



## Review

# From conflict management to reward-based decision making: Actors and critics in primate medial frontal cortex



Massimo Silvetti<sup>a,\*\*</sup>, William Alexander<sup>a,b</sup>, Tom Verguts<sup>a</sup>, Joshua W. Brown<sup>b,\*</sup>

<sup>a</sup> Ghent University, Department of Experimental Psychology, Henri Dunantlaan 2, B-9000 Gent, Belgium

<sup>b</sup> Indiana University, Department of Psychological and Brain Sciences, 1101 E Tenth Street, Bloomington, IN 47405, USA

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## ABSTRACT

The role of the medial prefrontal cortex (mPFC) and especially the anterior cingulate cortex has been the subject of intense debate for the last decade. A number of theories have been proposed to account for its function. Broadly speaking, some emphasize cognitive control, whereas others emphasize value processing; specific theories concern reward processing, conflict detection, error monitoring, and volatility detection, among others. Here we survey and evaluate them relative to experimental results from neurophysiological, anatomical, and cognitive studies. We argue for a new conceptualization of mPFC, arising from recent computational modeling work. Based on reinforcement learning theory, these new models propose that mPFC is an Actor–Critic system. This system is aimed to predict future events including rewards, to evaluate errors in those predictions, and finally, to implement optimal skeletal-motor and visceromotor commands to obtain reward. This framework provides a comprehensive account of mPFC function, accounting for and predicting empirical results across different levels of analysis, including monkey neurophysiology, human ERP, human neuroimaging, and human behavior.

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\* Corresponding author. Tel.: +1 812 855 9282.

\*\* Corresponding author.

E-mail addresses: [massimo.silvetti@ugent.be](mailto:massimo.silvetti@ugent.be) (M. Silvetti),

[jwbrown@indiana.edu](mailto:jwbrown@indiana.edu) (J.W. Brown).

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## 1. Introduction

The medial prefrontal cortex (mPFC) has been intensively studied in recent years, both in humans and nonhuman primates. It has been cast as a system for adaptive control of behavior (Ridderinkhof et al., 2004). For example, it has been proposed that mPFC performs a key role in error processing (Critchley et al., 2005), in the estimation of the probability of committing an error (Brown and Braver, 2005), or in estimating the amount of conflict between two or more available options (Botvinick et al., 2001). Despite intense interest, consensus on its role in cognition has not been reached. Besides different theoretical views, there are also differences in experimental paradigms and different anatomical structures in mPFC.

In this paper, we discuss different theories and tasks relevant to mPFC functioning, paying attention to the historical evolution of these findings, and focusing on one specific structure of mPFC, whose function remained for years as much elusive as ubiquitous in behavioral neuroscience: the anterior cingulate cortex (ACC). Then, we discuss the recent application of a machine learning framework on mPFC investigation, namely Reinforcement Learning (RL). Finally, we discuss two very recent and similar neuro-computational models of mPFC. We show how these models, both belonging to the RL framework, are able to account for the varied and disparate data that have been described. Based on these models we develop a framework according to which this area signals a need for change. Finally, we point out novel directions for investigation.

