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Large-scale neural networks and the lateralization of motivation and emotion

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ABSTRACT

Several lines of research in animals and humans converge on the distinction between two basic large-scale brain networks of self-regulation, giving rise to predictive and reactive control systems (PARCS). Predictive (internally-driven) and reactive (externally-guided) control are supported by dorsal versus ventral corticolimbic systems, respectively. Based on extant empirical evidence, we demonstrate how the PARCS produce frontal laterality effects in emotion and motivation. In addition, we explain how this framework gives rise to individual differences in appraising and coping with challenges. PARCS theory integrates separate fields of research, such as research on the motivational correlates of affect, EEG frontal alpha power asymmetry and implicit affective priming effects on cardiovascular indicators of effort during cognitive task performance. Across these different paradigms, converging evidence points to a qualitative motivational division between, on the one hand, angry and happy emotions, and, on the other hand, sad and fearful emotions. PARCS suggests that those two pairs of emotions are associated with predictive and reactive control, respectively. PARCS theory may thus generate important new insights on the motivational and emotional dynamics that drive autonomic and homeostatic control processes.

1. Introduction

One of the great unresolved issues within modern neuroscience is the functional significance of the division between the left and right hemisphere. With respect to emotional and motivational aspects of behavior, the currently dominant view is that the left hemisphere supports approach motivation, and that the right hemisphere supports avoidance motivation (Davidson, 1998; Harmon-Jones, 2004). This view has yielded important insights. However, recent developments in animal research (Rogers et al., 2013) suggest a macro-level organization of neural networks that may have effects on the specialization of each hemisphere. This specialization of either hemisphere may work over and above approach versus avoidance motivation.

Recently, evidence from several lines of physiological research in animals and humans has converged on the notion of a macro-level organization of neural networks that is remarkably similar across vertebrates. This basic organization has not only been found in terms of laterality of functions, but also in terms of ventral versus dorsal corticolimbic networks that are systems for autonomic, homeostatic, emotional, and behavioral motor control (see Tops et al., 2014a). Ventral networks control behavior in unpredictable, unstable and novel environments. By contrast, dorsal networks control behavior in predictable, familiar, and stable environments. Hemispheric specialization may have led to asymmetric elaborations of the ventral and dorsal pathways (Tucker et al., 1995). In turn, these asymmetric elaborations of the ventral and dorsal pathways may explain different functions of each hemisphere in terms of emotion and motivation. Individual differences in the asymmetric elaborations or recruitment of these systems appear to give rise to individual differences in appraising and coping with challenges, leading to differences in emotion and motivation.

In what follows, we begin by outlining predictive and reactive control systems (PARCS) theory, an integrative framework for understanding the macro-level organization of predictive (driven by internal prediction) and reactive (guided by external stimuli) behavior control systems. Next, we discuss that reactive and predictive control systems manifest themselves in reactive and proactive coping styles that preferentially engage the right versus left hemisphere. Similar to the coping styles, this is evidenced by a wide range of behaviors across many vertebrate species. We go on to suggest that, based on predictive and reactive control systems, evolution favored the emergence of at least two additional coping styles in humans, namely conscientious and self-directed styles. Applying this framework, we show how the reactive-predictive

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distinction can integrate evidence from studies of affect, laterality of approach-avoidance motivation and studies of effects of affective priming on cardiovascular indication of effort mobilization during cognitive task performance. Finally, we discuss implications for research on health, resilience, sex differences, hemispheric lateralization and motivation.

2. Reactive and predictive systems as adaptations to environmental conditions

Theories of human motivation propose that metabolic requirements for survival need to be met before prospective functioning and investment can emerge. The most prominent of these theories is Maslow's (1954) hierarchy of needs, which proposes a hierarchical ordering of the most basic needs such as safety and physiological needs (e.g., food) through higher-order needs such as love/belonging and esteem/status to eventually self-actualization. Maslow's theory has been subsequently criticized mainly because it has not generated a systematic body of empirical evidence to back up a stable or specific order in which the needs tend to be fulfilled (Wahba and Bridwell, 1976). Still, evidence has been gathered for theories of personality and motivation that do not propose a specific hierarchy of needs, but do discriminate classes of motivation according to the level in which behavior is externally determined by the environment versus by the internal self (e.g., self-determination theory; Deci and Ryan, 1985). In addition to these humanistic theories, in both animals and humans, there is support for a basic distinction between survival (physiological and safety) needs and needs to invest in future benefits (Schneider et al., 2013; Tang and West, 1997).

Animal research suggests that neural systems are fundamentally organized to distinguish conditions of low resources and unmet energy need from conditions of high levels of resources and met energy needs, and to regulate behavior, effort, autonomic function and homeostasis accordingly. Energy acquisition and storage is an important prerequisite for reproductive success. Thus, in most species, behavioral sequences are organized so that a period of eating and fattening typically precedes a period of mating and caring for offspring. This is particularly important in habitats where food availability fluctuates in an unpredictable manner (Schneider et al., 2013). Perceptions of predictability and having a surplus of resources and energy shift the regulatory focus from immediate, momentary concerns and harm prevention towards future-directed behavior and long-term investments. Human evolution has taken this shift from immediate survival towards mating and caring for offspring further, exploiting environmental predictability through the development of a large neocortex and extended parental investment, facilitating the development and learning of prospective abilities (Tops and Carter, 2013).

