality.

Key Words: emotions, emotion regulation, mood, motivational system, personality

Evolutionary research on emotion is increasingly converging on the idea that emotions can be understood as superordinate *coordination mechanisms* or *coordination programs* (Al-Shawaf et al., 2016; Al-Shawaf & Lewis, 2017; Nesse, 1990, 2004; Sznycer, Cosmides, et al., 2017; Tooby & Cosmides, 1990, 2008, Chapter 2 in this volume). In a nutshell, emotions evolved to solve the *coordination problem*—the adaptive problem of how to orchestrate large suites of cognitive, physiological, and behavioral mechanisms so as to produce efficient but flexible responses to recurrent fitness-relevant situations. What we call emotions are organismic modes of operation that fulfill this crucial coordination function; the same applies to other feelings that are not usually categorized as emotions, such as hunger and sexual arousal.

Importantly, coordination mechanisms do not map in a one-to-one fashion on folk categories such as "anger" or "fear," which are often used to refer to multiple mechanisms with somewhat distinct features and functions (Al-Shawaf et al., 2016; Sznycer, Cosmides, et al., 2017; see also Fiske, 2020; Scarantino, 2012). And because emotions have evolved through a complex history of divergence and progressive specialization, they are best described as a multitude of overlapping neurocomputational mechanisms with somewhat fuzzy boundaries (Nesse, 1990, 2004, 2020). Thus, simple taxonomies based on a small number of distinct, sharply differentiated emotions are inevitably limited and artificial; while an adaptationist approach is the best way to "carve emotions at their functional joints" (Sznycer, Cosmides, et al., 2017), there are going to be multiple reasonable ways to do the carving, and inherent uncertainty about the number of mechanisms and their exact boundaries. The coordination approach suggests that the classic distinction between "basic" and "non-basic" emotions is not functionally meaningful (Al-Shawaf et al., 2016; Cosmides & Tooby, 2000); however, it is compatible with some recent updates of basic emotion theory, most notably the reformed version proposed by Scarantino (2015; see also Keltner et al., 2019).

The coordination approach to emotions is biologically plausible, heuristically powerful, and integrative in scope. I believe it has the potential to become the "standard model" in biologically oriented emotion research. However, the model is still incomplete in many respects, and some important issues have remained unaddressed so far. Perhaps the biggest conceptual gap concerns the relations between emotions and motivation. Proponents of the coordination approach have argued that one of the functions of emotion programs is to regulate the individual's motivational priorities (e.g., safety is prioritized when fear is activated; Al-Shawaf et al., 2016; Cosmides & Tooby, 2000; Tooby & Cosmides, 2008). The same authors have invoked the concept of *motivational systems*—computational mechanisms that regulate behavior and decision-making in fitness-relevant domains. For example, Tooby and colleagues (2008) discussed the sexual and altruistic motivational systems as examples of mechanisms that rely on the "kinship index," a hypothetical *internal regulatory variable* (IRV) that tracks the estimated genetic relatedness between the focal individual and other people (e.g., siblings). The sexual system is associated with emotions of lust and disgust, whereas the altruism system is associated with love and closeness. They argued that "[a] high kinship index produces feelings of disgust when accessed by the sexual motivation system at the possibility of sexual contact with the person, and impulses to help when accessed by the system regulating altruistic motivations" (p. 256). This seems to imply that motivational systems activate emotional programs in response to goal-relevant situations. However, the authors also stated that anger orchestrates the activity of "downstream" motivational systems that regulate cooperation and aggression (p. 266). In other papers, emotions such as pride are described as systems that include "motivational subcomponents" (e.g., Sznycer, Cosmides, et al., 2017). While the coordination approach postulates a tight coupling between emotions and motivational systems, the nature of this relation is not clearly specified. As noted by Beall and Tracy (2017), the concept of emotions as coordination mechanisms overlaps substantially with the concept of motivational systems in the literature on motivation (e.g., Kenrick et al., 2010), but the two have not been explicitly connected by evolutionary scholars.

In this chapter, I aim to fill this gap. I argue that the current view of emotions as coordination mechanisms should be extended—and partially revised—to include motivational systems as an additional (second-order) control layer, responsible for the activation and deactivation of specific emotions (Aunger & Curtis, 2013; Beall & Tracy, 2017; Bowlby, 1982; Del Giudice, 2018; Gilbert, 1989, 2005; Lichtenberg et al., 1992; Scott, 1980). Motivational systems regulate the pursuit of key biological goals and coordinate emotions in the service of those goals. From a computational perspective, they take up some of the functions that have been ascribed to emotion mechanisms, including the detection and evaluation of fitness-relevant situations. This reconceptualization has important theoretical implications: just like emotions can solve the basic coordination problem, motivational systems can efficiently solve the higher-order problems that arise in the pursuit of flexible, context-sensitive coordination. Motivational systems contribute to the robustness and evolvability of psychological architectures, by serving as central nodes in a regulatory network with a hierarchical "bow-tie" structure (Csete & Doyle, 2004). A motivational-systems perspective facilitates the analysis of folk emotion categories, and helps clarify the distinction between emotions and moods. At the end of the chapter, I illustrate how the extended coordination approach suggests new ways to think about emotion regulation, and provides a more natural interface to model the link between emotions and personality.

Motivational Systems

Historical Roots of the Concept

The theory of motivational systems originates in the psychology of the early 20th century, most notably in McDougall's concept of *instincts* (1908). McDougall took a strikingly modern approach (Boden, 1965) and described instincts as goal-directed processes that orient attention and perception (cognitive component), give rise to emotional experiences (affective component), and elicit specific action tendencies (conative component). On this view, instincts are not rigid or stereotyped—on the contrary, they motivate learning and enable adaptive behavioral change. McDougall (1908) proposed six "primary" human instincts, each with an associated primary emotion: *flight* (fear), *repulsion* (disgust), *curiosity* (wonder), *pugnacity* (anger), *self-abasement* or *subjection* (negative self-feeling), *self-assertion* or *self-display* (positive self-feeling or elation), and the *parental instinct* (tenderness). Four additional instincts lacked a clearly defined emotional component: *reproduction*, *gregarious instinct*, *acquisition*, and *construction*. From a functional perspective, McDougall's cognitive-affective-conative processes can be likened to the emotional coordination mechanisms envisioned by present-day evolutionary scholars.

In his later work, McDougall (1932) switched from "instincts" to "propensities," to avoid the former's connotations of deterministic rigidity. He also expanded the list to include *appeal* or help-seeking, *laughter*, a *migratory* propensity, and some basic physiological motivations (*food-seeking*, *comfort*, and *rest/sleep*). By that time, however, the popularity of instinct theories in psychology was fading. There were a number of reasons for this reversal of fortune. To begin with, some theorists had started using the concept of instincts in a circular fashion, raising doubts about the explanatory status of this approach. More importantly, behaviorism was on the rise, and its proponents kept attacking instinct theories as old-fashioned and unscientific.[1] On a deeper level, it seemed impossible to reconcile McDougall's "purposive" and goal-oriented view of the mind with a truly "mechanistic" explanation of behavior (see Heckhausen, 2018; Krantz & Allen, 1967; McDougall, 1921, 1924; Scheffer & Heckhausen, 2018). Instinct-like constructs like "needs" and "ergs" would keep resurfacing in the field of personality (e.g., Cattell, 1957; Maslow, 1954; Murray, 1938), but for most psychologists, the concept was going to remain scientifically suspect, if not outright taboo.

At the same time that they were being (prematurely) abandoned in psychology, instincts were taking center stage in the emerging discipline of ethology. Building on Craig's (1918) appetitive-consummatory model, Tinbergen (1951) advanced the notion that instincts can be redefined as hierarchically organized structures of behavior. For example, the stickleback fish's reproductive instinct includes the sub-instincts of fighting, nest building, mating, and offspring care; each of these sub-instincts can trigger a set of appropriate consummatory behaviors (e.g., chasing, biting, threatening as fighting behaviors). Tinbergen's seminal contribution was expanded and recast in the framework of control systems theory (cybernetics), yielding the concept of *behavioral* or *motivational systems*. (In the biological literature, these two labels are essentially synonymous, and I use them interchangeably in this chapter.) Behavioral/motivational systems were conceptualized as hierarchies of feedback-regulated processes, with dedicated goals and subgoals, that control the sequencing of behavior through complex loops of activation and inhibition (Baerends, 1976; McFarland, 1971, 1974; Toates & Archer, 1978).

Conceptual Developments

While behavioral systems theory has informed decades of animal research, ethologists have generally avoided the issue of emotions and affective states (Burghardt, 2019; Burghardt & Bowers, 2017). But as ethological ideas started to filter back into psychology, the connection between the operation of behavioral systems and the experience of emotions became an important topic of investigation. The key contributions in this respect were made by Scott (1980) and Bowlby (1982). In Bowlby's model, feelings are experienced in relation to the activation of a behavioral system, the progress of current behavior in relation to the system's "set goal," and the eventual consequences of behavior (success vs. failure to achieve the set goal).[2] For example, the *attachment system* in infants and children has the set goal of maintaining the proximity and/or availability of the caregiver (and the ultimate function of ensuring the child's survival). The system is activated by perceived dangers or separations (with feelings of anxiety, fear, distress, loneliness), and successfully deactivated by the attainment of proximity and protection (with feelings of relief, comfort, and "felt security"). Lack of progress in reaching proximity (e.g., because of an inconsistent or insensitive caregiver) can elicit anger and protest behaviors (e.g., crying, yelling), whereas protracted failure of the system leads to sadness, despair, and ultimately emotional detachment.

Bowlby's theory of motivation was extended by Gilbert (1989) and Lichtenberg and colleagues (1992). In addition to attachment, Lichtenberg's list of motivational mechanisms includes *defensive*, *exploration/competence*, *sexuality*, *caregiving*, and *affiliative* systems. Gilbert's work is focused on interpersonal relations, with an emphasis on what he calls the "social mentalities" related to *care eliciting* (attachment), *caregiving*, *social ranking* (competition), *formation of alliances* (cooperation, affiliation), and *mating/sexuality* (Gilbert, 2005). Along similar lines, Bugental (2000) argued for the existence of five basic systems that regulate social relationships in our species: *attachment*, *mating*, *reciprocity*, *hierarchical power*, and *coalitional group* (a system that has the goal of acquiring and defending shared group resources, and is involved in intergroup conflict). Bugental also tracked the emergence and development of these systems across the life span and considered their possible neurobiological correlates.

The model of motivation that emerges from this tradition has some notable implications. First, a motivational system can have multiple, thematically related goals, rather than a single overarching goal. For instance, the goals of a system that regulates status/dominance relations may include improving, maintaining, and displaying one's status, as well as deferring or submitting to higher-status individuals (e.g., Gilbert, 1989, 2005). These narrower motivations can be thought of as subsystems within a broader neurocomputational mechanism. Second, motivational systems can embody sophisticated and context-sensitive operation rules, that respond flexibly to the state of the environment and draw on internal representations (including internal regulatory variables) and models of the world (e.g., inferences about the caregiver's intentions and emotions, expectations about the caregiver's likely response, representations of the child's worth and value to the caregiver). Third, motivational systems can reciprocally potentiate and inhibit each other's activity, and thus achieve a degree of collective self-organization without the intervention of other prioritization mechanisms; for example, when the attachment system is activated, it quickly suppresses play and curiosity-driven exploration (Bowlby, 1982). Fourth, a given motivational system is not tied to a single emotion, but to a *set* of characteristic emotions (both "positive" and "negative"). Different emotions are activated depending on contextual factors, internal representations, and the moment-to-moment consequences of the individual's actions. Finally, emotions may be shared by more than one system. For example, anger—or, quite possibly, multiple domain-specific variants of the "anger" program—can be triggered in the context of attachment, but also in those of status competition, aggressive defense, pair bonding, or reciprocal exchange (in response to cheating and betrayal). One implication is that affective labels have low motivational specificity; simply knowing that someone feels "angry" says relatively little about their goals and motivational state.

A distinct and highly influential approach to motivation is Panksepp's research program on "basic emotional systems" (Panksepp, 1998, 2005, 2011; Davis & Panksepp, 2018). Working from a neurobiological and comparative perspective, Panksepp used a broad array of evidence from animal research to describe seven emotional systems shared by all mammals, which give rise to basic emotions or "core emotional feelings." These mechanisms are mainly implemented by subcortical circuits; they are labeled *RAGE* (anger/rage), *FEAR*, *PANIC* (separation panic/sadness), *LUST*, *CARE* (care/nurturance), *PLAY* (joy), and *SEEKING* (a generalized appetitive/exploratory system that regulates reward seeking). More recently, Toronchuk and Ellis (2013) suggested that the model should be expanded to include two additional systems, *DISGUST* and *POWER/dominance*.

One notable contribution of this research program is the attempt to specify in some detail how different systems interact by potentiating or inhibiting one another's activity. For example, Panksepp (1998) drew on neurobiological and pharmacological evidence to argue that RAGE inhibits the activity of FEAR, PANIC, and SEEKING, whereas FEAR potentiates the other three systems. An important limitation of the model—which self-consciously echoes McDougall's instinct theory—is the assumed one-to-one correspondence between each system and one specific emotion, which precludes the strategic flexibility and computational richness of the multi-emotion systems theorized by Bowlby and others. Another limitation is the insistence that, to be truly "basic," emotional systems must be shared across all mammalian species. Each species faces somewhat distinctive adaptive problems, and humans have evolved complex forms of social interaction that make them unique among mammals and primates (e.g., Borgerhoff Mulder & Beheim, 2011; Hrdy & Burkart, 2020, Chapter 47 in this volume; Kaplan et al., 2009; Pinker, 2010; Quinlan, 2008). Thus, humans can be expected to possess species-specific motivations and emotions, as well as many unique variations on pan-mammalian motives (Al-Shawaf et al., 2016; Aunger & Curtis, 2013).

Some Recent Contributions

In the last 10 years or so, there have been several notable contributions based on the concept of behavioral/motivational systems, including integrative works on the systems underlying caregiving (Brown et al., 2012; Schaller, 2018), pair-bonding (Fletcher et al., 2015), dominance and status (Anderson et al., 2015; Johnson et al., 2012), and play (Pellis et al., 2019). Woody and Szechtman (2011) presented a detailed analysis of the *security system* (or *precaution system*; Boyer & Liénard, 2006), a motivational system specialized to prevent rare, potential threats and associated with anxiety and apprehension (in contrast with fear triggered by imminent threats).

In their evolutionary renovation of Maslow's ever-popular "pyramid of needs" (1954), Kenrick and colleagues (2010) described seven fundamental motives—*immediate physiological needs*, *self-protection*, *affiliation*, *status/esteem*, *mate acquisition*, *mate retention*, and *parenting*. The ordering of the motives reflects both their cognitive priority (higher to lower precedence) and their timing of emergence during the life course (earlier to later development). Each motive is served by one or more motivational systems, which in turn are composed by "(a) a template for recognizing a particular class of relevant environmental threats or opportunities, (b) inner motivational/physiological states designed to mobilize relevant resources, (c) cognitive decision rules designed to analyze trade-offs inherent in various prepotent responses, and (d) a set of responses designed to respond to threats or opportunities represented by the environmental inputs (i.e., to achieve adaptive goals)" (Kenrick et al., 2010, p. 306). Neel and colleagues (2016) developed the framework by adding *disease avoidance* as distinct from fear-based self-protection, and replacing parenting with a broader motive of *kin care*.

