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The somatic marker hypothesis: revisiting the role of the 'body-loop' in decision-making

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The somatic marker hypothesis is one of the most influential neurocognitive theories of emotion and decision-making. A key aspect of the somatic marker hypothesis is the 'body-loop', which is the claim that emotive events that are expressed in the body can influence decision-making via afferent feedback to the brain. The body-loop has often been the subject of debate. However, evidence for the neural and peripheral mechanisms that support interactions between bodily states and cognitive functions has consistently emerged. The purpose of this article is to outline an updated neurophysiological account of how somatic states may be triggered, and how they bias decisions through afferent feedback. We largely focus on vagus nerve-dependent feedback mechanisms, which demonstrate how interoceptive signals can shape high order cognition and goal-directed behavior.

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Introduction

The somatic marker hypothesis has been one of the most influential neurocognitive theories of decision-making since its proposal by A. R. Damasio in the early 1990s [1]. The SMH is a systems-level neurocognitive framework for decision-making and its influence by emotion. The broad claim of the SMH is that decision-making is a process that is influenced by visceral and somatosensory markers that arise in bioregulatory processes, including those that express themselves in emotions and feelings. The ventromedial cortex (VMPFC), including the mesial orbitofrontal (OFC) region, is a critical component of a neural system subserving decision-making and affective processing. However, decision-making is not mediated by the VMPFC alone, it arises from large-scale systems that include other cortical and subcortical components. Such structures include the amygdala, the somatosensory and insular cortices, and the peripheral nervous system.

The SMH proposes that the VMPFC provides the substrate for learning an association between complex situations and the bio-regulatory or emotional state usually associated with that class of situation in the individual's experience, and how the VMPFC acts as a trigger region to re-activate somatic patterns when an individual faces a situation for which some aspects have been previously experienced. The re-activation can be carried out via a 'body-loop', in which the body changes in response to brain activity, and the ensuing changes are relayed to somatosensory and insular cortices. Alternatively, in the 'as-if body-loop', the body is bypassed and those re-activation signals from the VMPFC are conveyed to the somatosensory and insular cortices, which then adopt the appropriate neural pattern [2]. Most of the early empirical research on the SMH focused on how decision-making behaviors and autonomic responses were altered in patients with focal lesions to the VMPFC, amygdala, and insula [3]. These early lesion studies were able to address some aspects of the body-loop and its role in modulating decisions, such as by establishing that peripheral autonomic responses during various aspects of decision-making depend on lesion site [2]. However, these studies could not definitively demonstrate the influence of ascending feedback on decision-making. Indeed, historical criticism of the SMH has primarily concerned the plausibility of the influence of somatic feedback on high-order cognitive processes. Therefore, the purpose of this article is to provide an updated account for the body-loop by drawing from recent literature on how somatic states are triggered, and how somatic states may modulate decision-making through peripheral feedback. The evidence strongly suggests that visceral processes mediated by afferent vagus nerve signaling participate in shaping high-order cognition by influencing activity of brainstem-level neurotransmitter systems involved in learning, memory, and motivation and valuation. To begin, we review the current evidence for a system of cortical and subcortical structures which have an essential role in visceromotor and viscerosensory processing. These regions largely overlap with regions implicated in emotion and decision-making.

The role of ventral PFC and agranular insular cortex in triggering somatic states

