



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.

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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 proactive 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

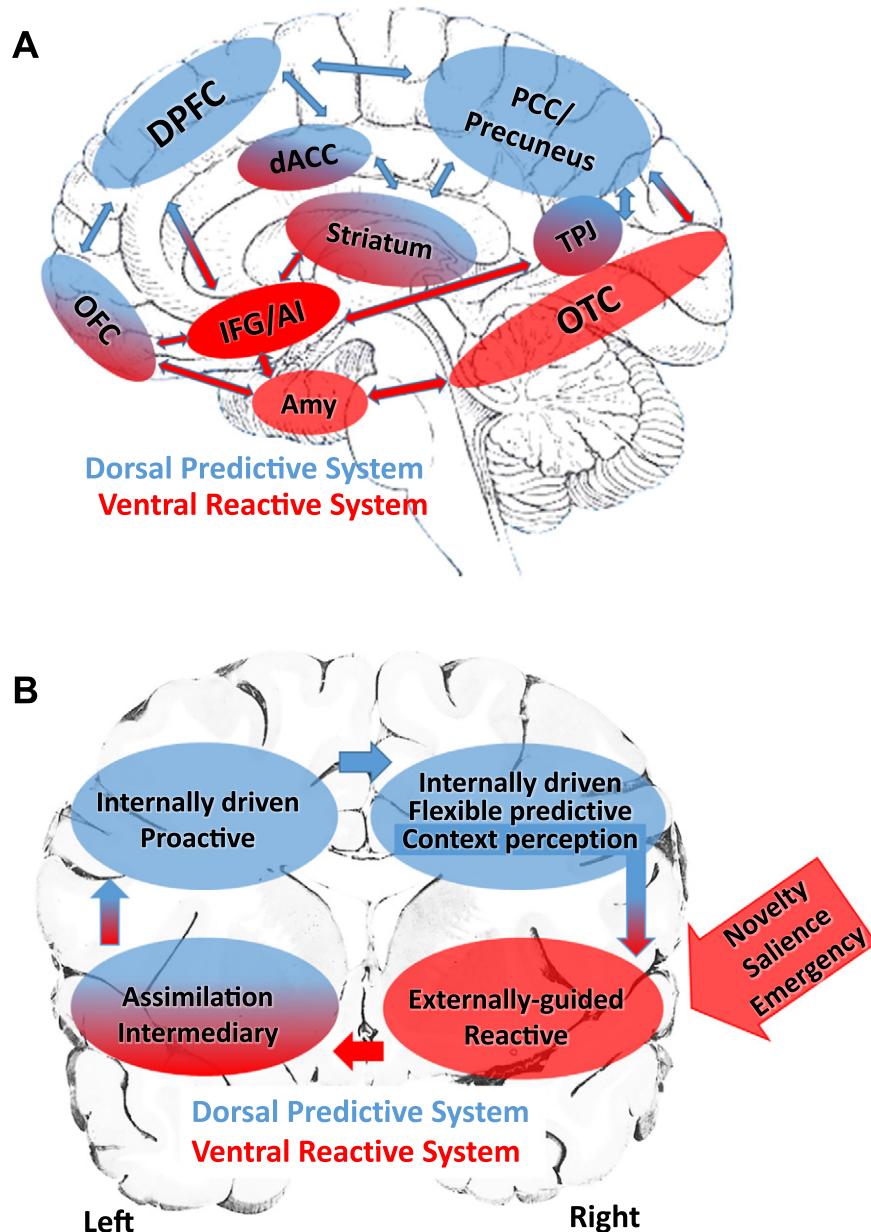


Fig. 1. A. Example areas and their interconnections as part of either the ventral reactive control system or the dorsal predictive control system. OFC = orbitofrontal cortex (and ventromedial prefrontal cortex), IFG = inferior frontal gyrus, AI = anterior insula, dACC = dorsal anterior cingulate cortex, DPFc = dorsal (medial & lateral) prefrontal cortex, PCC = posterior cingulate cortex, TPJ = temporo-parietal junction, OTC = occipito-temporal cortex, Amy = Amygdala. B. Flow of processing novel, salient or emergency information in dorsal predictive and ventral reactive control systems in the right and left hemispheres. Individual differences arise from relative elaborations of a particular process.