## 2. ACC functional anatomy

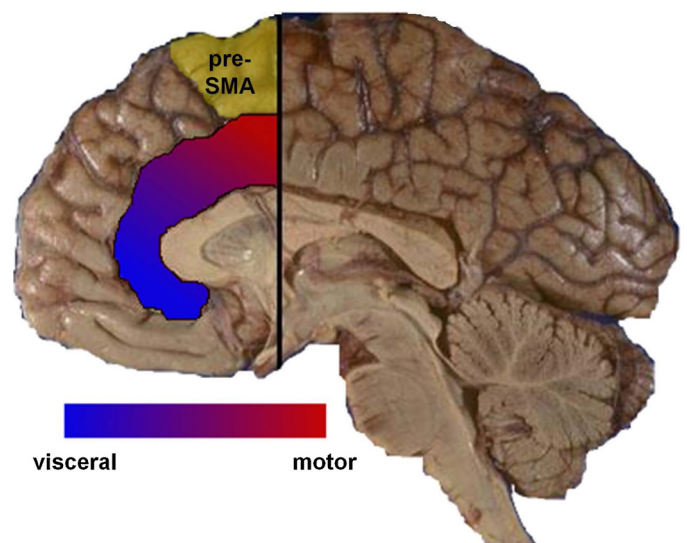
### 2.1. ACC as a limbic area

A useful way to focus the main functions of the ACC is to place it inside a specific network of sensory–limbic–motor areas, which may integrate limbic and motivational factors with sensorimotor functions (Bush et al., 2000). ACC is classically identified as part of the limbic system (MacLean, 1955; Papez, 1937). This area, including most of the cingulate cortex, is widely connected with the hippocampus via mainly efferent fibers to the parahippocampal gyrus (Nieuwenhuys et al., 1981). The hippocampus connects to the mammillary bodies (part of the hypothalamus) through the fornix. Finally the mammillary bodies are connected to the anterior thalamic nuclei through the mammillothalamic tract, which projects back to ACC, closing the Papez circuit (1937). Electrical stimulation of the ACC evokes both emotional (Meyer et al., 1973) and autonomic responses, such as variation of blood pressure and heart rate, pupil dilation, pyloric contraction and penile erection (Devinsky et al., 1995). From the anatomical viewpoint, the rostral ACC (Brodmann area 25) sends extensive efferents toward both sympathetic (Hurley et al., 1991) and parasympathetic (Terreberry and Neafsey, 1983; Willett et al., 1986; Hurley et al., 1991) nuclei. Although there is a rostro-caudal gradient in ACC from visceral to motor connectivity (Fig. 1), the caudal part of ACC is to some extent able to evoke autonomic responses via connections with BA25 (Vogt and Pandya, 1987). Experimental conditioning paradigms showed that the ACC is necessary to associate appropriate anticipatory autonomic nervous system responses to future stressful stimuli (e.g. Frysztak and Neafsey, 1991; Critchley and Mathias, 2003), suggesting a role of the ACC in regulating autonomic response as a function of effortful cognitive or motor tasks.

Finally, the ACC receives and processes nociceptive information from thalamic nuclei (Vogt et al., 1979). Nociceptive information in ACC does not adhere to somatotopic organization, and it seems linked to avoidance learning and emotional and autonomic response to pain (Gabriel et al., 1991).

### 2.2. ACC: motor properties

The ACC contains wide populations of motor and premotor neurons, with a caudal-to-rostral gradient (i.e. reversed with respect to the visceromotor gradient), showing maximal density of motor units in its caudal part, located ventrally to the (pre-) supplementary motor area (SMA and pre-SMA) (Dum and Strick, 2002; Fig. 1). Cingulate motor unit targets are the same as those of the dorsolateral premotor cortex: the ACC establishes reciprocal connections with the primary motor cortex and the SMA, and also direct efferents toward the spinal cord (Dum and Strick, 1991; Bates and Goldman-Rakic, 1993). Electrical stimulation of the ACC typically evokes complex motor patterns (Talairach et al., 1973), somatotopically organized and involving the mouth and forelimbs primarily (Wang et al., 2008; Luppino et al., 1991). ACC motor properties are not limited to limbs. Indeed stimulation of this area can evoke also vocalizations, often coordinated with corresponding autonomic reactions in emotional motor responses (Paus, 2001). Microstimulation of bat ACC evoked vocalizations organized in a tonotopic fashion, similarly to the somatotopic organization in primates, providing a highly specialized map of frequencies that are used for echolocation (Gooler and O'Neill, 1987). Interestingly, while autonomic and motor functions of ACC are similar across mammals (including humans), electrical stimulation in humans (in which vocalization evolved into language) seldom evokes vocal behavior (Devinsky et al., 1995). However, ACC lesions can lead to akinetic mutism (Paus, 2001), but only if the lesions are sufficiently widespread (Fellows and Farah, 2005). The examples of humans



**Fig. 1.** Anatomical–functional gradients in the ACC. Color nuances indicate the density of neurons specialized in different functions. Pre-SMA area is evidenced as reference point. Vertical line: vertical line on anterior commissure. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

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