Although Kenrick and colleagues repeatedly implied that evolved responses to threats and opportunities include the experience of feelings, they remained vague about the specific nature and adaptive role of those feelings. Beall and Tracy (2017) set out to complete the framework by linking the activation of each fundamental motivation with the onset of a distinct emotion: fear for self-protection, happiness for affiliation, pride for status/esteem, lust for mate acquisition, romantic love for mate retention, and tenderness for parenting/kin care. In line with the coordination approach, the emotion triggered by a motivational system orchestrates cognition, physiology, and behavior so as to reach the system's adaptive outcome (effectively working as an "effector" of the system). Beall and Tracy made a valuable contribution by explicitly linking the concept of motivational systems with the coordination approach to emotions. As they themselves acknowledged, the idea that complex computational mechanisms like the status/esteem system are associated with just *one* characteristic emotion (instead of multiple emotions, including not only pride but also shame, embarrassment, etc.) is problematic and should be revised. Luckily, more sophisticated models of motivation are readily available (see above) and can be integrated within the same basic framework.

Drawing on a century of literature on this topic, Aunger and Curtis (2013) presented a biologically informed taxonomy of human motivational systems (which they labeled "motives"). Their list comprises *hunger*, *comfort*, *fear*, *disgust*, *lust*, *attract* (a system specialized for mating competition), *love* (pair-bonding), *nurture*, *affiliate*, *status*, *justice* (a system that regulates reciprocal exchange), *hoard* (resource acquisition), *create*, *curiosity*, and *play*. I made a similar attempt to present an organized taxonomy of motivation in a book on psychopathology (Del Giudice, 2018). The admittedly partial list of systems I proposed includes *aggression*, *fear*, *security*, *disgust*, *status*, *mating*, *attachment*, *caregiving*, *pair bonding*, *affiliation*, *reciprocity*, *acquisition*, *play*, and *curiosity*.

A Map of Human Motivational Systems

Even though different scholars have proposed somewhat different taxonomies of motivational systems, there are more commonalities than differences. If one excludes "physiological needs" like hunger, thirst, and thermoregulation, human motivations can be related to five broad categories of adaptive problems: (a) prevention and avoidance of physical hazards; (b) acquisition and enhancement of resources (including "embodied" resources such as knowledge and skills; Kaplan et al., 2000, 2007); (c) mating and reproduction; (d) relations with kin; and (e) relations within and between groups. Each of these categories comprises several specific problems that can be solved by specialized motivational systems, each equipped with domain-relevant goals and algorithms.

Figure 5.1 shows a partial map of human motivational systems, derived from recent syntheses of the literature (mainly Aunger & Curtis, 2013; Del Giudice, 2018; Kenrick et al., 2010). I briefly describe each of the systems later in this section. Note that, while the taxonomy in Figure 5.1 has enough support to serve as a useful starting point, it is also provisional in many respects. Some systems (e.g., fear, attachment) have been studied extensively for decades, and we have detailed information on their adaptive goals, activating cues/situations, operating rules, associated emotions, neurobiological bases, and developmental patterns; other putative systems (e.g., acquisition, creation) are understood only in their generalities, or represent plausible but still largely hypothetical adaptations.

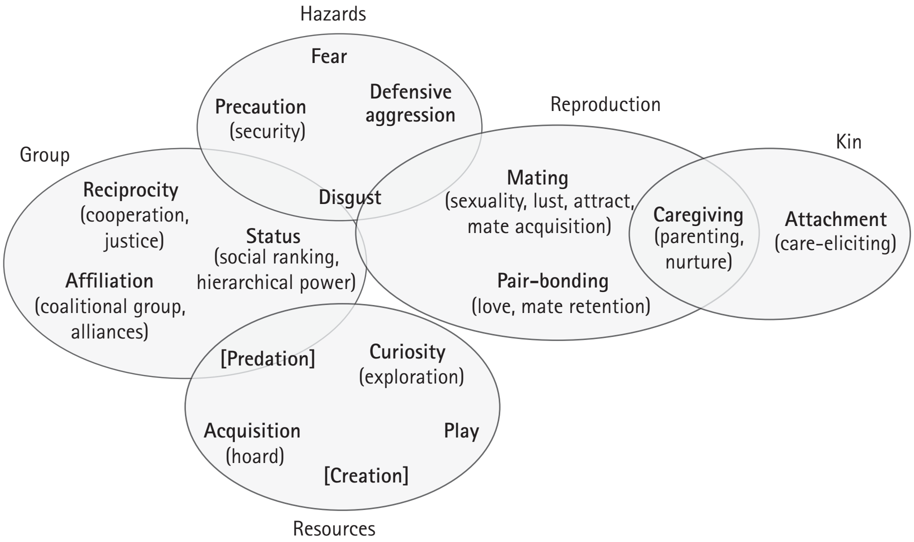

Figure 5.1. A partial map of human motivational systems, grouped into five broad categories of adaptive problems. Some alternative labels used in the literature are shown in parentheses. The systems in square brackets are still mostly hypothetical but warrant further investigation.

How Many Systems?

Questions about the "right" number of constructs are as old as the psychology of motivation; lack of agreement on the number of human instincts was a contributing factor to the waning of instinct theories in the 1920s (Krantz & Allen, 1967; Scheffer & Heckhausen, 2018). A hundred years later, we are much better equipped to deal with this problem, having realized that the evolution of complex biological mechanisms (including the brain) proceeds by reuse, duplication, partial differentiation, and gradual accrual of function (see Barrett, 2012, 2015a). This intricate process of "descent with modification" does not deliver neatly packaged mechanisms with simple, well-specified functions—instead, it produces overlapping mechanisms with somewhat indistinct boundaries, multiple functions, and a great deal of redundancy (Nesse, 2020). Moreover, most computational mechanisms are composed of simpler components or sub-processes, some of which may be shared with other mechanisms. The bottom line is that, as in the case of emotions, it may not be possible to converge on a single, unambiguous taxonomy of motivational systems; there will always be multiple defensible ways to draw boundaries between related systems, and multiple levels of resolution to describe the same computational processes (Kenrick et al., 2010). In fact, the problem of "how many motivational systems there are" is essentially the same problem of "how many emotions there are"—only somewhat more tractable, because there are many fewer motivational systems than distinguishable emotions.

To illustrate, Gilbert (2005) described a single *sexual system* that covers everything from sexual desire to romantic love; Kenrick and colleagues (2010) separated *mate acquisition* (sexual desire and attraction) from *mate retention* (including pair-bonding); while Aunger and Curtis (2013) drew a subtler distinction between systems that regulate sexual desire (*lust*), mate attraction and competition (*attract*), and pair-bonding (*love*). There is no doubt that sexual desire and romantic love share some deep functional connections; however, they can occur independently of one another, have different emotional constellations and evolutionary histories, and serve different goals within the broader task of reproduction (more on this below). I believe there is a strong case for treating mating and pair-bonding as distinct motivational systems that can become activated separately or in combination; but it is also possible to regard them as part of a larger, composite system with phylogenetically older and newer components. In the process of pair-bonding, passionate love gives way to affection and "loving attachment" (Tennov, 1999). These two phases of pair-bonding are emotionally distinct, and may or may not be best described as outputs of the same system. The case of sexual desire vs. mate attraction is even less clear-cut, and the decision to postulate one or two systems becomes more arbitrary (at least in the present state of knowledge) and dependent on one's preferences for "lumping" vs. "splitting." This ambiguity is a predictable consequence of the organic, evolved complexity of motivational mechanisms (Nesse, 2020).

Needless to say, these complications should not deter researchers from trying to map our species' motivational systems (and associated emotions) as accurately and meaningfully as possible. Evolutionary task analysis (Al-Shawaf, 2016; Al-Shawaf & Lewis, 2017; Lewis et al., 2017; Tooby & Cosmides, 2015) is a powerful tool to identify putative systems and draw functional distinctions among them—especially in combination with a rich database of behavioral, neurobiological, and comparative/phylogenetic evidence. This is no different from how evolutionary scholars approach the analysis and classification of individual emotions, as exemplified in many chapters of this volume.

A focus on the adaptive tasks and computational logic of motivational systems is essential to overcome the shortcomings of atheoretical correlational methods, such as factor analysis and principal component analysis (PCA). Patterns of correlations among multiple types of behaviors, emotional experiences, and so forth can be informative and heuristically useful; but when they are used to make inferences about the *mechanisms* that give rise to those behaviors, emotions, etc., correlational analyses are severely limited and can be downright misleading (see also Lukaszewski et al., 2020). The output of a motivational system is not fixed, but conditional on the nature of the current situation (e.g., threat vs. opportunity) and the individual's success or failure relative to the system's goal. These appraisals and the emotional responses they trigger are further modulated by individual differences in the system's working parameters and the value of the relevant regulatory variables. Activation of attachment needs can lead to vigorous crying but also withdrawal and detachment; a challenge to one's status can lead to pride and elevation but also shame, submission, or defeat. In other words, a system can be *functionally* coherent, but this coherence may not translate into simple patterns of correlations among the system's outputs. For example, infants' attachment behaviors in response to separation require at least two dimensions of variation to be adequately summarized (Fraley & Spieker, 2003). Moreover, between-person correlations do not simply reflect the dynamics of individual systems, but also patterns of co-activation and inhibition between multiple systems and individual differences at various timescales. And when the measured indicators include emotions, the use of standard labels makes it impossible to detect functional distinctions *within* folk categories such as "anger" or "anxiety."

Given all the above, it is rather unlikely that the dimensions identified by factor analysis or PCA will correspond to specific mechanisms. In practice, the situation is even worse: first, determining the "correct" number of dimensions to retain is an ill-specified task with no straightforward solution (see Del Giudice, 2021); and second, standard algorithms for rotating factors/components are designed to seek a "simple structure" in the data—a hopelessly unrealistic assumption for many complex biological systems (Lykken, 1971).[3] To illustrate, Brasini and colleagues (2020) performed factor analysis on a pool of behaviors and emotions selected to indicate the activation of seven motivational systems (attachment, caregiving, rank competition, sexuality, cooperation, affiliation, and social play). Unsurprisingly, the analysis failed to clearly identify the hypothesized systems; instead, it returned some composite factors (e.g., a "prosociality" factor mixing caregiving and cooperation; an "insecurity" factor mixing attachment, submission, and shame), as well as a separate factor for dominant and high-status behaviors. Because correlational methods are intrinsically limited in their ability to answer questions about mechanisms and processes (especially in the absence of strong theoretical models), the same problems arise in the study of personality (Baumert et al., 2017; Borsboom et al., 2009; Davis & Panksepp, 2018; Lukaszewski et al., 2020; more on this below).

In the remainder of this section, I outline the motivational systems shown in Figure 5.1. I want to stress that this is only intended as a brief summary, far from an in-depth evolutionary and computational analysis. For more detailed overviews, see Aunger and Curtis (2013); Bugental (2000); Kenrick and colleagues (2010); and Toronchuk and Ellis (2013), in addition to the literature cited in each subsection.[4]

Fear System

The fear system is an ancient defensive mechanism that motivates organisms to avoid or escape immediate threats. This system can be activated by a multitude of cues and situations, and many specific fears are acquired through learning. However, some types of stimuli elicit fear with no need for learning (e.g., sudden loud noises) or after minimal exposure (e.g., snakes, spiders, angry male faces; LoBue & Rakison, 2013; Mallan et al., 2013; Öhman, 2009). *Tonic* and *attentive immobility* are important components of the fear system. Attentive immobility or "freezing" occurs in preparation for escape or fighting; tonic immobility is a kind of paralysis or fainting without loss of consciousness, a last resort defense when harm is inevitable (Hagenaars et al., 2014; Roelofs, 2017). In contrast, successful escape/avoidance triggers feelings of safety and relief.

Defensive Aggression System

Aggression is a basic motivation to harm or threaten other organisms, including—but not limited to—individuals of the same species. Aggression is often deployed as a defensive strategy in response to immediate threats to oneself, one's kin, or one's allies. Defensive aggression has been labeled as *reactive*, *affective*, *emotional*, etc.; it is marked by intense arousal, anger, or rage, and can be triggered by high levels of fear (Panksepp, 1998, 2011). For this reason, defensive aggression and fear are sometimes discussed together as part of a unitary "fight-or-flight" or "fight-flight-freeze" system (e.g., Corr et al., 2013; Corr & Krupić, 2017). However, aggressive motivations are not always defensive. A prime example of *proactive*, *instrumental*, or *predatory* aggression is hunting, which involves extreme aggression toward prey but no anger. In fact, "proactive" aggression can be accompanied by feelings of pleasure and excitement (Chester, 2017; Chichinadze et al., 2011; Panksepp, 1998).

In humans, proactive aggression is also a key component of group conflicts and wars, in the course of which the enemy is dehumanized and effectively treated like prey (Wrangham, 1999, 2018). Proactive aggression can be employed to reinforce dominance hierarchies, take or steal resources, and more generally control the behavior of others. Whereas defensive aggression can be meaningfully treated as a distinct motivational system (in analogy with fear, disgust, etc.), I concur with Aunger and Curtis (2013) that—generally speaking—proactive aggression is best understood as a behavioral tactic in the service of other motivations (e.g., status, acquisition). On the other hand, humans have a long evolutionary history as predators, and a number of cognitive adaptations that seem to be specialized for interactions with prey (Barrett, 2015b). One can tentatively hypothesize the existence of a specialized motivational system for *predation*, which is activated both during hunting/fishing and in intergroup conflicts (Figure 5.1). A predation system would most likely develop in a sex-specific way, and may be only fully expressed in boys and men.

Precaution System

Like the fear system, the precaution system is a mechanism designed to protect organisms from threats. The crucial difference is that fear is triggered by immediate threats, whereas precautionary motivations are activated by *potential* threats—that is, threats that are comparatively rare and hard to detect but may have catastrophic consequences, such as dangerous predators or contaminating pathogens (Boyer & Liénard, 2006; Woody & Szechtman, 2011). Immediate threats evoke fear and escape/fight behaviors; in contrast, activation of the precaution system is marked by anxiety, wariness, and repetitive behaviors such as checking and exploration, which help gather further information about the presence of potential risks. Indeed, the precaution system tends to inhibit fear, preventing flight/panic responses to permit cautious exploration (Graeff, 2004). The precaution system is activated by subtle and indirect cues of danger; but the *absence* of a potential threat is hard or even impossible to determine with certainty, and there are no clear signals indicating whether precautionary behaviors have been successful. Thus, the system is not deactivated by situational cues, but by the precautionary behaviors themselves, provided that they have been correctly executed (Woody & Szechtman, 2011). In my previous work (Del Giudice, 2018), I adopted Woody and Szechtman's label of "security system," but "precaution" (Boyer & Liénard, 2006) is more transparent and less likely to generate confusion with affiliation and attachment.