intrinsically driven type of behavior and perseverance, and show reduced impulse control (behavioral inhibition) in operant conditioning paradigms. Nonaggressive animals in contrast are more *externally-guided*, show stronger orienting responses and neophobia, and are continuously highly reactive to environmental stimuli, i.e., they show larger cue dependency and conditioned immobility. For that reason, Koolhaas et al. (1999) suggested the terms “proactive coping” and “reactive coping”. Studies of animals in feral populations indicate that the proactive and the reactive coping style represent fundamental biological trait characteristics that can be observed in many species. The coping styles seem to play a role in the population ecology of the species. The optimal proportion of each temperament in a population changes with the predictability and stability of the environment. The reactive and proactive traits developed during evolution because they are adaptive in unpredictable or changing environments, and predictable and stable environments, respectively.

Their differential degree of flexibility may explain why proactive animals are more successful under stable colony conditions, whereas reactive animals do better in a variable or unpredictable environment, for example during migration (see Koolhaas et al., 1999).

The characteristics of the coping styles and neural systems involved suggest that externally-guided reactive coping and intrinsically-driven proactive coping may be associated with reactive and predictive control, respectively. For instance, in the context of stress-related challenges in relation to different positions in a dominance hierarchy, activity in the predictive system (dorsal striatum) is involved in autonomy by programming behavior on the basis of comparing information from the environment and interoception with internal objectives, i.e., behavior is self-determined rather than controlled by others. By contrast, the reactive system (ventral striatum) is involved in programming behavior on the basis of immediately present external input (Cools et al., 1990; van

den Bos, 2015). In the next section, we discuss evidence for different involvement of each hemisphere in reactive versus predictive control and reactive versus proactive coping.

4. Lateralization of reactive and predictive control systems

During evolution, demands increased for complex integration of information that is novel or of immediate concern into internal models for future-directed behavior, which may have led to a functional hemispheric asymmetry. In the right hemisphere, the reactive system is involved in responses to novel and salient stimuli that pose immediate, momentary concerns whereas in the left hemisphere this ventral system developed an intermediary role between reactive and predictive control, being implicated in assimilation of those stimuli and experiences in internal models and facilitating shifting towards future-directed behavior (Tops et al., 2014a). Similarly, based on evolutionary considerations, research on motor control, and semantic priming, Dien (2008) characterized left hemispheric specialization as “proactive” and right hemispheric specialization as “reactive.” That is, the left hemisphere has the role of anticipating future scenarios and choosing between them while the right hemisphere has the role of integrating ongoing information into a unitary view of the past in order to immediately detect and respond to novel and unexpected events; the left hemisphere is guided by internal predictions, planning and hypothesis testing whereas the right hemisphere is guided by external unforeseen events and characterized by trial-and-error learning (Dien, 2008). The right hemisphere uses internal models of past experience to detect deviations, anomalies and novel events.

Consistent with reactive and proactive hemispheric specializations, reactive and proactive coping appears to preferentially engage the right versus left hemisphere. Henry (1997) concluded from behavioural and neurophysiological evidence that the right (emotional perceptions) and the left (socially manipulative, action oriented) hemispheres subserve different emotional sets that correspond to “appraisal” and “control” (e.g., active coping, action planning and power), respectively. Reactive coping has been related to right hemisphere activation or dominance and proactive coping has been related to left hemisphere activation or dominance in primates and rabbits (Braccini and Caine, 2009; Pavlova et al., 2012). Right-handed primates (presumably left-hemisphere dominant) approach and touch novel objects sooner than do left-handed primates (Braccini and Caine, 2009; Rogers et al., 2013). Left-handed marmosets prefer to explore visually rather than handling a novel object, and they also show persistent elevation of cortisol after return to the home cage, following a period in a strange cage, whereas this response is absent in right-handed marmosets.