The different systems for behavioral control are the main focus of predictive and reactive control systems (PARCS) theory (Tops et al., 2013, 2014a, 2014b). PARCS theory proposes that people are equipped with separate neural systems for dealing with different types of environments. Reactive control systems are for dealing with unpredictable, unstable and novel environments. During reactive control, autonomic, homeostatic, and motor control is guided by feedback from stimuli or cues from the environment. By contrast, predictive control systems are for dealing with predictable, familiar, and stable environments. During predictive control, autonomic, homeostatic, and motor control is guided by internally organized model-based predictions and expectancies that are based on people's prior experiences.

PARCS theory acknowledges the network architecture of the frontal lobe that reflects the dual limbic origins of frontal cortex, in the dorsal archicortical and ventral paleocortical structures (see Goldberg, 1985; Tucker et al., 1995). PARCS theory suggests that the ventral system evolved early in evolutionary history for the purpose of reactive control, i.e., behavioral control in unpredictable environments. This system (see Fig. 1A) is composed of the mediodorsal thalamus, ventral pallidum, lateral limbic system structures such as the ventral striatum (“nucleus accumbens”), anterior hippocampal formation, and amygdala, the dorsal anterior cingulate cortex (dACC), as well as ventrolateral cortical structures such as the ventro-anterior temporoparietal junction, perirhinal cortex, inferotemporal cortex, temporal pole, anterior insula (AI), ventral lateral pre-frontal areas BA 44, 45 and 47 (together: inferior frontal gyrus; IFG), lateral orbital (lateral BA 11 and 13), aspects of the frontal pole (BA 10), and ventral third of dorsolateral area (ventral BA 46; cf. Faw, 2003). The ventral system is thought to specialize in the processing of novelty and biological salience in order to control behavior in unpredictable as well as in urgent and emergency situations. It responds in a feedback-guided manner to the immediate situation and narrows attention to local, central aspects of a situation or a stimulus.

The predictive control system, by contrast, is comprised of mostly dorsomedial structures (see Fig. 1A) such as the posterior cingulate cortex, precuneus, posterior temporoparietal junction/angular gyrus, parahippocampal cortex and retrosplenial cortex, posterior hippocampal formation, anteroventral thalamus, lateral pallidum, dorsal striatum, medial prefrontal cortex, frontal eye fields and dorsolateral prefrontal cortex (DLPFC). This network of systems is considered largely an outgrowth of evolutionary pressures that emerged in predictable and stable environments (Tops et al., 2014a). PARCS theory suggests that the dorsal (predictive) system creates internal models that predict future outcomes through simulation, and updates those models slowly during learning, in line with the idea that it responds to environmental predictability and familiarity.

Predictive and reactive control systems each support different ways of coping with challenges and situations. Reactive control leads to hyper-engagement: appraisal of unpredictability or emergency precludes prediction of efficient responses. Instead, reactive control tries to ensure that responses are sufficient through increased and undifferentiated sympathetic (and hypothalamus-pituitary-adrenal axis) activation. However, the high physiological costs of increased sympathetic activation and appraisal of unpredictability and low control also predispose to demotivation resulting in hypo-engagement: appraisal that the challenge cannot be overcome, or only at excessive costs. By contrast, predictive control will increase efficiency and perseveration informed by current and future-directed benefits. In section 3, we consider how the coping styles of reactive and (albeit lower level, see Section 5) predictive control are recognized in many animal species. In Section 4, we relate reactive and predictive control to the different hemispheres.

3. Manifestation in animal personality

Humans and animals show stable individual differences in coping style, i.e., in the behavioral and physiological efforts to master the situation. Much of the work on coping styles (also termed personality or behavioral syndrome) is inspired by the work of researcher of animal coping styles Henry and Stephens (1977). Henry suggested, on the basis of social stress research in animals and man, that two stress response patterns may be distinguished. The first pattern, the active response, was originally described by Cannon (1915) as fight-flight response. Behaviorally, the active response is characterized by territorial control and aggression. The second pattern, was originally termed the “conservation-withdrawal response” (Engel and Schmale, 1972). The second response pattern is characterized behaviorally by immobility and low levels of aggression. Overlapping descriptions and operationalizations of the two coping styles have been named variously high- versus low-aggressive, active versus passive, bold versus shy, Roman high versus low (active) avoidance (rats) (see Biro and Stamps, 2008; Koolhaas et al., 1999; Steimer and Driscoll, 2003; Wolf et al., 2007).

However, the aforementioned terms may not properly describe the fundamental difference between the two stress response patterns (Koolhaas et al., 1999). A fundamental difference seems to be the degree in which behavior is guided reactively by environmental stimuli (Benus et al., 1990). Aggressive animals easily develop routines, i.e. a rather