Disgust System

The disgust system is a defensive mechanism whose original function is preventing contact with pathogens and/or toxins through ingestion of contaminated foods, drinks, or waste products; manipulation of contaminated objects; and contact with infected people or animal pathogen vectors (*pathogen* disgust; Curtis, 2011; Toronchuk & Ellis, 2013). Pathogen disgust promotes physical avoidance, expulsion (e.g., vomiting), and cleaning behaviors. Disgust can also trigger activation of the precaution system, and the two systems often work in synergy. Over evolutionary history, the disgust system has been co-opted and differentiated to deal with other kinds of threats (Tybur et al., 2013). In particular, *sexual* disgust is designed to prevent sexual contact with partners that would be detrimental to fitness, for example because they are too old, too genetically similar (e.g., siblings and other close kin), or prone to sexually transmitted diseases (e.g., highly promiscuous individuals). Finally, disgust in our species is deeply connected to morality: violations of moral norms and taboos can elicit disgust and feelings of uncleanliness and contamination. A likely function of *moral* disgust is to motivate and coordinate social distancing from (and/or condemnation of) individuals who violate moral rules (Tybur et al., 2013). While failure to avoid contact with repulsive objects leads to intense physical discomfort, motivational failures in the sexual and moral domains may also evoke evaluative emotions such as shame and guilt.

Status System

In animals, dominance motivational systems have two complementary functions: (a) enhancing, defending, and displaying one's social rank; and (b) when necessary, submitting to higher-ranking individuals to avoid punishment and retaliation (Toronchuk & Ellis, 2013). In our species, social hierarchies reflect both physical dominance and skill-based *prestige*; the more general concept of a "status system" covers both aspects, emphasizing the complex nature of human competition (see Anderson et al., 2015; Aunger & Curtis, 2013; Cheng et al., 2010; Cheng et al., 2013; Johnson et al., 2012; Maner, 2017). The status system is activated by challenges to one's dominance rank or prestige (from provocations and disrespectful acts to situations that involve social judgments), but also by opportunities to rise in the social hierarchy; depending on the nature of the situation and the person's current rank and capabilities, the associated emotions may include anger, (performance) anxiety, envy, hope, and excitement. The main emotions triggered by success are pride and confidence, whereas failure tends to elicit shame, anger, frustration, and sadness. Importantly, voluntary deference to high-status individuals (leaders, teachers, etc.) can evoke a range of positive emotions such as admiration and awe (Keltner et al., 2006). The concept of a status system absorbs the motivational functions that have been ascribed to the emotional mechanisms of pride and shame, such as promoting and advertising the achievement of socially valued goals/characteristics (Sznycer, 2019; Sznycer, Al-Shawaf, et al., 2017; see also Durkee et al., 2019). Dominance competition often elicits aggression, and the two systems are deeply connected on a functional level (Anderson et al., 2015; Toronchuk & Ellis, 2013).

Mating System

The mating system plays a critical role in reproduction by motivating sexual behavior, from courtship and mate choice to intercourse. The system is activated by the presence or prospect of attractive partners and/or rivals; the emotional constellation of mating is varied, ranging from arousal, desire, excitement, and pleasure to embarrassment, anxiety, and shame (e.g., Al-Shawaf et al., 2016; Toronchuk & Ellis, 2013). In a broader perspective, it is important to note that mating and sexuality can be put in the service of other motivations and goals—for example, reinforcing a long-term bond, enhancing one's social status, exerting dominance, or exchanging sex for gifts and other resources (e.g., Gangestad & Haselton, 2015; Meston & Buss, 2007).

Attachment System

Like most young mammals, infants and children are vulnerable and depend on adults for feeding and protection. The attachment system is designed to monitor and maintain the proximity and availability of caregivers (see above). In infancy and childhood, attachment has high motivational priority, consistent with its critical role in ensuring survival. When activated, the attachment system inhibits play and curiosity; conversely, the presence of an available attachment figure works as a "secure base" for exploration (Cassidy, 2016). In our species, attachment has been co-opted as a building block of close relationships in adulthood, including those with romantic partners and friends (Fletcher et al., 2015; Mikulincer & Shaver, 2016; Zeifman & Hazan, 2016). Specifically, most intimate relationships involve an attachment component, as they provide comfort, reassurance, and safety in times of distress.

Caregiving System

Mirroring the biological function of the attachment system, the caregiving system motivates parents and other caregivers to protect and nurture their dependent young (Brown et al., 2012; Cassidy, 2016; Panksepp, 1998, 2011; Schaller, 2018). As a species, humans show many features of *cooperative breeding*: across societies, care and protection are provided not just by parents, but by multiple individuals including older siblings, grandparents, and friends (Hrdy, 2005; Kramer, 2010). Thus, caregiving motivations need not be restricted to one's biological offspring. Caregiving is primarily activated by displays of immaturity, vulnerability, and/or distress (e.g., crying, cute baby-like features) and can trigger a range of emotions: tenderness, "anxious solicitude," protectiveness, as well as parental love and pride. Failures of the caregiving motivation can trigger powerful negative emotions of sadness and guilt (e.g., Gilbert, Chapter 15 in this volume).

Pair-Bonding System

Pair-bonding is a central feature of human mating. It has plausibly evolved from the integration of sexual attraction with attachment and caregiving—two motivations rooted in parent–child relations—and reused to enable long-term bonding between sexual partners. In part, romantic love can be seen as a blend of emotions associated with these three systems; at the same time, the psychology of love also shows unique features and evidence of functional specialization. For example, being in love temporarily inhibits the desire for alternative sexual partners, thus working as a credible signal of interest and a "commitment device" in view of shared parental investment (Doherty & Brumbaugh, Chapter 11 in this volume; Eastwick, 2009; Fletcher et al., 2015; Gangestad & Thornhill, 2007; Quinlan, 2008). Also, love is powerfully associated with jealousy, an emotional mechanism designed to prevent infidelity by partners (Buss, 2013). For these reasons, it makes sense to postulate a specialized pair-bonding system with the specific goal of forming and maintaining long-term couple relationships (Aunger & Curtis, 2013; Kenrick et al., 2010; see also Barbaro, 2020).

Affiliation System

Affiliation is a key motivational substrate of group living; its function is to enable and sustain long-term relationships with extended kin and other group members, including friends and allies. As with pair bonding, the psychology of affiliation overlaps with that of attachment; at the same time, friendship and group membership are sufficiently distinct from parent–child relations to warrant the idea of a specialized motivational system (Aunger & Curtis, 2013; Bugental, 2000; Kenrick et al., 2010). The affiliation system can be activated not only by the perception of shared interests and goals, but also by threatening situations, lack of social resources (isolation, rejection), and intergroup conflict. Successful affiliation evokes feelings of security and belonging, promotes the formation of a shared group identity, and sustains cooperation and reciprocity.

Reciprocity System

While the affiliation system promotes affective bonding with other group members, the reciprocity system deals with cooperation and with the exchange of favors and resources. Its main tasks are selecting cooperation partners, optimizing joint and personal benefits, and monitoring/enforcing fairness (Bugental, 2000; Keltner et al., 2006). Even though extensive cooperation networks of non-kin are unique to humans, other primates do engage in more limited forms of reciprocity, for example in the context of grooming and food sharing (Engelmann et al., 2015; Jaeggi et al., 2013; Jaeggi & Gurven, 2013). The reciprocity system can be activated by opportunities such as the presence of a capable and trustworthy partner, or by threats such as cheating and unfairness. The corresponding emotions include trust, benevolence, suspiciousness, and moral indignation. In humans, reciprocity is supported by specialized cognitive mechanisms that monitor violations of rules and keep track of partners' contributions and reputations over time (Cosmides & Tooby, 2015). While successful exchanges engender satisfaction and gratitude, failures of reciprocity may arouse intense anger and contempt or guilt, depending on whether one is the victim or the perpetrator.

Acquisition System

An obvious but sometimes overlooked characteristic of our species is the extent to which we store and accumulate resources for future use. Material wealth—in the form of land, cattle, houses, or money—provides immediate adaptive benefits as it improves both mating success (especially in men) and the survival of children (see Borgerhoff Mulder & Beheim, 2011; Nettle & Pollet, 2008). Moreover, stored resources reduce risk by working as a buffer against periods of scarcity and can be passed down from one generation to the next, with cumulative effects on long-term fitness (Borgerhoff Mulder et al., 2009; Winterhalder et al., 1999). Unsurprisingly, humans have strong motivations to acquire resources, accumulate them, and defend them against theft, as well as a distinct psychology of ownership based on emotions such as desire, envy, and greed. The acquisition system likely has its evolutionary roots in the mechanisms that mediate foraging and food hoarding (Aunger & Curtis, 2013; Preston, 2014; Preston & Vickers, 2014). The specific goals of the acquisition system depend on its interaction with other motivations such as mating and pair-bonding. For example, saving resources for future family needs in the context of a long-term relationship is not the same as acquiring costly luxury goods to boost success in courtship and short-term mating (Griskevicius et al., 2007; Sundie et al., 2011).

Aunger and Curtis (2013) argued that humans possess a specific motive to improve and maintain their habitat, making it more conducive to survival and reproduction. The relevant behaviors include building dwellings, removing parasites and other dangers, tidying and repairing habitat, and producing tools and artifacts. While there is little evolutionary work on creation as a motivational system, the construct is plausible enough to be tentatively included in the map of human motivation (Figure 5.1).

Curiosity System

Acquiring knowledge and exploring new environments have long been recognized as fundamental motives in animals (Aunger & Curtis, 2013; Loewenstein, 1994). Information-seeking is essential to building models of the world and improving one's ability to make inferences and predictions (Gottlieb et al., 2013). In humans, knowledge can be used to build prestige or increase one's value as a social partner. Far from being a "cold" cognitive task, the acquisition of information is regulated by a wide range of emotions and feelings, from excitement and surprise to boredom, frustration, and anxiety. Curiosity and exploration are often discussed in association with play, and play is certainly a powerful way to gather information about oneself, other people, and the environment. Even pretend play based on unrealistic scenarios can play a critical role in building sophisticated causal models of the world (Weisberg & Gopnik, 2013). However, there are many ways to acquire knowledge that do not rely on play; moreover, language permits massive transfer of information without the need for firsthand experience. In humans, adaptations for learning seem to be matched by adaptations for *teaching*, the deliberate transmission of knowledge and skills (Csibra & Gergely, 2006; Fogarty et al., 2011).

Play System

Play behaviors are widespread in mammals and absorb a large fraction of juveniles' time and energy. The overarching function of play is to enable self-training in a range of adaptive skills; fighting, parenting, and foraging are prominent recurring themes across species. More specific functions are regulating neuromuscular development, learning how to cope with unexpected events, and testing the limits of one's abilities (Burghardt, 2005; Byers & Walker, 1995; Spinka et al., 2001). While playful motivation in mammals seems to be mediated by a specialized mechanism (Panksepp, 1998, 2005, 2011; Pellis et al., 2019), it always works in synergy with other motivational systems that provide the momentary goals of play and the relevant behavioral/emotional repertoires. For example, rough-and-tumble play stems from the playful coordination of the fear, defensive aggression, predation, and status systems (see Pellis et al., 2019). Cognitive skills are also exercised through play, as when children play games of memory, numbers, and language (e.g., Locke & Bogin, 2006). Finally, play promotes social bonding in synergy with the affiliation system (Toronchuk & Ellis, 2013) and can also be an effective way to *display* skills and other attractive traits (e.g., strength, intelligence) to potential allies and partners.

Extending the Coordination Approach

The standard coordination approach to emotions makes certain assumptions about the computational architecture of emotions. Specifically, emotion mechanisms are thought to comprise two kinds of components: (a) *situation-detecting algorithms* that monitor for situation-defining cues, and perform computations of variable complexity to identify the presence of the activating situation; and (b) *coordination programs* that signal to the downstream mechanisms (e.g., memory, attention, autonomic, and other physiological systems), switching them into the appropriate functioning mode. Because more than one emotion-eliciting situation may occur at the same time (e.g., an animal may be hungry *and* being attacked by a predator), emotion mechanisms are supervised by *prioritizing algorithms* that determine the degree of compatibility between multiple emotion modes, and resolve conflicts by giving priority to the most important or pressing situations (Cosmides & Tooby, 2000; Tooby & Cosmides, 2008, Chapter 2 in this volume). This architecture is sketched in Figure 5.2A. Note that, for clarity, the figure depicts emotions and motivational systems as separate mechanisms with clear-cut boundaries; as I discussed earlier, this is a dramatic simplification of reality.

A motivational-systems perspective suggests some modifications to the standard approach, as illustrated in Figure 5.2B. Most notably, motivational systems take up the task of detecting situations, and subsequently activate different emotions depending on the state of the organism and its environment vis à vis the system's goal(s). This revision has two main consequences. First, emotion mechanisms are effectively reduced to coordination programs. Second, situation-detecting algorithms are decoupled from emotion mechanisms, so that similar situations may give rise to different emotions depending on the motivational state of the individual, while situations pertaining to different motivational domains may trigger the same emotion (possibly with alternative motivation-specific "flavors").

In addition to detecting goal-relevant situations, motivational systems monitor the progress of current behavior in relation to the active goals, evaluate situations in terms of success vs. failure, and strategically deploy emotions in order to increase the chances of success, avoid failure, or deal with failure and mitigate its costs if necessary. In the diagram of Figure 5.2B, these computational tasks are carried out by *goal pursuit/evaluation algorithms*. Note that multiple motivational systems may make use of the same information to perform their computations. For example, information about the possession of socially valued traits such as attractiveness and trustworthiness (see Sznycer & Lukaszewski, 2019) is going to affect evaluations (and the intensity of the corresponding emotions) across a number of distinct motivational domains—from status, reciprocity, and affiliation to mating and pair-bonding (Scrivner et al., Chapter 4 in this volume).