A similar pattern was found in a longitudinal study of seventy-six human subjects that examined whether differences in the structure of the ventromedial or orbitofrontal cerebral cortex at age 18 years are associated with observed high or low reactivity at 4 months of age (Schwartz et al., 2010). High-reactive infants are characterized at age 4 months by vigorous motor activity and crying in response to unfamiliar visual, auditory, and olfactory stimuli, whereas low-reactive infants show low motor activity and low vocal distress to the same stimuli. High-reactive infants are biased to become behaviorally inhibited in the second year of life, defined by timidity with unfamiliar people, objects, and situations. By contrast, low-reactive infants are biased to develop into uninhibited children who spontaneously approach novel situations. Adults with a low-reactive infant coping style, compared with those categorized as high reactive, showed greater thickness in the left IFG/orbitofrontal cortex. Subjects categorized as high reactive in infancy, compared with those previously categorized as low reactive, showed greater thickness in the right ventromedial prefrontal cortex.

Similar conclusions were drawn from evidence from a wide range of behaviors across many vertebrate species (MacNeilage et al., 2009; Rogers, 2008; Rogers et al., 2013). Asymmetry of the brain and behavior (lateralization) was originally believed to be unique to humans.

However, research has shown that this phenomenon is widespread throughout the vertebrate kingdom. Evidence of a similar basic plan of organization across vertebrates has been summarized in a recent book by three authorities on animal asymmetries, Rogers et al. (2013). With respect to emotional and motivational aspects of behavior, the overall evidence from different taxonomic groups seems to indicate a common and shared pattern of lateralization. In fish, reptiles and mammals, the right hemisphere controls responding to unpredicted, urgent and novel environmental events, whereas the left hemisphere controls well-established patterns of behavior performed in familiar and often safe environmental conditions (Rogers et al., 2013).

The right hemisphere reactive system is involved in appraisal and conditioning and detects novel, unpredicted, and salient stimuli that require elaboration or scrutiny from reactive control (see Tops et al., 2014a). By contrast, the left hemisphere reactive (or “intermediary”, see Table 1 and Fig. 1B) system, which includes Broca's language area in the IFG, takes control in processes of reappraisal or rumination when elaboration or scrutiny is needed to ensure consistency of new information with internal models. In this manner, the left intermediary system can take new information and communicate with predictive systems to update internal predictive models promoting greater predictive control in the future (Tops et al., 2014a). This function involves the verbalization functions in the left IFG. Functional neuroimaging has revealed that using cognitive reappraisal to increase or decrease affective responses involves left IFG activation and goal-appropriate increases or decreases in amygdala activation (e.g., Ray et al., 2005). Successful encoding during reappraisal was uniquely associated with greater co-activation of the left IFG, amygdala, and hippocampus (Hayes et al., 2010). According to a model by Perlovsky (Perlovsky and Ilin, 2013) the language semantic areas in the left hemisphere guide the development of internal models using information and restrictions from culture and collective wisdom that have accumulated in language. Consistent with the idea that this function predates language development, it has even been argued that language originally evolved as a cognitive tool for exploring and exploiting the full potential of acquired knowledge about the world (i.e., internal models) and only later came to include communication functions that enabled sharing of knowledge (Lupyan and Clark, 2015; Reboul, 2015).

A similar function in reappraisal and assimilation of novel information in preexisting internal models was proposed to explain findings of a “left-brain interpreter” in split-brain patients. A left-brain interpreter refers to the construction of explanations (in terms of internal models) by the left hemisphere in order to make sense of the world by reconciling novel information with what was known before (Gazzaniga, 2000). Similarly, a right-hemisphere mechanism for anomaly or novelty detection has been proposed, versus a left-hemisphere mechanism for maintaining our current beliefs (internal models) about the world (Ramachandran, 1995). Recent evidence from neuroimaging and brain stimulation studies points to a role of the left IFG in relating novel information to beliefs (internal models) about the world (see also Quirin et al., 2015). Disruption of left IFG activity by applying transcranial magnetic stimulation (TMS) impaired reasoning that was congruent with beliefs but improved incongruent reasoning (Tsujii et al., 2011). Similarly, inhibiting conceptual knowledge and expectations of the world by means of TMS at the left IFG/temporal pole improved accuracy in describing raw sensory data (Snyder, 2009).