The SMH proposed that primary or secondary inducers trigger somatic states. Primary inducers are sensory stimuli that are innate or learned to be pleasurable or aversive, and automatically elicit a somatic response. Secondary inducers are entities generated by the recall of a personal or hypothetical emotional event concerning a primary inducer, which, when brought to working memory, elicit a somatic state. The amygdala was shown to be important for triggering somatic states from primary inducers, whereas the VMPFC was viewed as the essential region for the trigger of somatic states from secondary inducers. The amygdala and VMPFC were proposed to accomplish this by coupling sensory-cognitive input to effector structures in the brainstem and hypothalamus [2,4]. Prefrontal structures are increasingly recognized as having an essential function in regulating somatic states through efferent communication with brainstem nuclei and the hypothalamus [5••,6,7]. A model proposed by Barrett and Simmons [5••] identifies a system of prefrontal agranular visceromotor cortices that includes the posterior OFC, posterior VMPFC, anterior cingulate (ACC), and anterior insula (aINS). Agranular cortices control visceral outputs through connections to the amygdala, ventral striatum, hypothalamus, and the periaqueductal gray to deploy the autonomic, immunological, metabolic, hormonal resources necessary to predict and respond to the sensory world. These are regions reliably involved in fMRI studies of emotion [8], and recent lesion studies continue to support the view that prefrontal regions participate in coordinating autonomic responses to affective stimuli. For example, patients with VMPFC damage demonstrate exaggerated amygdala responses but reduced cardiac deceleration when viewing aversive images [9•]; and in macaques, lesions of the subgenual ACC impairs autonomic arousal during reward anticipation [10]. Thus, damage to areas of the PFC alters interactions with sites governing sympathetic-parasympathetic balance, which could manifest as altered vagal tone, or sympathetic-adrenal-medullary and hypothalamic-pituitary-adrenal responses [6,7,11•,12].

The earlier lesion work on the SMH also identified roles for the insula in subjective feelings of arousal to positively and negatively valenced stimuli [13] and risky choice [14]. The proposed role of the insula in the original SMH model was visceral sensory processing. Yet, the insula is also increasingly implicated in efferent autonomic regulation, with the most evidence so far detailing its role in reflex cardiovascular control [15]. More generally, the insula is identified in correlational neuroimaging studies of autonomic function. Takotsubo cardiomyopathy, for example, is associated with abnormal responses to autonomic challenges and structural abnormalities of the insula and amygdala [16], while aINS atrophy has been correlated with blood pressure responses in frontotemporal dementia [17]. The posterior insula (pINS) and aINS are consistently correlated with parasympathetic and sympathetic measures across affective, cognitive, somatosensory, and motor domains [18]. Moreover, from a network perspective, the salience network canonically includes the aINS and appears to be strongly related to the deployment of sympathetic outputs (or parasympathetic withdrawal) such as spontaneous pupil dilations [19] and spontaneous increases in heart rate [20]. It is difficult to distinguish viscerosensory versus visceromotor processing based on correlational studies, but the functional role of the insula in both visceral sensory and visceral motor processing is not contradictory. Many visceral sensory afferents reach the pINS. From there, interconnections make it to the aINS. The dorsal aINS links to motor regions and executive control networks, while the ventral aINS links to limbic structures connected to visceromotor output centers, including the amygdala, hypothalamus, and brainstem nuclei [21]. Thus, the insula is poised to play both visceral-sensory and visceral-motor roles in a series of feedforward and feedback regulatory loops that interface with motor, cognitive, somatosensory and exteroceptive sensory regions.

Dysfunction in agranular prefrontal cortices should predictably generate inappropriate mobilization of energetic resources in response to sensory events, as well as for the enactment of allostasic goals (the processes by which homeostasis is achieved). Decision-making, learning, and reward processing can be seen as being closely coupled with allostatic regulation (e.g. the release of insulin in response to cues predicting food allows us to tolerate food intake [22,5••]). This perspective can help reconcile the fact that these same visceromotor regions also appear to participate in the computations underlying learning, rewards and punishments, and decision-making in general. Nevertheless, these facts do not explain how bodily feedback mechanisms work to influence these central processes. The next sections discuss the interactions of peripheral feedback on decision-making and other cognitive activities, with emphasis on the role of the vagus nerve, which is a critical route of information flow from the body to the brain.

The afferent side of the body-loop: the role of the vagus nerve

Some early empirical work on the SMH suggested that the vagus nerve, rather than the spinal cord, is a critical conduit for communicating somatic states to the brain [23]. The vagus nerve is a complex autonomic, endocrine, and immune regulatory interface through which the body communicates with the brain, and the brain with the body. Primarily parasympathetic vagal efferent fibers innervate thoracic (e.g. cardiac) and abdominal organs and exert effects on these end organ systems through largely cholinergic mechanisms. However, the vagus is