Figure 5.2B makes the additional assumption that control signals flow in one particular direction, that is, from motivational systems to emotion mechanisms but not vice versa (i.e., emotions do not directly coordinate motivational systems). This simplifying assumption is open to revision, as future research unveils the computational logic of various motivational

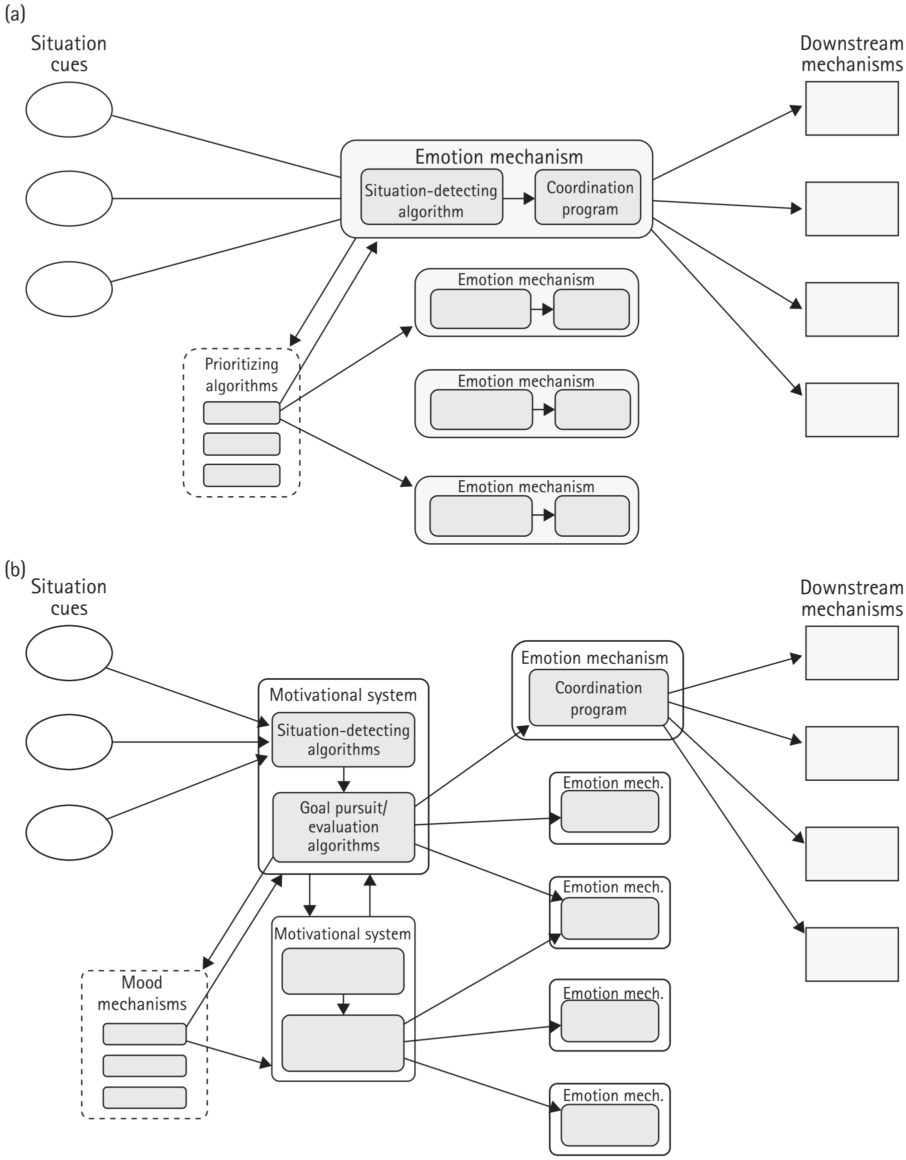

Figure 5.2. Schematic diagram of the computational architectures underlying (A) the standard coordination approach; and (B) the extended coordination approach, in which emotion mechanisms are themselves coordinated by a layer of motivational systems. Each motivational system detects a range of situations, integrates them over time, evaluates them in relation to its specific goals, activates the appropriate emotions, and modulates the activity of other systems. Note that a given emotion may be activated by more than one motivational system, and thus may play a role in the pursuit of more than one adaptive goal. Moods are produced by superordinate mechanisms that use information from motivational systems (and/or other inputs, such as the immune system) to assess/predict the state of the organism and its environment on a more global scale, and to regulate the activity of several motivational systems at once.

systems. To be clear, even if emotions do not directly control motivational systems, they still "motivate behavior" in the sense of activating certain action tendencies. The point is that, according to this model, motivational *goals* are processed upstream of emotions rather than downstream (e.g., pride is triggered by the successful pursuit of status-enhancement goals).

The extended architecture in Figure 5.2B is characterized by a hierarchical "bow-tie" structure, in which a large number of inputs and outputs flow through a small set of common, highly conserved processes that form the "knot" of the tie (Csete & Doyle, 2004). In this case, the central knot corresponds to the layer of motivational systems. Bow-tie architectures are ubiquitous in biological systems, from genetic regulation and immunity to cellular and neural signaling (Doyle & Csete, 2011; Kitano, 2004; Kitano & Oda, 2006). The compact size of the knot (e.g., a small set of regulatory genes or second messenger molecules) permits rapid, efficient control of the entire system in response to challenges and fluctuations. At the same time, the comparatively weak linkages between the central knot and input/output processes increase both the flexibility of the system and its evolvability. For example, a given motivational system can easily evolve to process different situation cues, or trigger additional emotions that were previously specific to other systems, with few or no changes to its set-goals and core algorithms ("plug-and-play modularity").

The Achilles' heel of bow-tie architectures lies in the same features that make them versatile and robust to perturbations—that is, the small size and centralized control function of the knot. If knot processes get damaged or successfully hijacked (for example by parasites), the consequences can be catastrophic. As a result, central processes are more tightly regulated than the ones in the periphery, and tend to evolve at a much slower pace (Csete & Doyle, 2004; Kitano, 2004). These properties of bow-tie architectures could have interesting implications for the study of motivation and emotion from a phylogenetic and comparative perspective.

Higher-Order Coordination Problems

In the standard coordination approach, the need to postulate the existence of prioritizing algorithms (Figure 5.2A) points to what I will call the *second-order* coordination problem. Emotions evolved to efficiently coordinate a large number of psychological and physiological mechanisms, by "centralizing" the detection of situations and the generation of appropriate activity patterns. However, there are not just a handful of emotion mechanisms, but dozens of them—and hence dozens of potential modes of operation for the organism, many of which have mutually contradictory effects;[5] hence, the second-order problem of how to coordinate the activity of this teeming multitude of emotion mechanisms, resolving potential conflicts and maintaining a coherent sequence of behavior. In the standard approach, this role is fulfilled by prioritizing algorithms, whose architecture and functional properties are left unspecified. In the extended approach I am proposing, motivational systems directly control the activation of emotion mechanisms, and thus solve the second-order coordination problem without the need for a dedicated supervisory system.

Although motivational systems solve the second-order coordination problem, they still necessitate ways to resolve conflicts and prioritize certain goals over others, giving rise to a *third-order* coordination problem. This may sound like infinite regress, but it is not: as the number of mechanisms that have to be coordinated shrinks, it becomes possible to use coordination strategies that would be impractical or intractable at lower levels of the control hierarchy. For example, cross-modulation (e.g., reciprocal inhibition between functionally incompatible systems) may allow motivational systems to self-coordinate to a certain degree, and make it possible to "arbitrate" simple priority conflicts without the intervention of superordinate mechanisms. Cross-modulation is feasible within a relatively small set of motivational systems, but would become cumbersome (and potentially unworkable) if scaled up to dozens of emotion mechanisms with thousands of potential connections among them.

Moods as Third-Order Coordination Programs

The concept of higher-order coordination problems shines new light on the old and perplexing question of what differentiates emotions from moods. Phenomenologically, moods are long-lasting and have a diffuse rather than focused quality; unlike emotions, they do not have a specific cause or triggering object, and do not prompt specific behaviors or action tendencies (Beedie et al., 2005; Gendolla, 2000). At the same time, they have a powerful (if nonspecific) impact on motivation, and dispose people to appraise new situations in affect-congruent ways (e.g., attributing hostile intentions to others when one is in an irritable mood; see Siemer, 2009).

Current biological models of mood resonate with Nesse's (1990) suggestion that mood encodes a global estimate of the "propitiousness" of the environment, or the expected rate of reward per unit of effort invested (a plausible internal regulatory variable). Similarly, Morris (1992) framed mood as a system that regulates goal-directed behavior so as to maintain a balance between goal-relevant resources and demands; mood improves when (personal and environmental) resources are more plentiful than necessary to meet demands, and deteriorates when resources are perceived as inadequate. Nettle and Bateson (2012) argued that, as organisms experience rewards and punishments, they revise their estimates of the probability of the two types of outcomes, and adjust the thresholds that determine how easily a new situation is perceived as a potential reward or a potential threat. In this model, the organism's "core" mood reflects the settings of two separate thresholds for detecting/responding to rewards and punishments (e.g., a depressed mood corresponds to high thresholds for both rewards and punishments). Trimmer and colleagues (2013) proposed a somewhat different two-dimensional scheme that distinguishes between the organism's general positive vs. negative expectations and its level of preparedness to act (e.g., a depressed mood corresponds to a combination of negative expectations and low preparedness). In his later work, Nesse (2004) focused on the relation between high vs. low mood and the rate of progress in the pursuit of domain-specific goals. Across domains, reaching one's goals faster than expected elicits positive moods, which in turn facilitate investing more effort; whereas the perception that goals keep getting farther away despite increasing effort is a trigger for low mood and depression, which promote disengagement and effort withdrawal. Eldar and colleagues (2016) echoed these ideas with the notion that mood is especially influenced by prediction errors, and specifically by positive vs. negative discrepancies between expected and actual outcomes (e.g., rewards). In the same paper, they argued that mood encodes the *momentum* of recent outcomes (i.e., their improving or declining trend), and noted that forming global expectations about future rewards based on specific events can be adaptive if different sources of reward (e.g., material resources, social status, sexual partners) tend to be correlated with one another.

From the standpoint of the extended coordination approach, moods are easily understood as the product of third-order coordination mechanisms that (a) receive information from motivational systems about success and failure in the pursuit of domain-specific goals (together with other inputs that encode the state of the organism, for example its immunological condition, energetic balance, and level of fatigue); (b) compute integrative estimates of the present/future state of the organism in relation to its environment, for example based on the momentum of recent outcomes; and (c) strategically modulate the functioning of multiple motivational systems—not just by generically "activating" or "inhibiting" them, but also by selectively influencing their sensitivity to threats vs. opportunities (as in the threshold model by Nettle and Bateson, 2012). Computationally, some of these modulation effects may be construed as changes in the settings of global or motivation-specific regulatory variables. According to this model (Figure 5.2B), moods act as superordinate programs that function to coordinate the activity of motivational systems. They affect cognition, behavior, and physiology on a broad scale, but do so *indirectly* through the action of multiple motivational systems and the corresponding emotions (see also Morris, 1992). To the extent that motivational systems directly modulate one another, some aspects of the phenomenology of moods may reflect self-coordination instead of regulation by superordinate programs; precisely how much top-down regulation is needed to produce moods will become clearer as we learn more about the dynamic interplay between motivational systems.

The extended coordination approach accommodates the main insights of other biological models and accounts for key aspects of the phenomenology of moods, including the combination of high motivational potency and low motivational specificity. It also provides a simple, principled answer to the long-standing question of what the difference is between emotions and moods. Both are coordination adaptations; but emotions are first-order coordination mechanisms activated by motivational systems, whereas moods are third-order coordination mechanisms whose primary function is to modulate the activity of motivational systems. From this vantage point, some putative emotions such as *lassitude* (the feeling of being sick; Schrock et al., 2020, Chapter 16 in this volume) should be classified more precisely as moods. Lassitude does not entail specific goals or action tendencies; but when triggered by cues of infection, it modulates a wide range of motivational systems, including the ones that control mating, parenting, hunger, and thermoregulation (Schrock et al., 2020). The effects on cognition and behavior are profound, and can last for days or even weeks (i.e., until the acute phase of the infection is resolved).

The Sequence Integration Problem

In many cases, the meaning of emotion-eliciting situations is not entirely determined by immediate circumstances, but depends on the preceding sequence of situations, outcomes, and emotions. Winning an unlikely victory after suffering humiliation and shame does not just arouse pride and satisfaction, but intoxicating feelings of triumph. In fact, important situations like revenge, betrayal, and reconciliation are *defined* by their place within thematic sequences of events and emotions, which can be represented as movements toward and away from certain motivational goals. This adds a layer of complexity to the task of detecting and evaluating situations, raising what I will call the *sequence integration problem*. In principle, it would be possible to solve the sequence integration problem with a complex system of regulatory variables whose values are updated and accessed by individual emotion mechanisms. However, a control layer of motivational systems addresses this problem in a more straightforward way. Tracking goals over time and evaluating new events in relation to those goals are crucial functions of motivational systems; sequence integration arises naturally out of these functions, without the need for additional computational machinery.

A Note on Feedback vs. Feedforward Control

Both the classic ethological perspective and contemporary theories of self-regulation (e.g., Carver & Scheier, 2013; DeYoung, 2015; DeYoung & Krueger, 2018; Revelle & Condon, 2015) emphasize the critical role of feedback control in the pursuit of goals. Feedback controllers work by reducing the discrepancy between the current state of the world (as sensed and interpreted by the controller) and a desired state or "set point." The set point can be static (*homeostasis*) but need not be—it is possible for a feedback controller to track a "moving target" that changes based on previous events and/or predictions about the future state of the world (*allostasis*; Sterling & Eyer, 1988).

Here I want to briefly note that feedback regulation is not the only possibility, and suggest that the goal-pursuit algorithms employed by motivational systems will often include both feedback and feedforward processes. Instead of continuously self-correcting based on the consequences of previous actions, feedforward controllers *anticipate* the future state of the system, and execute the appropriate action(s) without further course correction. In the simplest forms of feedforward control, no actual predictions are computed and the response has a fixed and "ballistic" quality, as in the case of rapid protective reflexes (e.g., blinking, pain-induced limb retraction). In more sophisticated instances, the controller computes a model of the system and uses the resulting prediction to generate an action, or a prespecified sequence of actions (see Albertos & Mareels, 2010). A thermostat that turns on and off a heater to maintain the target temperature within a house is a classic example of feedback control. A device that automatically turns on the heater at a certain time in the evening to preempt an (expected) temperature drop during the night would be an example of feedforward control based on a simple model of the system. (For an introduction to the basic concepts of control theory, see Del Giudice, 2015: Del Giudice et al., 2018.)

Feedback and feedforward regulation have complementary strengths and weaknesses. For example, feedforward controllers are more resistant to noise and delays in the system, but are unable to deal with unanticipated events; feedback controllers can function without an accurate model of the system, but can only respond to events "after the fact," without the ability to anticipate them (Albertos & Mareels, 2010; Bechhoefer, 2005). In many situations, combining the two strategies yields dramatically improved performance, and I see no reason why motivational systems should not take advantage of this option (see also Tops et al., 2010; Tops et al., 2021). To give a simple example, encountering a dangerous predator at night activates the fear system and the emotion of fear, which in turn may promote escape behaviors (Tooby & Cosmides, 2008). Like other avoidance goals, escaping from danger can be described as a feedback-regulated process, in which the intensity of fear and the urge to flee diminish as one moves farther away from the threat (Ballard et al., 2017). However, this feedback mechanism is vulnerable to noisy information—e.g., the predator may be closer than it seems, it may be hiding in the dark, or there may be *other* predators lurking in the surroundings. At least initially, the escape response is more likely to operate under feedforward control (just run away as fast as possible); indeed, the optimal strategies for defensive mechanisms that deal with uncertain dangers almost invariably involve an initial feedforward phase (Shudo et al., 2003). Likewise, the (feedback-regulated) goal of increasing the distance from the threat may be supplemented by the (feedforward-regulated) goal of reaching a safe hiding place or some other known refuge. In many cases, a regulatory system that combines the strengths of feedback and feedforward control is going to outcompete a system that relies on just one of these principles.

Other Benefits of an Extended Approach

Throughout this section, I have emphasized the theoretical benefits of extending the coordination approach to include a central role for motivation. Another advantage of an extended approach is that it makes it easier to "carve emotions at their functional joints" (Sznycer, Cosmides, et al., 2017; see also Scarantino, 2015), using motivational systems as a guide to plausible functional distinctions. For example, the folk category of "anger" may be usefully analyzed in view of the distinct adaptive problems posed by reciprocal cooperation, pair-bonding, parent–child attachment, status competition, and defensive aggression. I speculate that, when viewed through this lens, the recalibration theory of anger (Sell et al., 2009; Sell et al., 2017; Sell et al., Chapter 8 in this volume) will turn out to apply only to some domains, or will require modifications to match the specifics of the various motivational systems that deploy "angry" emotions. To illustrate: open defiance by a subordinate may signal a bid for dominance; the implications of this gesture go beyond the fact that the subordinate does not place enough weight on the welfare of the dominant individual, and an adaptive response should take this into account. The anger expressed by infants and children toward unresponsive caregivers is not amplified by self-perceived formidability (Sell et al., 2009), but by self-perceived *vulnerability*—and the associated behaviors also function to display heightened vulnerability and immaturity, rather than strength and competence. Anger and rage in the context of defensive aggression may lack a recalibration function altogether, and terminate when the aggressor is gone or incapacitated. Are these "varieties" of anger produced by the same neurocomputational mechanism, or by distinct mechanisms? Answering this question is going to require sustained research effort, and the task will be much facilitated by a working map of the main motivational systems and their adaptive logic.