Reappraisal by the left hemisphere not only facilitates assimilation of information but also improves selection of motor actions. After reappraisal resolves conflicts between novel information and internal models, those internal models are again available for predictive and habitual action control. Moreover, reappraisal may curtail deliberative processing to facilitate implementation of action (Düsing et al., 2016). The left hemisphere has a predominant role in the control of motor ‘manipulative’ responses towards objects. Whereas the information stored by the left hemisphere is about the properties of objects to be

Table 1

Overview of brain networks, coping styles and personality, laterality and dorsal-ventral systems according to PARCS theory.

	Left ventral	Left dorsal	Right dorsal	Right ventral
Hemisphere	Left	Left	Right	Right
Ventral-dorsal	Ventral	Dorsal	Dorsal	Ventral
Control type	Intermediary, reactive/proactive	Proactive	Flexible predictive	Reactive
Cognition	Reappraisal, familiar, deliberation, assimilation, categorization, invariance	Implementation	Perspective taking	Appraisal, error-detection, novel, variance
Coping style	Conscientious	Proactive	Self-determined	Reactive
Personality	Conscientiousness	Drive for reward	Self-directedness	Absorption

manipulated, the detailed representation encoded in the right hemisphere involves mainly elements such as position and spatial context (Rogers et al., 2013). The left hemisphere is specialized to attend to similarities or invariances between stimuli, in order to allocate stimuli and events into categories so that they can be responded to appropriately by practiced responses and skills. It has the ability to select a goal and to sustain response towards it, shielding it against distraction and increasing goal-directed persistence (Rogers et al., 2013).

5. Reactive, proactive and flexible predictive control in humans

The association between predictability and proactive coping described in the animal personality literature (see Section 3) only applies to simpler adaptations to predictable environments that benefit from rigid routines (Tops, 2014). For more sophisticated, future-oriented control in predictable environments, lowered impulsivity and reduced overt aggressive behavior seem to be beneficial. The fact that most species do not engage in the kind of long-term planning typical of human adults may explain the apparent consistency of the animal literature, in which predictability is almost invariably associated with traits that indicate primacy of proactive control. In PARCS theory, we have proposed that evolution produced at least two more coping styles in humans (Tops, 2014; Tops et al., 2016).

First, we suggest that evolution favored the emergence of a conscientious type of personality. This personality type exploits the advantages of collaboration and of moral and authority rule structures in order to protect obtained (ingroup) resources from aggression and other threats. More specific, predictability enables long-term investments if those investments can be protected against aggressive competition. However, similar to proactive personality, the conscientious personality type is still associated with rigidity (Ferguson et al., 2014). For example, conscientiousness has been associated with higher probability of obsessive-compulsive disorder (Tops, 2014; Del Giudice, 2014).

Second, we suggest that, in humans, also a "self-directed" coping style evolved that makes use of more flexible predictive control (see Table 1 and Fig. 1B). Although proactive animals seem to a certain degree able to exploit environmental predictability, humans appear to be able to go beyond such rigid predictive (i.e., proactive) control by using more flexible predictive control. Evolutionary psychologists reasoned that through increased encephalization, prolonged learning and development of language, humans evolved flexible predictive behavior control that could be applied in a wider variety of environments and circumstances such as in separation from the ingroup or to allow increased exchange with outgroups (Chiappe and MacDonald, 2005; Jones, 2011; Potts, 1998), i.e., groups with different moral and authority rule structures and culture. In PARCS theory, flexible predictive control is achieved by flexibility in switching between alternative models and by faster updating of internal models in light of novel information and evidence compared to slower updating in proactive traits (Tops, 2014). However, the original reactive and proactive coping styles were optimized for specific environments and may have retained adaptive value for individuals who were born in or select specific environments, or in an optimal proportion in the population (Koolhaas et al., 1999).

