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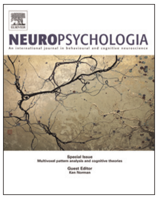

Understanding the role of the primary somatosensory cortex: Opportunities for rehabilitation

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ABSTRACT

Emerging evidence indicates impairments in somatosensory function may be a major contributor to motor dysfunction associated with neurologic injury or disorders. However, the neuroanatomical substrates underlying the connection between aberrant sensory input and ineffective motor output are still under investigation. The primary somatosensory cortex (S1) plays a critical role in processing afferent somatosensory input and contributes to the integration of sensory and motor signals necessary for skilled movement. Neuroimaging and neurostimulation approaches provide unique opportunities to non-invasively study S1 structure and function including connectivity with other cortical regions. These research techniques have begun to illuminate casual contributions of abnormal S1 activity and connectivity to motor dysfunction and poorer recovery of motor function in neurologic patient populations. This review synthesizes recent evidence illustrating the role of S1 in motor control, motor learning and functional recovery with an emphasis on how information from these investigations may be exploited to inform stroke rehabilitation to reduce motor dysfunction and improve therapeutic outcomes.

1. Introduction

The planning, execution, and control of motor behaviors is a complex neural process in part dependent on correct sampling of multiple sensory modalities from the body periphery (e.g., somatosensation, vestibular, etc.) and external environment (e.g., vision, hearing, etc.) (Hummelsheim et al., 1988; Riemann and Lephart, 2002; Wolpert et al., 2013; Zarzecki et al., 1978). Without correct processing and translation of sensory input, both before and during movement, motor outputs are abnormal and/or inaccurate. Thus, there is a tight link between sensory processing and movement production. Accordingly, emerging evidence suggests abnormal processing of somatosensory information by the primary somatosensory cortex (S1) contributes to deficits seen in neurological disorders typically classified by motor dysfunction (e.g. stroke, Parkinson's disease, dystonia, ataxia, etc.) (Elbert et al., 1998; Hummelsheim et al., 1988; Jacobs et al., 2012; Konczak and Abbruzzese, 2013; Rub et al., 2003; Wolpert et al., 2013).

There is a growing body of literature regarding the effects of altered S1 function on M1 activity and the control of movement. Increased M1 excitability has been noted in animal models of neurological conditions involving S1 damage, such as stroke (Harrison et al., 2013; Winship and Murphy, 2009) and idiopathic dystonia (Domenech et al., 2013). Focal lesions to sensorimotor areas, similar to injuries resulting from stroke, have resulted in difficulty with a battery of motor behavioral tasks assessing gross motor function and reflexes in rats (Gerlai et al., 2000; Kleim et al., 2007; McIntosh et al., 1996), and impaired fine motor skills involving small objects in monkeys (Brinkman et al.,1985; Hikosaka et al., 1985).

Motor deficits observed after S1 lesions may not always be due to difficulty with executing motor commands but rather attributed to disrupted learning of new motor tasks, as motor deficits are attenuated if the task had been learned prior to S1 injury (Pavlides et al.,1993; Sakamoto et al., 1989,1987). Another phenomenon that could affect motor function is the alteration of somatosensory maps within S1. Studies in rodents have found a shift in the sensory map after experimentally-induced stroke that results in an overlap with a portion of the motor representation where the

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neurons originally devoted to encode exclusively motor commands take on a small role in sensory processing, reducing their capacity for involvement in the motor system (Harrison et al., 2013; Winship and Murphy, 2009).

In the following sections, the importance of S1 to motor function will be considered using theoretical models, neuroimaging approaches, non-invasive neural stimulation technologies, and combined neuroimaging–neurostimulation paradigms. Finally, future clinical implications of a comprehensive understanding of the relationship between motor functioning and S1 structure, function, and connectivity will be discussed.

2. Modeling the role of S1 in sensorimotor integration

The balance between sensory input and motor output is essential for efficiently acting within the environment. For example, when grasping a previously visualized object, first the visual information about the object's location is identified based on input from the retina (e.g. Becke et al., 2015). Then the information integrated with the (currently available) visual and/or somatosensory information about the location and configuration of the body. During movement, somatosensory input from the primary effector (s) also is transmitted to the motor system in order to fine-tune the movement (e.g. Blakemore et al., 1998; Wolpert et al., 1995). For successful motor execution of most tasks, real-time somatosensory feedback must be encoded and provided to the motor system through integrative loops for a precise motor control (see also Perruchoud et al., 2014).

Nevertheless, the basic mechanisms, anatomo-functional neural underpinnings, and rehabilitation of sensorimotor function are still under investigation. In particular, current models of S1 function lack precision in defining the multifaceted role in processing afferent sensory information and regulating efferent motor commands of this cortical region. This section will review the available data on the anatomo-functional role of S1 in motor control, aiming at describing the reciprocal influence between somatosensory information and motor commands.