Conversely, the conceptual precision and careful analytic style that characterize the coordination approach could greatly improve the current understanding of motivational systems. To begin, the lists of emotions associated with the activation, success, and failure of most motivational systems are plausible but still impressionistic (and most likely incomplete). There is urgent need for a fine-grained, empirically rigorous map of the emotional constellations of human motivations. Similarly, existing attempts at specifying the computational logic of human motivational systems are no more than bare-bones outlines, heuristically useful but lacking in detail and precision (e.g., Bugental, 2000; Kenrick et al., 2010). Needless to say, the computational logic of a motivational system is likely to be more complex than that of a single emotion, as it involves more elaborate decision rules and goal-directed control strategies. Hence, the toolkit of the coordination approach will need to be supplemented, for example with concepts and models from mathematical control theory.

Another problem that would benefit from detailed computational analysis concerns the nature of the interplay between multiple systems. The vague notion that motivational systems "activate" or "inhibit" one another (e.g., Bowlby, 1982; Panksepp, 1998) is rooted in simplistic cybernetic and/or neurobiological models, and should be updated with a modern understanding of psychological adaptations. To illustrate, inhibition of a system may be understood as a change in its general threshold for activation, but also as a change in the evaluation of certain activating cues, a strategic adjustment of the system's goals or criteria for success/failure, a selective suppression of some emotional responses, and so forth. Evolutionary models of emotion and motivation naturally complement one another, and there are no good reasons to maintain a separation between these areas of research (Beall & Tracy, 2017).

Implications for Emotion Regulation

From "Emotion Regulation" to "Motivation Regulation"

After decades of research, emotion regulation remains a scientific puzzle. The slow progress on this topic is largely due to a persistent neglect of function beyond immediate proximate concerns. With few exceptions, work in this area has been guided by the "hedonic assumption" that people are motivated by a desire to feel good and avoid feeling bad, and the related notion that emotion regulation is "adaptive" if it leads to more positive (or less negative) feelings (see Aldao, 2013; Erber & Erber, 2000; Tamir, 2009, 2016). These ingrained assumptions have been challenged by another line of work, showing that people have multiple reasons to change their emotional state in ways that are potentially counter-hedonic (e.g., getting important work done, eliciting help and compassion, displaying empathy, matching the emotions of other group members; see Tamir, 2016). While this more realistic approach has been gaining traction in recent years, the focus is still on immediate goals; so far, there have been very few attempts to understand emotion regulation from an explicitly adaptationist perspective. Kisley (Chapter 39 in this volume) has started to lay the groundwork for this enterprise. Here I adopt the working assumption that, while emotions coordinate the state of the organism to deal with *recurrent* adaptive problems, other cognitive mechanisms have a (limited) ability to second-guess emotional responses based on the *unique* features of a situation (see Kisley, Chapter 39). For example, certain situations may cause detection errors, and trigger emotions that are inappropriate or harmful. (This is especially likely when situation cues are ambiguous, inconsistent, or occur in evolutionarily novel contexts.) In other cases, algorithms correctly detect the current situation, but circumstances make it undesirable to express the relevant emotions or act on them (e.g., because doing so would incur social costs, or interfere with other prioritized goals). In yet other cases, the situation may pose multiple contradictory demands, causing a regulatory conflict that cannot be resolved by low-level arbitration processes.

My goal is not to delve into the details of these scenarios, but to suggest a general shift in perspective that may facilitate their functional and evolutionary analysis. Specifically, many phenomena that are currently studied under the rubric of emotion regulation can be understood more accurately and fruitfully as instances of *motivation* regulation. Consider the social situations in which people prefer to "feel bad" for instrumental reasons. One common example is that people who prepare for competitions and other conflictual interactions (e.g., negotiations with strangers) often want to feel at least somewhat angry (e.g., Tamir & Ford, 2012; Tamir et al., 2008; Tamir et al., 2013). I argue that what people are trying to do is not to feel anger per se, but to strategically upregulate specific motivational systems that include anger as a characteristic emotion. In this case, "feeling angry" likely corresponds to the threat-mode activation of either the status system ("dominance challenge") or the reciprocity system ("unfairness"). Note how a motivational perspective helps one to move beyond the folk concept of anger, and consider alternative functional accounts of the same self-reported emotions. This perspective also suggests new hypotheses about the mechanisms of regulation and their proximate functions. To illustrate: activating the status system before a competitive interaction may work not just for its communicative effects (e.g., van Kleef et al., 2004), but also because it indirectly inhibits the reciprocity and affiliation systems—thus making one less inclined to compromise with the adversary, or less receptive to manipulative cues of affiliation.

Regulation Strategies

It is instructive to apply the same lens to the literature on emotion-regulation strategies (Gross, 2015; McRae & Gross, 2020). Cognitive *reappraisal* involves reinterpreting or re-evaluating the situation to change the way one thinks about it. In some cases, "reinterpreting the situation" means downregulating the motivational system activated by the situation, by re-evaluating the meaning of ambiguous or inconsistent cues ("he didn't mean to disrespect me; he was just in a hurry"). In other cases, it means activating a new system whose activity is incompatible with that of the previous one (e.g., caregiving instead of status: "he didn't mean to disrespect me; he's nervous and depressed because his daughter is sick—poor guy!"). The activation of incompatible motivations may also underlie *distraction* strategies, when the distracting thoughts and/or actions are not merely neutral but engage a different motivational system. Indeed, strategies that belong to different categories according to current taxonomies may share functional commonalities when viewed through a motivational lens.

A motivational perspective could have interesting implications for the efficacy of different self-regulation strategies. For example, strategies that exploit the interplay between different motivational systems may be especially effective, compared with strategies that lack that functional leverage. Also, the success of a certain strategy may depend not just on the specific emotion that one is experiencing, but on the role played by that emotion in the economy of the relevant motivational system. When an emotion is triggered by the *activation* of a system by certain situation cues, it should be relatively easy to deactivate the system through reappraisal, as long as the cues are sufficiently weak or ambiguous. But when a negative emotion marks the *failure* of a system at the end of a sequence of goal-directed actions, reappraisal may become significantly harder, as it demands a complete re-evaluation of the entire course of events and their psychological meaning.

Finally, the model I presented in this chapter may help clarify the differences between the regulation of emotions (or motivations) and that of moods (e.g., Erber & Erber, 2000; Morris, 2000). As third-order coordination programs, moods are not driven by specific events, but by integrative evaluations of the state of the organism in relation to the environment. In this sense, they are harder to regulate than emotions/motivations, and less susceptible to targeted strategies such as reappraisal and suppression. On the other hand, the fact that mood mechanisms integrate over multiple inputs—including the immune system, digestive system, etc.—creates some opportunities for regulation that are not available for lower-order mechanisms. For example, it becomes possible to employ compensatory strategies, so that success in one motivational domain balances out failure in another. Just as importantly, the range of potential regulation mechanisms broadens to include physiological channels such as sleep, eating, and exercise. As Morris (2000) noted, "The most reliable form of mood repair is probably a good night's sleep" (p. 201).

Implications for Personality and Emotion

The Motivational Basis of Personality

The idea that motivations are the basic building blocks of personality has a long history (e.g., Cattell, 1957; Murray, 1938), and is gaining renewed popularity as the field begins to move from the description of individual differences to genuine, process-based explanation (e.g., Corr & Krupić, 2017; Davis & Panksepp, 2018; Dweck, 2017; Read et al., 2010; Read et al., 2017; Schultheiss, 2020). In an influential paper, Denissen and Penke (2008) argued that individual differences in the Big Five traits of the Five Factor Model (Neuroticism/Emotional Stability, Conscientiousness, Agreeableness, Extraversion, and Openness to Experience; McCrae & Costa, 2003) reflect differences in "motivational reaction norms," or response patterns to specific classes of evolutionarily relevant situational cues. Ashton and Lee (2001, 2007) linked the six traits of the HEXACO model to five behavioral domains with a biological interpretation: reciprocal altruism/cooperation (Agreeableness and Honesty-Humility), kin altruism (Emotionality), social engagement (Extraversion), task-related engagement (Conscientiousness), and idea-related engagement (Openness to experience). While these authors did not explicitly discuss motivational systems, the domains they described show some correspondences with more detailed models of human motivation, like the one I have presented in this chapter.

These and similar models (such as DeYoung's [2015] "cybernetic Big Five theory") share a fundamental limitation: because they take factor-analytic traits at face value, they cannot provide a mechanistic, process-focused explanation of personality. Human behavior is not controlled by a handful of general-purpose mechanisms, but by large number of specialized adaptations—certainly much larger than five or six (Michalski & Shackelford, 2010). The traits described by factor-analytic models arise from patterns of *covariation* among multiple mechanisms, including—but not limited to—motivational systems. Covariation between mechanisms can be explained at various levels of analysis, both proximate (e.g., shared genetic and environmental influences, regulation by the same hormones/neuromodulators, reliance on shared regulatory variables, reciprocal activation/inhibition) and ultimate (e.g., synergistic effects on fitness, coordinated expression of life history strategies; see Del Giudice, 2018). Correlated mechanisms produce patterned behaviors, which are then filtered through evolved heuristics for person perception, translated into intuitive person-description concepts, and imperfectly captured by the lexical terms of human languages (Buss, 2011; Lukaszewski, 2020). To be sure, correlations among lexical descriptors can be quite informative; but they provide very little information about the structure, number, and function of the underlying psychological mechanisms (Davis & Panksepp, 2018; Lukaszewski, 2020; Lukaszewski et al., 2020).

The solution to this problem is to invert the direction of analysis, and leverage our knowledge of psychological mechanisms to reconstruct personality from the bottom up ("ground-up adaptationism"; Lukaszewski, 2020). Neel and colleagues (2016) took an initial step in this direction, by assessing Kenrick et al.'s (2010) fundamental motives and correlating them to a host of other individual-difference variables (including the Big Five). However, these authors did not include emotions in the picture. In contrast, Davis and Panksepp (2011, 2018) sought to build an alternative model of personality based on putative basic emotional systems such as RAGE, SEEKING, CARE, and PLAY. This approach to personality puts emotions front and center; unfortunately, it adopts a simplistic conception of the link between motivation and emotion, and covers only a small portion of the human motivational landscape (see above for details). For these reasons, I view Davis and Panksepp's model as an interesting proof of concept, but not a realistic candidate for a general theory of personality.

Even if they do not explicitly include emotions, the computational models of personality developed by Read and colleagues (2010, 2017, 2020) deserve special attention. In these models, personality arises from the behavior of multiple motivational systems that interact with situational affordances and are able to learn from experience. This conception of personality agrees very well with the approach I am proposing, and I see the authors' computational approach as an important step in the right direction (see also Revelle & Condon, 2015). Still, the specifics of the models reveal some notable theoretical limitations. To begin, the lists of motivational systems included in the models are somewhat ad hoc and do not follow a principled taxonomy. Second, the models lack an explicit theory of how different systems interact with one another. Third, all the motivational systems in these models employ the same control algorithm, regardless of their adaptive domain and specific goals. The algorithm is based on a feedback loop, without the possibility of anticipatory feedforward control. Finally, Read and colleagues introduce a separation between "approach motives" such as hunger, dominance, and affiliation; and "avoidance motives" such as avoidance of harm, rejection, and interpersonal conflict. This is a major conceptual problem, because many motivational goals require both approach *and* avoidance, depending on the situation and the state of the organism (e.g., approach food when hungry, avoid it when satiated; approach subordinates if dominant, avoid dominants if subordinate). It is reasonable to postulate that, when emotion programs are activated by motivational systems, the behavioral adaptations they orchestrate include some general-purpose mechanisms that promote approach vs. avoidance of salient stimuli. Stated differently, approach and avoidance mechanisms may function as common behavioral pathways for the action of multiple domain-specific motivations. On the other hand, treating approach and avoidance as distinct *categories* of motivations is a confusing move, and I believe it will prove a theoretical dead end (see also Davis & Panksepp, 2018).[6]

Motivation as the Bridge between Personality and Emotion

If personality is largely the product of individual differences in motivation (in combination with other regulatory processes; e.g., Tops et al., 2010; Tops et al., 2021; Volk & Masicampo, 2020), the extended coordination approach suggests a two-pronged strategy for bridging personality and emotion. First, one should think about personality in explicitly motivational terms, without assuming the functional coherence of standard personality traits. As a rule, factor-analytic traits arise from the (correlated) activity of multiple motivational systems. Second, one should think about emotions not as isolated mechanisms, but as effectors of motivational systems, without assuming the functional coherence of folk emotion labels. A key insight is that emotions do not correspond to motivations in a simple one-to-one fashion; instead, they are deployed *conditionally*, depending on the meaning of a situation in relation to the system's adaptive goals.

As an illustration, consider the broad personality trait of Agreeableness in the Five Factor Model (FFM). People high in Agreeableness are described as kind, trusting, altruistic, and accommodating. Across countries, girls and women score higher than on this trait than boys and men (Lippa, 2010; Mac Giolla & Kajonius, 2019; Murphy et al., 2021; Soto et al., 2011). Agreeableness is associated with low proneness to anger, but high proneness to both guilt and shame (Cohen et al., 2011; Einstein & Lanning, 1998; Reisenzein & Weber, 2009). It correlates negatively with the experience of "hubristic" or dominance-related pride, and positively with "authentic" or prestige-related pride (Beall & Tracy, 2020; Cheng et al., 2010; Tracy & Robins, 2007). From a motivational systems perspective, Agreeableness is a functionally complex trait that reflects individual differences in reciprocity, affiliation, and status (specifically dominance-seeking; see Cheng et al., 2010; DeYoung et al., 2013; Graziano & Tobin, 2017). Beyond this motivational core, Agreeableness is also associated with increased investment in parental and kin care (caregiving system; Buckels et al., 2015; Neel et al., 2016), reduced mate-seeking, lack of interest in short-term mating, and high investment in long-term mating and stable romantic relationships (mating and pair-bonding systems; see Baams et al., 2014; Banai & Pavela, 2015; Bourdage et al., 2007; Holtzman & Strube, 2013; Neel et al., 2016; Schmitt & Buss, 2000).[7]

In functional terms, this pattern of covariation among motivational systems may be explained as a manifestation of individual differences along a "fast-slow continuum" of life-history strategies (see Del Giudice, 2020; Del Giudice et al., 2015; Figueredo et al., 2007; Sela & Barbaro, 2018). From this perspective, the trade-off between mating and parenting—a central aspect of human life-history strategies—drives the observed associations between status, mating, pair-bonding, and caregiving motivations (e.g., Neel et al., 2016); the future-oriented nature of slow strategies promotes increased cooperation and affiliation in addition to lower mating and higher parenting effort (see Del Giudice, 2018).