6. Implications for motivation

Reactive, proactive, conscientious and self-directed coping are fundamental in the human coping repertoire. Moreover, relative inclinations to use one of those coping styles are implicated in the personality traits absorption, drive for reward, conscientiousness, and self-directedness respectively (Table 1). Drive for reward is associated with social dominance, aggression and reward-motivated persistence. Conscientiousness has relationships with impulse control, reappraisal coping, problem solving, dutifulness, effortful control of behavior in the service of long-range goals and with engagement, but not disengagement, responses to adversity. Absorption is the tendency to get absorbed in intense appraisal of sensory or emotional experiences, a unifying focus on limited stimuli, to the exclusion of other stimuli. Self-directedness is a personality trait of self-determination, that is, the ability to regulate and adapt behavior to the demands of a situation in order to achieve personally chosen goals and values. See Tops et al. (2016) for discussion and references.

Elsewhere, we presented and discussed evidence that those traits each predict task engagement in a different manner and context (Tops and Boksem, 2010; Tops et al., 2016). For instance, drive for reward and conscientiousness related in unique ways to goal-directed persistence that is consistent with the capacity of the left hemisphere to shield goals and sustain response (Rogers et al., 2013, p. 165). Here, we show the potential of PARCS theory to integrate evidence from studies of laterality of approach-avoidance motivation and studies of effects of affective priming on cardiovascular indication of effort mobilization during cognitive task performance. A strength of PARCS theory is that it integrates such separate fields of research. Despite very different techniques and manipulations, both lines of research suggest a qualitative motivational division between, on the one hand, angry and happy emotions, and, on the other hand, sad and fear emotions.

6.1. Affect and PARCS theory

PARCS theory suggests that the distinction between angry and happy emotions versus sad and fearful emotions may be associated with predictive and reactive control, respectively. The balance between future-directed and momentary control is bidirectionally connected to affective states and cues of high resources and power (happiness, anger) versus low resources (sadness) and immediate concern (fear). Negative moods such as fear imply that the immediate environment is threatening and these concerns must be addressed. Individuals become more motivated to identify, alleviate, and eliminate the problem. They process information more effortfully and analytically to achieve this goal. By contrast, positive moods imply that the immediate environment is safe and no urgent action is required; heuristic and effortless processing prevails instead (Schwarz, 1990). According to Bless (2001), when individuals experience negative moods, their attention focuses on the stimuli and feedback from the immediate environment. That is, a negative mood implies the context deviates from norms or expectations provided by predictive control, undermining the utility of generic principles or knowledge from internal models.

By contrast, when individuals experience a positive mood, they are more inclined to apply knowledge in predictive control and disregard

the immediate stimuli. A positive mood implies that context aligns with their expectations. The application of generic knowledge, hence, is adaptive (Bless, 2001). Hence, when their mood is negative, individuals confine their attention to more immediate stimuli to predict their performance on a subsequent task. In particular, they will restrict their attention to the social support in the immediate environment and their abilities in the relevant domain only. Conversely, when their mood is positive, individuals consider more generic principles, such as their ability and social support resources in general, to predict subsequent performance.

Additionally, cues such as emotional facial expressions may trigger specific coping strategies. Research shows that angry expressions signal rejection or threat to social inclusion or rank, and that happy expressions signal acceptance to observers (Heerdink et al., 2016). Anger, dominance and aggression have increased prevalence in individuals who are high on drive for reward and aggression characterizes proactive coping (Section 3). Situations are fairly predictable for individuals who determine what is going on and aggression can be a means of actively controlling the social environment (Henry and Stephens, 1977). Happy faces may be cues for a conscientious coping strategy of defending one's social inclusion by looking for positive social support cues. Both the proactive and the conscientious coping strategy or style are associated with predictive control and the left hemisphere (Table 1). In a forthcoming paper we discuss evidence of involvement of the hormone testosterone in proactive coping and of the neuropeptide oxytocin in conscientious coping.