Two main features of S1 function deserve particular attention. First, S1 can drive movements in coordination with or independent of M1 activity. Converging evidence from animal research shows that rich fiber pathways interconnect S1 and M1 (Donoghue and Parham, 1983; Veinante and Deschenes, 2003; White and DeAmicis, 1977). These cortico-cortical connections are considered to modulate the relationship between sensory and motor components of sensorimotor processes (Petreanu et al., 2009; Xu et al., 2012). Recent theorizations about the directionality of such an exchange between S1 and M1 emphasize the dominant (probably disinhibitory) role of M1 over S1, both in rodents (Lee et al., 2013) and humans (Gandolla et al., 2014). In accordance with this view, animal research showed that lesions of S1 are associated with increased excitability of M1 (Domenech et al., 2013; Harrison et al., 2013). Furthermore, clinical observations in humans report increased peripheral somatosensory inflow facilitates functional reorganization of M1 (Hamdy et al., 1998) and that non-invasive stimulation of S1 induces shorter latencies to initiate movements (Meehan et al., 2011). These findings support a continuous mutual communication between sensory inflow and motor outflow (Kleinfeld et al., 2006; Lee et al., 2008). Other evidence conversely shows that S1 can drive motor commands without the intervention of M1. In particular, the behavioral outcome in response to a specific somatosensory stimulus, further associated with the earliest recorded cortical activity (in S1), can be triggered also by the stimulation of the same S1 subregion with latencies shorter than those of the motor region evoking the same movement, even when the motor region is pharmacologically inactivated (Matyas et al., 2010). In the same vein, motor deficits are less prominent if a particular movement is learned prior to a lesion of S1 (Sakamoto et al., 1989) and movement execution improves following the administration of S1-facilitating drugs (McIntosh et al., 1996).

The second important feature of S1 is that it is interconnected with other primary sensory cortices (e.g. visual and auditory; V1 and A1, respectively) and with subcortical structures encoding different sensory modalities. Unlike conventional views of the primary sensory cortices as unisensory regions, different perspectives propose that multisensory integration processes begin to take place in these regions prior to moving on to secondary association areas (Driver and Noesselt, 2008). The neural underpinnings of such crossmodal integration may be provided by the cortico-cortical connections between S1 and V1, described both in primates (Cappe and Barone, 2005) and humans (Ro et al., 2013), as well as by the modulation of human S1 activity in response to non-corresponding stimulation (Liang et al., 2013), e.g. acoustic (Murray et al., 2005) and visual information (Meyer et al., 2011). In addition, subcortico-cortical connections transmit information about different sensory modalities to non-matching primary sensory areas (Henschke et al., 2014).

In light of these findings, how can S1 contributions to movement control be modeled? In accordance with the multisensory nature of S1, initially multimodal sensory input must be combined with actual intentions and previous knowledge in order to initiate movements (Genewein and Braun, 2012). Current theoretical conceptualizations propose the existence of two internal movement prediction components. The first component can be defined as a “forward” model used by the nervous system to predict the behavioral outcome of a given motor command generated by M1 (Desmurget et al., 2009). The forward model is based on a copy of the motor command generated in M1, defined as an “efference copy” that, instead of being sent to the periphery, is to be processed by parietal regions (Sirigu et al., 1996). Simultaneously, the forward model contributes information to a so-called “feedforward model” used to anticipate the sensory consequence of the movement itself (Wolpert and Ghahramani, 2000). The feedforward model combines together the actual sensory consequences associated with an executed motor command and the sensory component of the predicted motor outcome (based on the forward model) to provide information on the potential mismatch between expected and real bodily states during the movement. In this way both the actual sensory information and the motor outcome are compared to the expected sensory consequences and the real movement, respectively. As a result of these recalibration mechanisms, the potential mismatch between the actual and predicted sensorimotor states can be used to update subsequent motor commands and may be used as an error signal facilitate motor learning.

Two different options may explain the reciprocal role the sensory and motor components of such a complex interaction (Fig. 1). The "optimal control" theory postulates that the motor command contains purely motor information (Wolpert et al., 1995) and M1 only generates the movement (Wolpert and Kawato, 1998). In this view, the motor command contains purely motor information and the motor command is context-independent (Fig. 1a). The alternative "active inference" theory proposes that, instead of being uniquely motor, the motor command also contains information used to predict the sensory consequences of the triggered movement (Fig. 1b; Adams et al., 2013). According to this view, motor commands are context-dependent and modulate activity in S1. In other words, M1 activity has a direct effect on S1 activity both in terms of a facilitation of the M1-S1 connections and stronger S1 self-inhibition (in order to diminish sensitivity to unrelated information), which has been recently demonstrated in the human

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