A motivational analysis of Agreeableness indicates that people high on this trait should experience (and express) less anger in response to violations of reciprocity and affiliation, dominance challenges, and threats to long-term relationships (e.g., romantic jealousy; Lukaszewski et al., 2020). But it also suggests some new hypotheses that run against a simple negative correlation with anger. For example, high-Agreeableness people may react intensely with protective ("parental") anger when their children or other dependents are threatened. And while they tend to get less angry when they experience unfairness and transgressions, things may change when the victims are *other* innocent people (for indirect evidence, see Bizer, 2020). If these hypotheses were supported, they would also raise interesting questions about the existence of functionally distinct variants of anger (e.g., how is "caregiving anger" different from "reciprocity anger" or "dominance anger"? Are these variants expressed differently in males and females?). The same kind of reasoning could be used to develop finer-grained hypotheses about the contexts in which Agreeableness should predict the experience of shame, guilt, and many other less-studied emotions like gratitude and sexual arousal. A more ambitious goal would be not just to refine the concept of Agreeableness, but to develop an alternative, functional model of personality based on a fine-grained understanding of human motivation.

Motivation and Person Perception

The flip side of this view of personality and motivation is that evolved heuristics for person perception ("difference-detecting mechanisms"; Buss, 2011) should be designed to make inferences about people's *motivational* processes, because this is the level of analysis that affords the largest predictive payoffs. An important corollary is that information about people's *emotions* is often going to be interpreted in relation to their (probabilistically inferred) motivational states. This is already implicit in the evolutionary literature on person perception. To illustrate the kinds of problems that person-perception algorithms are designed to solve, Lukaszewski and colleagues (2020) offered a list of questions, including: Who will be a reliable ally or long-term mate? Who is likely to defect on social contracts? Who will rise in the social hierarchy? Who is sexually permissive? To a large extent, these questions concern individual differences in motivational priorities and in the calibration of specific motivational systems.

In the same paper, Lukaszewski and colleagues presented convergent evidence that experiences, facial expressions, and behaviors associated with anger are systematically translated into descriptions that map onto the construct of Agreeableness.[8] I suggest that people employ the outputs of the anger program mainly as cues to the motivational processes of the angry individual. And because motivational systems covary in meaningful patterns, these inferences should often "spill over" to motivational domains that are not directly tapped by the target situation. For example, imagine someone who consistently gets angry and aggressive in the context of cooperative, reciprocal exchanges. That person is also more likely to be driven by dominance concerns, sensitive to behaviors that could be interpreted as dominance challenges, unreliable as a long-term romantic partner, interested in short-term mating opportunities, and so forth. (For evidence that people tend to possess accurate models of the correlations among personality traits, see Stolier et al., 2020.) In general, motivational inferences are so powerful precisely because they allow one to make predictions about people's emotions and behaviors beyond the current situation, including hypothetical events and unlikely yet fitness-critical scenarios ("would he protect me if someone assaulted us?"). Note that, depending on context, observed emotions may convey other kinds of predictive information besides motivation—for example about a person's beliefs, plans, and social alliances.

Based on the motivational analysis presented earlier, one can advance some hypotheses about situations in which anger should *not* trigger inferences of low Agreeableness, or would do so in a much-attenuated fashion. Possible examples are a parent getting angry at someone who is threatening their child, and a witness of blatant injustice getting angry at the perpetrator. Note that, in both scenarios, the emotion labeled as "anger" does not match the recalibration theory of anger (Sell et al., 2009; Sell et al., 2017), except in a loose and indirect sense. This is a nice example of how motivation and emotion can illuminate each other—and why they should be studied together as two sides of the same coin.

Conclusion

As this volume clearly testifies, the evolutionary study of emotion has made tremendous progress over the past few decades. The coordination approach has played a major role by clearing some important conceptual hurdles, emphasizing the computational level of analysis, providing a common language for alternative models, grounding and suggesting productive directions for empirical research. But motivation and emotion are inextricably linked, and it is becoming increasingly apparent that a successful theory of emotion requires an explicit theory of motivation (and vice versa). Here I have taken a step in this direction, by showing how the theory of motivational systems can be used to extend and partially revise the standard coordination approach. I hope that other researchers will find these ideas as exciting as I do, and use the extended framework as a springboard to refine existing theories, explore new hypotheses, and draw fruitful connections within and across disciplines.

Acknowledgments

I am grateful to Laith Al-Shawaf, Romina Angeleri, Steve Gangestad, and Daniel Sznycer for their generous and constructive feedback on this chapter.

Notes

1. On the ideological side, instinct theories were often portrayed as not merely old-fashioned but also politically conservative; in contrast, behaviorism aligned with the tenets of the Progressive movement, including a view of human behavior as radically malleable and an unshakable faith in top-down social engineering (see, e.g., Burnham, 1960).
2. Note that Bowlby (1982) remained agnostic as to whether feelings *cause* behavior, or only serve as intra- and interpersonal signals of the individual's motivational state. In contrast, Scott (1980) argued that the feelings triggered during the operation of behavioral systems contribute to motivate specific goal-relevant behaviors.
3. Intuitively, a simple structure obtains when each of the factors/components shows strong correlations with some indicators, and near-zero correlations with the remaining ones. For technical discussion, see Browne (2001) and Sass & Schmitt (2010).
4. Parts of this section are adapted with permission from Del Giudice (2018).
5. Recent large-scale analyses of emotional expressions and self-reports (see Cowen et al., 2019) suggest at least 25–30 dimensions of variation (extracted with PCA), with denser regions corresponding to "fuzzy" emotion categories. This is almost certainly a lower bound on the numerosity of emotion *mechanisms*, because the resolution of the analysis is limited by the use of folk labels, and the choice of the number of dimensions to retain is somewhat arbitrary. More generally, these results are based on correlational rather than functional analyses, and suffer from the same problems I have discussed in regard to the numerosity of motivational systems.
6. In Gray and McNaughton's (2000) reinforcement sensitivity theory (RST), behavior is regulated by three general-purpose systems that control reward approach (*behavioral activation system* or BAS), punishment avoidance (*fight-flight-freeze system* or FFFS), and approach-avoidance conflicts (*behavioral inhibition system* or BIS). I do not discuss this theory in detail because it provides an extremely partial account of motivation and emotion. For reviews of RST as a model of personality, see Corr et al. (2013) and Corr and Krupić (2017). The recent discussion by Corr & Krupić seems compatible with the idea that approach/avoidance mechanisms function as common pathways for other, domain-specific motivational systems.
7. As a further indication that Agreeableness is not a functionally unitary construct, the HEXACO model defines this trait in a somewhat different way by excluding sentimentality and including (low) irritability, which is a facet of Neuroticism in the FFM (see Ashton & Lee, 2007). Both versions of Agreeableness show a similar motivational profile with respect to reciprocity, affiliation, dominance/status, mating, and pair-bonding; however, the association with caregiving may be more specific to the FFM version (see Ashton & Lee, 2001, 20017; Ashton et al., 2010; Bourdage et al., 2007; Lee et al., 2013). Also, the available data suggest that sex differences on the HEXACO version of Agreeableness are smaller and less consistent than those on the FFM version (Lee & Ashton, 2020).
8. Note that these authors employed the HEXACO version of Agreeableness.

References

Albertos, P., & Mareels, I. (2010). *Feedback and control for everyone*. Springer.

Aldao, A. (2013). The future of emotion regulation research: Capturing context. *Perspectives on Psychological Science*, *8*, 155–172.

Al-Shawaf, L. (2016). The evolutionary psychology of hunger. *Appetite*, *105*, 591–595.

Al-Shawaf, L., Conroy-Beam, D., Asao, K., & Buss, D. M. (2016). Human emotions: An evolutionary psychological perspective. *Emotion Review*, *8*, 173–186.

Al-Shawaf, L., & Lewis, D. M. (2017). Evolutionary psychology and the emotions. In V. Zeigler-Hill & T.K. Shackelford (Eds.), *Encyclopedia of personality and individual differences* (pp. 1452–1461). Springer.

Anderson, C., Hildreth, J. A. D., & Howland, L. (2015). Is the desire for status a fundamental human motive? A review of the empirical literature. *Psychological Bulletin*, *141*, 574–601.

Ashton, M. C., & Lee, K. (2001). A theoretical basis for the major dimensions of personality. *European Journal of Personality*, *15*, 327–353.

Ashton, M. C., & Lee, K. (2007). Empirical, theoretical, and practical advantages of the HEXACO model of personality structure. *Personality and Social Psychology Review*, *11*, 150–166.

Ashton, M. C., Lee, K., Pozzebon, J. A., Visser, B. A., & Worth, N. C. (2010). Status-driven risk taking and the major dimensions of personality. *Journal of Research in Personality*, *44*, 734–737.

Aunger, R., & Curtis, V. (2013). The anatomy of motivation: An evolutionary-ecological approach. *Biological Theory*, *8*, 49–63.

Baams, L., Overbeek, G., Dubas, J. S., & Van Aken, M. A. (2014). On early starters and late bloomers: The development of sexual behavior in adolescence across personality types. *Journal of Sex Research*, *51*, 754–764.

Baerends, G. P. (1976). The functional organization of behaviour. *Animal Behaviour*, *24*, 726–738.

Ballard, T., Yeo, G., Vancouver, J. B., & Neal, A. (2017). The dynamics of avoidance goal regulation. *Motivation and Emotion*, *41*, 698–707.

Banai, B., & Pavela, I. (2015). Two-dimensional structure of the Sociosexual Orientation Inventory and its personality correlates. *Evolutionary Psychology*, *13*, 1474704915604541.

Barbaro, N. (2020). The nature of attachment systems. *Social and Personality Psychology Compass*, *14*, e12570.

Barrett, H. C. (2012). A hierarchical model of the evolution of human brain specializations. *Proceedings of the National Academy of Sciences USA*, *109*, 10733–10740.

Barrett, H. C. (2015a). *The shape of thought: How mental adaptations evolve*. Oxford University Press.

Barrett, H. C. (2015b). Adaptations to predators and prey. In D. M. Buss (Ed.), *The handbook of evolutionary psychology*, Vol 1: *Foundations* (2nd ed., pp. 246–263). Wiley.

Baumert, A., Schmitt, M., Perugini, M., Johnson, W., Blum, G., Borkenau, P., Costantini, G., Denissen, J. J. A., Fleeson, W., Grafton, B., Jayawickreme, E., Kurzius, E., MacLeod, C., Miller, L. C., Read, S. J., Roberts, B., Robinson, M. D., Wood, D., & Wrzus, C. (2017). Integrating personality structure, personality process, and personality development. *European Journal of Personality*, *31*, 503–528.

Beall, A. T., & Tracy, J. L. (2017). Emotivational psychology: How distinct emotions facilitate fundamental motives. *Social and Personality Psychology Compass*, *11*, e12303.

Beall, A. T., & Tracy, J. L. (2020). Evolution of pride and shame. In L. Workman, W. Reader, & J. H. Barkow (Eds.), *Cambridge handbook of evolutionary perspectives on human behavior* (pp. 179–193). Cambridge University Press.

Bechhoefer, J. (2005). Feedback for physicists: A tutorial essay on control. *Reviews of Modern Physics*, *77*, 783–836.

Beedie, C., Terry, P., & Lane, A. (2005). Distinctions between emotion and mood. *Cognition & Emotion*, *19*, 847–878.

Bizer, G. Y. (2020). Who's bothered by an unfair world? The emotional response to unfairness scale. *Personality and Individual Differences*, *159*, 109882.

Boden, M. A. (1965). McDougall revisited. *Journal of Personality*, *33*, 1–19.

Borgerhoff Mulder, M., & Beheim, B. A. (2011). Understanding the nature of wealth and its effects on human fitness. *Philosophical Transactions of the Royal Society of London B*, *366*, 344–356.

Borgerhoff Mulder, M., Bowles, S., Hertz, T., Bell, A., Beise, J., Clark, G., et al. (2009). Intergenerational wealth transmission and the dynamics of inequality in small-scale societies. *Science*, *326*, 682–688.

Borsboom, D., Kievit, R. A., Cervone, D., & Hood, S. B. (2009). The two disciplines of scientific psychology, or: The disunity of psychology as a working hypothesis. In J. Valsiner, P. C. Molenaar, M. C. D. P. Lyra, & N. Chaudhary (Eds.), *Dynamic process methodology in the social and developmental sciences* (pp. 67–97). Springer.

Bourdage, J. S., Lee, K., Ashton, M. C., & Perry, A. (2007). Big Five and HEXACO model personality correlates of sexuality. *Personality and Individual Differences*, *43*, 1506–1516.

Bowlby, J. (1982). *Attachment and loss*, Vol. I: *Attachment* (rev. ed.). Basic Books.

Boyer, P., & Liénard, P. (2006). Precaution systems and ritualized behavior. *Behavioral and Brain Sciences*, *29*, 635–641.

Brasini, M., Tanzilli, A., Pistella, J., Gentile, D., Di Marco, I., Mancini, F., Lingiardi, V., & Baiocco, R. (2020). The social mentalities scale: A new measure for assessing the interpersonal motivations underlying social relationships. *Personality and Individual Differences*, *167*, 110236.

Brown, S., Brown, R., & Preston, S. D. (2012). A model of human caregiving motivation. In S. L. Brown, R. M. Brown, & L. A. Penner (Eds.), *Moving beyond self interest: Perspectives from evolutionary biology, neuroscience, and the social sciences* (pp. 75–88). Oxford University Press.

Browne, M. W. (2001). An overview of analytic rotation in exploratory factor analysis. *Multivariate Behavioral Research*, *36*, 111–150.

Buckels, E. E., Beall, A. T., Hofer, M. K., Lin, E. Y., Zhou, Z., & Schaller, M. (2015). Individual differences in activation of the parental care motivational system: Assessment, prediction, and implications. *Journal of Personality and Social Psychology*, *108*, 497–514.

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

Burghardt, G. M. (2005). *The genesis of animal play*. MIT Press.

Burghardt, G. M. (2019). A place for emotions in behavior systems research. *Behavioural Processes*, *166*, 103881.

Burghardt, G. M., & Bowers, R. I. (2017). From instinct to behavior systems: An integrated approach to ethological psychology. In J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowdon, & T. Zentall (Eds.), *APA handbook of comparative psychology: Basic concepts, methods, neural substrate, and behavior* (p. 333–364). American Psychological Association.

Buss, D. M. (2011). Personality and the adaptive landscape: The role of individual differences in creating and solving social adaptive problems. In D. M. Buss & P. Hawley, *The evolution of personality and individual differences* (pp. 29–57). Oxford University Press.

Buss, D. M. (2013). Sexual jealousy. *Psychological Topics*, *22*, 155–182.

Byers, J. A., & Walker, C. (1995). Refining the motor training hypothesis for the evolution of play. *The American Naturalist*, *146*, 25–40.

Carver, C. S., & Scheier, M. F. (2013). Goals and emotion. In M. D. Robinson, E. R. Watkins, & E. Harmon-Jones (Eds.), *Guilford handbook of cognition and emotion* (pp. 176–194). Guilford Press.

Cassidy, J. (2016). The nature of the child's ties. In J. Cassidy & P. R. Shaver (Eds.), *Handbook of attachment* (3rd ed., pp. 3–24). Guilford Press.

Cattell, R. B. (1957). *Personality and motivation: Structure and measurement*. World Book.