Mood effects on effortful cognition can be complex and context-dependent. Also task-context variables like objective task difficulty and incentive can moderate mood effects on effortful cognition (see Gendolla, 2012). Discussing this literature in detail is beyond the scope of the present paper, which focuses on lateralization of motivation. However, we address some of those variables elsewhere in the context of cost-benefit analyses (Boksem and Tops, 2008) and the Protective Inhibition of Self-regulation and Motivation (PRISM) model (Tops et al., 2015, 2016). PRISM details on the regulation of costly engagement of reactive control. In section 6.3 we touch upon PRISM when we discuss the findings and mood-behavior model of Chatelain et al. (2016) and Gendolla (2012).

6.2. Approach – avoidance motivation

Optimism is a cognitive construct related to appraisal of predictability and resources, and consequently to motivation; optimists exert effort and approach, whereas pessimists disengage from effort and withdraw (or avoid; Carver et al., 2000). Differential involvement of the hemispheres in future-directed versus momentary control in predictable versus unpredictable environments may explain a large neuropsychological and EEG literature relating respectively the left versus right hemisphere to approach versus avoidance motivation (see Davidson, 1998; Harmon-Jones, 2004), optimism versus pessimism, believing to be in control versus being controlled, proactive versus passive or inhibitive, as well as to high versus low power, self-esteem, and persistence (see for a review Hecht, 2013). The functional hemispheric asymmetry that underlies PARCS theory's personality model is consistent with a large literature on frontal EEG (alpha power suppression) relative activation asymmetry. In this literature, left frontal activity has been associated with approach motivation, power, anger, dominance and drive for reward, while right frontal activity has been associated with avoidance or withdrawal motivation, submission, social anxiety, inhibition or high arousal (Boksem et al., 2012; Davidson, 1998; Demaree et al., 2005; Harmon-Jones, 2004; Heller et al., 1998; Moscovitch et al., 2011; Quirin et al., 2013; Santesso et al., 2008). Moreover, PARCS theory integrates this literature with findings (Tops and Boksem, 2010) that left hemisphere reactive control is involved in conscientiousness or constraint (consistent with an earlier theoretical claim by Tucker et al., 1995).

Being one of three subscales of a measure of reward processing and approach motivation (Behavior Activation System; BAS), studies that reported results separately for each subscale consistently found specific or largest associations of drive for reward (i.e., proactive coping) with leftward frontal EEG asymmetry (De Pascalis et al., 2010; Diego et al., 2001; Tops and Boksem, 2010) and functional Magnetic Resonance Imaging (fMRI) (Berkman and Lieberman, 2010). Additional support for this laterality in motivation to expend effort to obtain reward was found in Parkinson's patients with asymmetric dopamine loss (Porat et al., 2014). Predominant left-sided loss impaired the expending of effort to increase gains whereas right-sided loss impaired the expending of effort to minimize losses. fMRI studies demonstrated similar associations between promotion focus to increase gain, optimism and left IFG activation, and between prevention focus to avoid loss, pessimism and right IFG activation (Eddington et al., 2007; Garrett et al., 2014; Sharot et al., 2011).

Hemispheric asymmetry in proactive versus reactive coping may have consequences for psychopathology. In line with the continuous, dimensional approach to health and psychopathology, mental disorders appear to associate with similar relative lateralized activity as their cognitive and motivational characteristics do. Depression (low approach motivation, power and self-esteem) has been associated with decreased left frontal activity (Nusslock et al., 2015; Tomarken et al., 2004). The opposite seems to be the case for mania (increased left frontal activity, high approach motivation, power and drive for reward; Nusslock et al., 2015). Anxiety (low control, high avoidance motivation, subordination in social anxiety) and exposure to trauma-related stimuli in post-traumatic stress disorder (emergency, high arousal and avoidance motivation) have been associated with right frontal activity (Meyer et al., 2015; Moscovitch et al., 2011). However, the dynamic and multifaceted nature of psychopathology suggests that there won't likely be a stable one-on-one relationship between disorder and hemisphere. This can be seen in the example of rumination, which is often displayed in both mood and anxiety disorders. High-arousal rumination (brooding) has been associated with right frontal activity, whereas reflective and problem-solving types of rumination have been associated with left frontal activity and left IFG activation (Engels et al., 2007; Nusslock et al., 2015). PARCS suggests that the former type of rumination reflects emergency processing by the right reactive system, whereas the latter types of rumination reflect the involvement of the left hemisphere intermediate system (Table 1) in deliberative attempts to integrate (past or expected) experiences with internal models (Düsing et al., 2016; Tops et al., 2014a).

If the human hemispheric asymmetry in approach versus avoidance motivation and optimism versus pessimism is related to hemispheric asymmetry in proactive versus reactive coping, then similar asymmetry should be present in other vertebrate species. Optimism is determined in animals using an ambiguous-cue interpretation paradigm. This paradigm showed that "optimistic" rats were significantly more motivated to gain reward than their "pessimistic" conspecifics (Rygula et al., 2015). In line with the other evidence that the basic laterality pattern is found across vertebrates, laterality of optimistic versus pessimistic bias has been found in primates. Common marmosets were trained to expect a food reward from a bowl with a black lid and not from one with a white lid, or vice versa. In probe tests with ambiguous, grey-lidded bowls a left-handed group (presumably right-hemisphere dominant) were less likely to remove the lid to inspect the bowl than a right-handed group (presumably left-hemisphere dominant; Gordon and Rogers, 2015). Furthermore, retrospective examination of colony records of 39 marmosets revealed that more aggression was directed towards left-than right-handed marmosets, believed to reflect subordinate status.

6.3. Affective priming and effort

The implicit affect primes effort (IAPE) model (Gendolla, 2012) posits that affect primes (e.g., facial expressions or emotion words)

implicitly activate mental representations of the respective affective states, containing information about ease and difficulty. This, in turn, influences the extent of subjective task demand during performance. In empirical tests of this model, priming with happy and angry faces resulted in lower experienced task demand and lower mental effort (weaker cardiac contractility assessed as shortened pre-ejection period) during cognitive task performance compared to priming with sad or fearful faces (Gendolla and Silvestrini, 2011; also Chatelain and Gendolla, 2015, 2016; Chatelain et al., 2016). PARCS theory explains this pattern in terms of implicit activation of predictive control by social cues that trigger conscientious coping (happy faces) or proactive coping (angry faces), coupled with predictive homeostatic control that is efficient and subjectively less effortful (Tops et al., 2015, 2016). By contrast, sad and fearful faces may be implicit cues of respectively low resources and immediate threat that tend to activate reactive control. Reactive homeostatic control increases resource (effort) mobilization to cope with unpredictable challenges that may put a large demand on one's resources (Tops et al., 2015, 2016).

Furthermore, this research also uncovered effects that are predicted by PRISM (Tops et al., 2015, 2016). That is, sadness and fear primes compared to happy and anger primes decreased resource mobilization (increased physiological disengagement) for difficult tasks (e.g., Chatelain et al., 2016; Gendolla, 2012). Consistent with PRISM, this result indicated disengagement in conditions where demand exceeds the low level of perceived resources primed by the emotion cue. As we discussed in Section 2, 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 activation. However, PRISM predicts that the high physiological costs of increased sympathetic activation and appraisal of unpredictability and low control also predispose to disengagement: appraisal that the challenge (e.g., difficult task) cannot be overcome, or only at excessive costs. By contrast, predictive control will increase efficiency and perseveration informed by current and future-directed benefits.

Finally, there was no decreased mobilization of resources for difficult tasks after sadness or fear primes when there were high success incentives (Chatelain and Gendolla, 2016; Gendolla, 2012). Here, PRISM joins other theories that propose that an incentives-induced increase in resources and potential motivation can offset costs (Boksem and Tops, 2008; Brehm and Self, 1989; Tops et al., 2015).