Cheng, J. T., Tracy, J. L., Foulsham, T., Kingstone, A., & Henrich, J. (2013). Two ways to the top: Evidence that dominance and prestige are distinct yet viable avenues to social rank and influence. *Journal of Personality and Social Psychology*, *104*, 103–125.

Cheng, J. T., Tracy, J. L., & Henrich, J. (2010). Pride, personality, and the evolutionary foundations of human social status. *Evolution and Human Behavior*, *31*, 334–347.

Chester, D. S. (2017). The role of positive affect in aggression. *Current Directions in Psychological Science, 26*, 366–370.

Chichinadze, K., Chichinadze, N., & Lazarashvili, A. (2011). Hormonal and neurochemical mechanisms of aggression and a new classification of aggressive behavior. *Aggression and Violent Behavior*, *16*, 461–471.

Cohen, T. R., Wolf, S. T., Panter, A. T., & Insko, C. A. (2011). Introducing the GASP scale: A new measure of guilt and shame proneness. *Journal of Personality and Social Psychology*, *100*, 947–966.

Corr, P. J., DeYoung, C. G., & McNaughton, N. (2013). Motivation and personality: A neuropsychological perspective. *Social and Personality Psychology Compass*, *7*, 158–175.

Corr, P. J., & Krupić, D. (2017). Motivating personality: Approach, avoidance, and their conflict. In A. J. Elliot (Ed.), *Advances in motivation science* (Vol. 4, pp. 39–90). Academic Press.

Cosmides, L., & Tooby, J. (2000). Evolutionary psychology and the emotions. In M. Lewis & J. M. Haviland-Jones (Eds.), *Handbook of emotions* (2nd ed., pp. 91–115). Guilford Press.

Cosmides, L., & Tooby, J. (2015). Adaptations for reasoning about social exchange. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (2nd ed., pp. 625–668). Wiley.

Cowen, A., Sauter, D., Tracy, J. L., & Keltner, D. (2019). Mapping the passions: Toward a high-dimensional taxonomy of emotional experience and expression. *Psychological Science in the Public Interest*, *20*, 69–90.

Craig, W. (1918). Appetites and aversions as constituents of instincts. *Biological Bulletin*, *34*, 91–107.

Csete, M., & Doyle, J. (2004). Bow ties, metabolism and disease. *Trends in Biotechnology*, *22*, 446–450.

Csibra, G., & Gergely, G. (2006). Social learning and social cognition: The case for pedagogy. In Y. Munakata & M. H. Johnson (Eds.), *Processes of change in brain and cognitive development*, Vol. XXI: *Attention and performance* (pp. 249–274). Oxford University Press.

Curtis, V. (2011). Why disgust matters. *Philosophical Transactions of the Royal Society of London B*, *366*, 3478–3490.

Davis, K. L., & Panksepp, J. (2018). *The emotional foundations of personality: A neurobiological and evolutionary approach*. W. W. Norton.

Del Giudice, M. (2015). Self-regulation in an evolutionary perspective. In G. H. E. Gendolla, M. Tops, & S. Koole (Eds.), *Handbook of biobehavioral approaches to self-regulation* (pp. 25–42). Springer.

Del Giudice, M. (2018). *Evolutionary psychopathology: A unified approach*. Oxford University Press.

Del Giudice, M. (2020). Rethinking the fast-slow continuum of individual differences. *Evolution and Human Behavior*, *41*, 536–549.

Del Giudice, M. (2021). Effective dimensionality: A tutorial. *Multivariate Behavioral Research*, *56,* 527–542. https://doi.org/10.1080/00273171.2020.1743631

Del Giudice, M., Buck, C. L., Chaby, L. E., Gormally, B. M., Taff, C. C., Thawley, C. J., Vitousek, M. N., & Wada, H. (2018). What is stress? A systems perspective. *Integrative and Comparative Biology*, *58*, 1019–1032.

Del Giudice, M., Gangestad, S. W., & Kaplan, H. S. (2015). Life history theory and evolutionary psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology*, Vol 1: *Foundations* (2nd ed., pp. 88–114). Wiley.

Denissen, J. J., & Penke, L. (2008). Motivational individual reaction norms underlying the Five-Factor model of personality: First steps towards a theory-based conceptual framework. *Journal of Research in Personality*, *42*, 1285–1302.

DeYoung, C. G. (2015). Cybernetic Big Five theory. *Journal of Research in Personality*, *56*, 33–58.

DeYoung, C. G., & Krueger, R. F. (2018). A cybernetic theory of psychopathology. *Psychological Inquiry*, *29*, 117–138.

DeYoung, C. G., Weisberg, Y. J., Quilty, L. C., & Peterson, J. B. (2013). Unifying the aspects of the Big Five, the interpersonal circumplex, and trait affiliation. *Journal of Personality*, *81*, 465–475.

Doyle, J. C., & Csete, M. (2011). Architecture, constraints, and behavior. *Proceedings of the National Academy of Sciences USA*, *108*, 15624–15630.

Durkee, P. K., Lukaszewski, A. W., & Buss, D. M. (2019). Pride and shame: Key components of a culturally universal status management system. *Evolution and Human Behavior*, *40*, 470–478.

Dweck, C. S. (2017). From needs to goals and representations: Foundations for a unified theory of motivation, personality, and development. *Psychological Review*, *124*, 689–719.

Eastwick, P. W. (2009). Beyond the Pleistocene: Using phylogeny and constraint to inform the evolutionary psychology of human mating. *Psychological Bulletin*, *135*, 794–821.

Einstein, D., & Lanning, K. (1998). Shame, guilt, ego development and the five-factor model of personality. *Journal of Personality*, *66*, 555–582.

Eldar, E., Rutledge, R. B., Dolan, R. J., & Niv, Y. (2016). Mood as representation of momentum. *Trends in Cognitive Sciences*, *20*, 15–24.

Engelmann, J. M., Herrmann, E., & Tomasello, M. (2015). Chimpanzees trust conspecifics to engage in low-cost reciprocity. *Proceedings of the Royal Society of London B*, *282*, 20142803.

Erber, R., & Erber, M. W. (2000). The self-regulation of moods: Second thoughts on the importance of happiness in everyday life. *Psychological Inquiry*, *11*, 142–148.

Figueredo, A. J., Vásquez, G., Brumbach, B. H., & Schneider, S. M. (2007). The K-factor, covitality, and personality. *Human Nature*, *18*, 47–73.

Fiske, A. P. (2020). The lexical fallacy in emotion research: Mistaking vernacular words for psychological entities. *Psychological Review*, *127*, 95–113.

Fletcher, G. J. O., Simpson, J. A., Campbell, L., & Overall, N. C. (2015). Pair-Bonding, romantic love, and evolution: The curious case of Homo sapiens. *Perspectives on Psychological Science*, *10*, 20–36.

Fogarty, L., Strimling, P., & Laland, K. N. (2011). The evolution of teaching. *Evolution*, *65*, 2760–2770.

Fraley, R. C., & Spieker, S. J. (2003). Are infant attachment patterns continuously or categorically distributed? A taxometric analysis of strange situation behavior. *Developmental Psychology*, *39*, 387–404.

Gangestad, S. W., & Haselton, M. G. (2015). Human estrus: Implications for relationship science. *Current Opinion in Psychology*, *1*, 45–51.

Gangestad, S. W., & Thornhill, R. (2007). The evolution of social inference processes: The importance of signaling theory. In J. P. Forgas, M. G. Haselton, & W. von Hippel (Eds.), *Evolutionary psychology and social cognition* (pp. 33–48). Psychology Press.

Gendolla, G. H. (2000). On the impact of mood on behavior: An integrative theory and a review. *Review of General Psychology*, *4*, 378–408.

Gilbert, P. (1989). *Human nature and suffering*. Lawrence Erlbaum Associates.

Gilbert, P. (2005). Compassion and cruelty: A biopsychosocial approach. In P. Gilbert (Ed.), *Compassion: Conceptualisations, research and use in psychotherapy* (pp. 9–74). Routledge.

Gottlieb, J., Oudeyer, P. Y., Lopes, M., & Baranes, A. (2013). Information-seeking, curiosity, and attention: Computational and neural mechanisms. *Trends in Cognitive Sciences*, *17*, 585–593.

Graeff, F. G. (2004). Serotonin, the periaqueductal gray and panic. *Neuroscience & Biobehavioral Reviews*, *28*, 239–259.

Gray, J. A., & McNaughton, N. (2000). *The neuropsychology of anxiety: An enquiry into the functions of the septo-hippocampal system*. Oxford University Press.

Graziano, W. G., & Tobin, R. M. (2017). Agreeableness and the five factor model. In T. A. Widiger (Ed.), *The Oxford handbook of the five factor model* (pp. 105–132). Oxford University Press.

Griskevicius, V., Tybur, J. M., Sundie, J. M., Cialdini, R. B., Miller, G. F., & Kenrick, D. T. (2007). Blatant benevolence and conspicuous consumption: When romantic motives elicit strategic costly signals. *Journal of Personality and Social Psychology*, *93*, 85–102.

Gross, J. J. (2015). The extended process model of emotion regulation: Elaborations, applications, and future directions. *Psychological Inquiry*, *26*, 130–137.

Hagenaars, M. A., Oitzl, M., & Roelofs, K. (2014). Updating freeze: Aligning animal and human research. *Neuroscience & Biobehavioral Reviews*, *47*, 165–176.

Heckhausen, H. (2018). Historical trends in motivation research. In J. Heckhausen & H. Heckhausen (Eds.), *Motivation and action* (3rd ed., pp. 15–66). Springer.

Holtzman, N. S., & Strube, M. J. (2013). Above and beyond short-term mating, long-term mating is uniquely tied to human personality. *Evolutionary Psychology*, *11*, 1101–1129.

Hrdy, S. B. (2005). Comes the child before the man: How cooperative breeding and prolonged postweaning dependence shaped human potentials. In M. E. Lamb & B. S. Hewlett (Eds.), *Hunter-gatherer childhoods: Evolutionary, developmental, and cultural perspectives* (pp. 65–91). Aldine.

Hrdy, S. B., & Burkart, J. M. (2020). The emergence of emotionally modern humans: Implications for language and learning. *Philosophical Transactions of the Royal Society B*, *375*, 20190499.

Jaeggi, A. V., De Groot, E., Stevens, J. M., & Van Schaik, C. P. (2013). Mechanisms of reciprocity in primates: Testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evolution and Human Behavior*, *34*, 69–77.

Jaeggi, A. V., & Gurven, M. (2013). Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: A phylogenetic meta-analysis. *Proceedings of the Royal Society of London B*, *280*, 20131615.

Johnson, S. L., Leedom, L. J., & Muhtadie, L. (2012). The dominance behavioral system and psychopathology: Evidence from self-report, observational, and biological studies. *Psychological Bulletin*, *138*, 692–743.

Kaplan, H. S., Gurven, M., & Lancaster, J. B. (2007). Brain evolution and the human adaptive complex: An ecological and social theory. In S. W. Gangestad & J. A. Simpson (Eds.), *The evolution of mind: Fundamental questions and controversies* (pp. 269–279). Guilford Press.

Kaplan, H. S., Hill, K., Lancaster, J. B., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology*, *9*, 156–185.

Kaplan, H. S., Hooper, P. L., & Gurven, M. (2009). The evolutionary and ecological roots of human social organization. *Philosophical Transactions of the Royal Society B*, *364*, 3289–3299.

Keltner, D., Haidt, J., & Shiota, L. (2006). Social functionalism and the evolution of emotions. In M. Schaller, D. Kenrick, & J. Simpson (Eds.), *Evolution and social psychology* (pp. 115–142). Psychology Press.

Keltner, D., Tracy, J. L., Sauter, D., & Cowen, A. (2019). What basic emotion theory really says for the twenty-first century study of emotion. *Journal of Nonverbal Behavior*, *43*, 195–201.

Kenrick, D. T., Griskevicius, V., Neuberg, S. L., & Schaller, M. (2010). Renovating the pyramid of needs: Contemporary extensions built upon ancient foundations. *Perspectives on Psychological Science*, *5*, 292–314.

Kitano, H. (2004). Biological robustness. *Nature Reviews Genetics*, *5*, 826–837.

Kitano, H., & Oda, K. (2006). Robustness trade-offs and host–microbial symbiosis in the immune system. *Molecular Systems Biology*, *2*, 2006.0022.

Kramer, K. L. (2010). Cooperative breeding and its significance to the demographic success of humans. *Annual Review of Anthropology*, *39*, 417–436.

Krantz, D. L., & Allen, D. (1967). The rise and fall of McDougall's instinct doctrine. *Journal of the History of the Behavioral Sciences*, *3*, 326–338.

Lee, K., & Ashton, M. C. (2020). Sex differences in HEXACO personality characteristics across countries and ethnicities. *Journal of Personality*, *88*, 1075–1090.

Lee, K., Ashton, M. C., Wiltshire, J., Bourdage, J. S., Visser, B. A., & Gallucci, A. (2013). Sex, power, and money: Prediction from the Dark Triad and Honesty–Humility. European *Journal of Personality*, *27*, 169–184.

Lewis, D. M., Al-Shawaf, L., Conroy-Beam, D., Asao, K., & Buss, D. M. (2017). Evolutionary psychology: A how-to guide. *American Psychologist*, *72*, 353–373.

Lichtenberg, J. D., Lachmann, F. M., & Fosshage, J. I. (1992). *Self and motivational systems*. Analytic Press.

Lippa, R. A. (2010). Gender differences in personality and interests: When, where, and why? *Social and Personality Psychology Compass*, *4*, 1098–1110.

LoBue, V., & Rakison, D. H. (2013). What we fear most: Developmental advantage for threat-relevant stimuli. *Developmental Review*, *33*, 285–303.

Locke, J. L., & Bogin, B. (2006). Language and life history: A new perspective on the development and evolution of human language. *Behavioral and Brain Sciences*, *29*, 259–280.

Loewenstein, G. (1994) The psychology of curiosity: A review and reinterpretation. *Psychological Bulletin*, *116*, 75–98.

Lukaszewski, A. W. (2020). Evolutionary perspectives on the mechanistic underpinnings of personality. In J. F. Rauthmann (Ed.), *The handbook of personality dynamics and processes* (pp. 523–550). Academic Press.

Lukaszewski, A. W., Lewis, D. M., Durkee, P. K., Sell, A. N., Sznycer, D., & Buss, D. M. (2020). An adaptationist framework for personality science. *European Journal of Personality*, *34*, 1151–1174.

Lykken, D. T. (1971). Multiple factor analysis and personality research. *Journal of Experimental Research in Personality*, *5*, 161–170.

Mac Giolla, E., & Kajonius, P. J. (2019). Sex differences in personality are larger in gender equal countries: Replicating and extending a surprising finding. *International Journal of Psychology*, *54*, 705–711.

Mallan, K. M., Lipp, O. V., & Cochrane, B. (2013). Slithering snakes, angry men and out-group members: What and whom are we evolved to fear? *Cognition and Emotion*, *27*, 1168–1180.

Maner, J. K. (2017). Dominance and prestige: A tale of two hierarchies. *Current Directions in Psychological Science*, *26*, 526–531.

Maslow, A. H. (1954). *Motivation and personality*. Harper.