7. Conclusion

Most people would probably want to get out of the grip of immediate concerns and instead invest in future profits in more relaxed conditions. It may be thought that in prosperous countries the energy needs would be met for most people and they would experience sufficient predictability and control to invest in future profits. However, in social animals including primates, resources and predictability are highly dependent on social status. Subordinate animals need to be vigilant so they are able to react to the whims of superordinates. Also to humans, social evaluation and threats to social inclusion, status or control are potent elicitors of physiological stress responses (Dickerson and Kemeny, 2004; Mason, 1968). Irrespective of coping style and dominance hierarchy, novel challenges may initially trigger cortisol and sympathetic responses. The goal of active coping responses is to shift from reactive control in response to novel challenges or threats, to predictive control in which physiological responses habituate. Similarly, the pattern of hemispheric asymmetry that we discussed suggests that active coping involves a shift from right hemisphere control towards left hemisphere control. One important challenge for the future is to combine neuroscientific studies on mechanisms with biological, ecologically relevant studies to fully appreciate the implications of PARCS theory for the outcome of stress-related behavior and underlying brain activity as well as in the development of stress-associated neuropsychiatric disorders. For

instance, reactive coping versus proactive coping individuals tend to develop other types of stress-related psychopathology (van den Bos, 2015).

PARCS is also able to make connections with, and between, other theories. As an example, we point out relationships between PARCS and the generalized unsafety theory of stress (GUTS; Brosschot et al., 2017). Based on neurobiological and evolutionary arguments, GUTS hypothesizes that the stress response is a default response, and that chronic stress responses are caused by generalized unsafety (GU), independent of stressors or their cognitive representation. As long as safety is perceived, the subcortically-mediated stress response is under tonic prefrontal inhibition. This default unsafety responding is comparable with the default or starting role of reactive control in PARCS, which switches to predictive control when metabolic and safety requirements for survival are met. Alternatively put, reactive control and sympathetic activation habituate and parasympathetic activity takes over when stimuli have been integrated and represented as being safe in internal models, along with ways to cope with them. Similar to GUTS, PARCS proposes that the shift from novel/unsafety to familiar/safety is dependent on the perception of resources, including physical/body resources and social resources (Tops et al., 2015, 2016). Different from GUTS, PARCS goes beyond the familiar dichotomies of cortical/prefrontal versus subcortical, and higher-level versus primitive. PARCS recognizes that the respective systems are represented at all levels of the brain, albeit differently expressed in ventral-dorsal and left-right dimensions. Moreover, each system developed higher level (e.g., prefrontal) cognitive controls during evolution (Tops et al., 2014a). PARCS recognizes as well that not only chronic reactive system (unsafety) activation can compromise health. Predictive system activation in safe conditions appears sometimes associated with exaggerated perseveration (persistence in the pursuit of a goal) capable of compromising health (Tops et al., 2016).

The framework of PARCS theory is capable of integrating various extensive literatures on laterality of behavior control, stress coping, motivation and effort regulation. However, our discussion of the evidence has been limited by space restrictions and the specific focus of the present paper. For instance, coping styles, stress coping, and laterality all are associated with sex differences (Bao and Swaab, 2010; Martel, 2013; van den Bos, 2015). Hence, this early presentation needs to be followed by a more comprehensive analysis of the interactions between sex, hemisphere and ventral versus dorsal corticolimbic systems. The consistency of the laterality literature may be increased further by explicating for each assumingly-lateralized function, whether it reflects elaboration of the dorsal or ventral pathway in that hemisphere, or their collaboration. Moreover, most laterality of function is relative and may be different in non-right-handers, which we ignored for the simplicity of argument.

A strength of PARCS theory is that it may connect separate fields of research, such as research on the motivational correlates of EEG frontal alpha power asymmetry and research on implicit affective priming on cardiovascular indicators of effort during cognitive task performance. Despite very different techniques and manipulations, both lines of research suggest a qualitative motivational division between, on the one hand, angry and happy emotions, and, on the other hand, sad and fear emotions. PARCS theory suggests that a distinction may be an association with predictive and reactive control, respectively. This leads to novel predictions, such as how frontal asymmetrical activity and cardiovascular indicators of effort relate to externally-guided versus internally-driven behavior.

Disclosure/conflict-of-interest statement

The research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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