McCrae, R. R., & Costa, P. T. (2003). *Personality in adulthood: A five-factor theory perspective* (2nd ed.). Guilford Press.

McDougall, W. (1908). *An introduction to social psychology*. Luce.

McDougall, W. (1921). The use and abuse of instinct in social psychology. *Journal of Abnormal Psychology and Social Psychology*, *16*, 285–333.

McDougall, W. (1924). Can sociology and social psychology dispense with instincts? *Journal of Abnormal Psychology and Social Psychology*, *19*, 13–41.

McDougall, W. (1932). *The energies of men: A study of the fundamentals of dynamic psychology*. Methuen.

McFarland, D. J. (1971). *Feedback mechanisms in animal behaviour*. Academic Press.

McFarland, D. J. (1974). *Motivational control systems analysis*. Academic Press.

McRae, K., & Gross, J. J. (2020). Emotion regulation. *Emotion*, *20*, 1–9.

Meston, C. M., & Buss, D. M. (2007). Why humans have sex. *Archives of Sexual Behavior*, *36*, 477–507.

Michalski, R. L., & Shackelford, T. K. (2010). Evolutionary personality psychology: Reconciling human nature and individual differences. *Personality and Individual Differences*, *48*, 509–516.

Mikulincer, M., & Shaver, P. R. (2016). *Attachment in adulthood: Structure, dynamics, and change* (2nd ed.). Guilford Press.

Morris, W. N. (1992). A functional analysis of the role of mood in affective systems. *Review of Personality and Social Psychology*, *13*, 256–293.

Morris, W. N. (2000). Some thoughts about mood and its regulation. *Psychological Inquiry*, *11*, 200–202.

Mulder, M. B., & Beheim, B. A. (2011). Understanding the nature of wealth and its effects on human fitness. *Philosophical Transactions of the Royal Society B*, *366*, 344–356.

Murphy, S. A., Fisher, P. A., & Robie, C. (2021). International comparison of gender differences in the five-factor model of personality: An investigation across 105 countries. *Journal of Research in Personality*, *90*, 104047.

Murray, H. A. (1938). *Explorations in personality*. Oxford University Press.

Neel, R., Kenrick, D. T., White, A. E., & Neuberg, S. L. (2016). Individual differences in fundamental social motives. *Journal of Personality and Social Psychology*, *110*, 887–907.

Nesse, R. M. (1990). Evolutionary explanations of emotions. *Human Nature*, *1*, 261–289.

Nesse, R. M. (2004). Natural selection and the elusiveness of happiness. *Philosophical Transactions of the Royal Society of London B*, *359*, 1333–1347.

Nesse, R. M. (2020). Tacit creationism in emotion research. In C. Price & E. Walle (Eds.), *Emotion Researcher, ISRE's sourcebook for research on emotion and affect*. International Society for Research on Emotion. https://emotionresearcher.com/tacit-creationism-in-emotion-research

Nettle, D., & Bateson, M. (2012). The evolutionary origins of mood and its disorders. *Current Biology*, *22*, R712–R721.

Nettle, D., & Pollet, T. V. (2008). Natural selection on male wealth in humans. *The American Naturalist*, *172*, 658–666.

Öhman, A. (2009). Of snakes and faces: An evolutionary perspective on the psychology of fear. *Scandinavian Journal of Psychology*, *50*, 543–552.

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

Panksepp, J. (2005). Affective consciousness: Core emotional feelings in animals and humans. *Consciousness and Cognition*, *14*, 30–80.

Panksepp, J. (2011). Cross-species affective neuroscience decoding of the primal affective experiences of humans and related animals. *PLoS ONE*, *6*, e21236.

Pellis, S. M., Pellis, V. C., Pelletier, A., & Leca, J. B. (2019). Is play a behavior system, and, if so, what kind? *Behavioural Processes*, *160*, 1–9.

Pinker, S. (2010). The cognitive niche: Coevolution of intelligence, sociality, and language. *Proceedings of the National Academy of Sciences USA*, *107*, 8993–8999.

Preston, S. D. (2014). Hoarding in animals: The argument for a homology. In R. O. Frost & G. Steketee (Eds.), *The Oxford handbook of hoarding and acquiring* (pp. 187–205). Oxford University Press.

Preston, S. D., & Vickers, B. D. (2014). The psychology of acquisitiveness. In S. D. Preston, M. L. Kringelbach, & B. Knutson (Eds.), *The interdisciplinary science of consumption* (pp. 127–146). MIT Press.

Quinlan, R. J. (2008). Human pair-bonds: Evolutionary functions, ecological variation, and adaptive development. *Evolutionary Anthropology*, *17*, 227–238.

Read, S. J., Brown, A. D., Wang, P., & Miller, L. C. (2020). Virtual personalities and neural networks: Capturing the structure and dynamics of personality. In J. F. Rauthmann (Ed.), *The handbook of personality dynamics and processes* (pp. 1037–1057). Academic Press.

Read, S. J., Monroe, B. M., Brownstein, A. L., Yang, Y., Chopra, G., & Miller, L. C. (2010). A neural network model of the structure and dynamics of human personality. *Psychological Review*, *117*, 61–92.

Read, S. J., Smith, B. J., Droutman, V., & Miller, L. C. (2017). Virtual personalities: Using computational modeling to understand within-person variability. *Journal of Research in Personality*, *69*, 237–249.

Reisenzein, R., & Weber, H. (2009). Personality and emotion. In P. J. Corr & G. Matthews (Eds.), *The Cambridge handbook of personality psychology* (pp. 54–71). Cambridge University Press.

Revelle, W., & Condon, D. M. (2015). A model for personality at three levels. *Journal of Research in Personality*, *56*, 70–81.

Roelofs, K. (2017). Freeze for action: Neurobiological mechanisms in animal and human freezing. *Philosophical Transactions of the Royal Society B*, *372*, 20160206.

Sass, D. A., & Schmitt, T. A. (2010). A comparative investigation of rotation criteria within exploratory factor analysis. *Multivariate Behavioral Research*, *45*, 73–103.

Scarantino, A. (2012). How to define emotions scientifically. *Emotion Review*, *4*, 358–368.

Scarantino, A. (2015). Basic emotions, psychological construction, and the problem of variability. In L. F. Barrett & J. A. Russell (Eds.), *The psychological construction of emotion* (pp. 334–376). Guilford Press.

Schaller, M. (2018). The parental care motivational system and why it matters (for everyone). *Current Directions in Psychological Science*, *27*, 295–301.

Scheffer, D., & Heckhausen, H. (2018). Trait theories of motivation. In J. Heckhausen & H. Heckhausen (Eds.), *Motivation and action* (3rd ed., pp. 67–112). Springer.

Schmitt, D. P., & Buss, D. M. (2000). Sexual dimensions of person description: Beyond or subsumed by the Big Five? *Journal of Research in Personality*, *34*, 141–177.

Schrock, J. M., Snodgrass, J. J., & Sugiyama, L. S. (2020). Lassitude: The emotion of being sick. *Evolution and Human Behavior*, *41*, 44–57.

Schultheiss, O.C. (2020). Motives and goals, or: The joys and meanings of life. In J. F. Rauthmann (Ed.), *The handbook of personality dynamics and processes* (pp. 295–322). Academic Press.

Scott, J. P. (1980). The function of emotions in behavioral systems: A systems theory analysis. In R. Plutchick & H. Kellerman (Eds.), *Emotion: Theory, research, and experience*, Vol. 1: *Theories of emotion* (pp. 35–56). Academic Press.

Sela, Y., & Barbaro, N. (2018). Evolutionary perspectives on personality and individual differences. In V. Zeigler-Hill & T. K. Shackelford (Eds.), *The SAGE handbook of personality and individual differences* (Vol. 1, pp. 203–228). SAGE.

Sell, A., Sznycer, D., Al-Shawaf, L., Lim, J., Krauss, A., Feldman, A., Rascanu, R., Sugiyama, L., Cosmides, L., & Tooby, J. (2017). The grammar of anger: Mapping the computational architecture of a recalibrational emotion. *Cognition*, *168*, 110–128.

Sell, A., Tooby, J., & Cosmides, L. (2009). Formidability and the logic of human anger. *Proceedings of the National Academy of Sciences USA*, *106*, 15073–15078.

Shudo, E., Haccou, P., & Iwasa, Y. (2003). Optimal choice between feedforward and feedback control in gene expression to cope with unpredictable danger. *Journal of Theoretical Biology*, *223*, 149–160.

Siemer, M. (2009). Mood experience: Implications of a dispositional theory of moods. *Emotion Review*, *1*, 256–263.

Soto, C. J., John, O. P., Gosling, S. D., & Potter, J. (2011). Age differences in personality traits from 10 to 65: Big Five domains and facets in a large cross-sectional sample. *Journal of Personality and Social Psychology*, *100*, 330–348.

Spinka, M., Newberry, R. C., & Bekoff, M. (2001). Mammalian play: Training for the unexpected. *Quarterly Review of Biology*, *76*, 141–168.

Sterling, P., & Eyer, J. (1988). Allostasis: A new paradigm to explain arousal pathology. In S. Fisher & J. Reason (Eds.), *Handbook of life stress, cognition, and health* (pp. 629–650). Oxford University Press.

Stolier, R. M., Hehman, E., & Freeman, J. B. (2020). Trait knowledge forms a common structure across social cognition. *Nature Human Behaviour*, *4*, 361–371.

Sundie, J. M., Kenrick, D. T., Griskevicius, V., Tybur, J. M., Vohs, K. D., & Beal, D. J. (2011). Peacocks, Porsches, and Thorstein Veblen: Conspicuous consumption as a sexual signaling system. *Journal of Personality and Social Psychology*, *100*, 664–680.

Sznycer, D. (2019). Forms and functions of the self-conscious emotions. *Trends in Cognitive Sciences*, *23*, 143–157.

Sznycer, D., Al-Shawaf, L., Bereby-Meyer, Y., Curry, O. S., De Smet, D., Ermer, E., Kim, S., Kim, S., Li, N. P., Lopez Seal, M. F., McClung, J., O, J., Ohtsubo, Y., Quillien, T., Schaub, M., Sell, A., van Leeuwen, F., Cosmides, L., & Tooby, J. (2017). Cross-cultural regularities in the cognitive architecture of pride. *Proceedings of the National Academy of Sciences USA*, *114*, 1874–1879.

Sznycer, D., Cosmides, L., & Tooby, J. (2017). Adaptationism carves emotions at their functional joints. *Psychological Inquiry*, *28*, 56–62.

Sznycer, D., & Lukaszewski, A. W. (2019). The emotion-valuation constellation: Multiple emotions are governed by a common grammar of social valuation. *Evolution and Human Behavior*, *40*, 395–404.

Tamir, M. (2009). What do people want to feel and why? Pleasure and utility in emotion regulation. *Current Directions in Psychological Science*, *18*, 101–105.

Tamir, M. (2016). Why do people regulate their emotions? A taxonomy of motives in emotion regulation. *Personality and Social Psychology Review*, *20*, 199–222.

Tamir, M., & Ford, B. Q. (2012). When feeling bad is expected to be good: Emotion regulation and outcome expectancies in social conflicts. *Emotion*, *12*, 807–816.

Tamir, M., Ford, B. Q., & Gilliam, M. (2013). Evidence for utilitarian motives in emotion regulation. *Cognition and Emotion*, *27*, 483–491.

Tamir, M., Mitchell, C., & Gross, J. J. (2008). Hedonic and instrumental motives in anger regulation. *Psychological Science*, *19*, 324–328.

Tennov, D. (1999). *Love and limerence: The experience of being in love*. Scarborough House.

Tinbergen, N. (1951). *The study of instinct*. Clarendon Press.

Toates, F. M., & Archer, J. (1978). A comparative review of motivational systems using classical control theory. *Animal Behaviour*, *26*, 368–380.

Tooby, J., & Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology*, *11*, 375–424.

Tooby, J., & Cosmides, L. (2008). The evolutionary psychology of the emotions and their relationship to internal regulatory variables. In M. Lewis, J. M. Haviland-Jones, & L. F. Barrett (Eds.), *Handbook of emotions* (3rd ed., pp. 114–137). Guilford Press.

Tooby, J., & Cosmides, L. (2015). The theoretical foundations of evolutionary psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology*, Vol 1: *Foundations* (2nd ed., pp. 3–87). Wiley.

Tooby, J., Cosmides, L., Sell, A., Lieberman, D., & Sznycer, D. (2008). Internal regulatory variables and the design of human motivation: A computational and evolutionary approach. In A. J. Elliot (Ed.), *Handbook of approach and avoidance motivation* (pp. 252–271). Taylor & Francis.

Tops, M., Boksem, M. A. S., Luu, P., & Tucker, D. M. (2010). Brain substrates of behavioral programs associated with self-regulation. *Frontiers in Cognition*, *1*, 152.

Tops, M., IJzerman, H., & Quirin, M. (2021). Personality dynamics in the brain: Individual differences in updating of representations and their phylogenetic roots. In J. F. Rauthmann (Ed.), *The handbook of personality dynamics and processes* (pp. 126–155). Academic Press.

Toronchuk, J. A., & Ellis, G. F. (2013). Affective neuronal selection: The nature of the primordial emotion systems. *Frontiers in Psychology*, *3*, 589.

Tracy, J. L., & Robins, R. W. (2007). The psychological structure of pride: A tale of two facets. *Journal of Personality and Social Psychology*, *92*, 506–525.

Trimmer, P. C., Paul, E. S., Mendl, M. T., McNamara, J. M., & Houston, A. I. (2013). On the evolution and optimality of mood states. *Behavioral Sciences*, *3*, 501–521.

Tybur, J. M., Lieberman, D., Kurzban, R., & DeScioli, P. (2013). Disgust: Evolved function and structure. *Psychological Review*, *120*, 65–84.

van Kleef, G. A., De Dreu, C. K., & Manstead, A. S. (2004). The interpersonal effects of anger and happiness in negotiations. *Journal of Personality and Social Psychology*, *86*, 57–76.

Volk, S., & Masicampo, E. J. (2020). Self-regulatory processes and personality. In J. F. Rauthmann (Ed.), *The handbook of personality dynamics and processes* (pp. 345–363). Academic Press.

Weisberg, D. S., & Gopnik, A. (2013). Pretense, counterfactuals, and Bayesian causal models: Why what is not real really matters. *Cognitive Science*, *37*, 1368–1381.

Winterhalder, B., Lu, F., & Tucker, B. (1999). Risk-sensitive adaptive tactics: Models and evidence from subsistence studies in biology and anthropology. *Journal of Archaeological Research*, *7*, 301–348.

Woody, E. Z., & Szechtman, H. (2011). Adaptation to potential threat: The evolution, neurobiology, and psychopathology of the security motivation system. *Neuroscience & Biobehavioral Reviews*, *35*, 1019–1033.

Wrangham, R. W. (1999). Evolution of coalitionary killing. *American Journal of Physical Anthropology*, *110*, 1–30.

Wrangham, R. W. (2018). Two types of aggression in human evolution. *Proceedings of the National Academy of Sciences USA*, *115*, 245–253.

Zeifman, D. M., & Hazan, C. (2016). Pair bonds as attachments: Mounting evidence in support of Bowlby's hypothesis. In J. Cassidy & P. R. Shaver (Eds.), *Handbook of attachment* (3rd ed., pp. 416–434). Guilford Press.