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Understanding body representations

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EDITORIAL

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A number of different yet interacting systems are involved in representing our bodies. Our ability to perceive our bodies is the product of a complex multisensory system, integrating information from vision, touch, proprioception, and vestibular systems. Information from these representations is tightly integrated with systems for motor control, allowing us to effectively act on our environment. Finally, along with sensory and motor systems, our bodies are strongly related to our sense of self – including the feeling that a body part is our own, and that we can have control over our bodies.

The manner in which the brain represents the body may be profitably studied by investigating the effects of damage to these systems. Subsequent to brain and peripheral nervous system damage, a wide variety of deficits of body representation have been reported, ranging anywhere from relatively simple deficits in tactile detection and mislocalization to loss of control, or even sense of ownership, of one's own body parts. Disorders of perception, motor control, and embodiment after brain damage have provided key insights into the mental processes involved in representing our bodies. These studies have a long history, including Head and Holmes' (1911) seminal work proposing the existence of body schemas, Gerstmann's documentation of somatoparaphrenia (1942) and finger agnosia (1940), Critchley's (1953) review of body representation deficits subsequent to parietal damage, Bender's (1952) reports of sensory phenomena, including tactile extinction and allochiria, and many other studies not listed here.

In recent years, however, the study of how the mind represents the body has lagged behind other domains (e.g., language, attention, memory). Part of this may be due to the multisensory nature of body representations, the difficulty in studying concepts such as embodiment, and the often unhelpful predominance of overly broad concepts with limited explanatory power (see Poeck & Orgass, 1971). Fostered in part by the development of additional experimental methodologies in cognitive neuroscience, there has been a renewed interest in understanding how the mind/brain represents the body with a substantial increase in empirical papers on the topic (for reviews, see Berti & Pia, 2006; Cardinali, Brozzoli, & Farne, 2009; Haggard & Wolpert, 2005; Heed & Azañon, 2014; Longo, Azañon, & Haggard, 2010; Medina & Coslett, 2010; Schwoebel & Coslett, 2005). The goal of this special issue is to provide a forum for authors to present theoretical frameworks for understanding how the mind represents the body, in a number of different sub-domains. A brief review of these contributions follows.

Papers in this issue

The study of error patterns in neurologically intact and brain-damaged individuals has provided a wealth of information in developing our understanding of various cognitive domains. This approach is adopted by several contributors to this issue. Medina and Coslett (2016) examine how errors in tactile perception inform us regarding how the brain represents the body. First, they discuss whether participants with numbtouch – who are thought to be able to localize touch without feeling touch – provide evidence in support of a double dissociation between processes for tactile detection and localization. Second, they discuss the necessity of secondary representations for mapping information encoded in somatosensory maps to a representation of the skin surface, and review how evidence from plasticity and sensory uncertainty provide information regarding how we localize touch. Third, they review studies reporting referred sensations in amputees and conclude that better evidence is needed to support the "remapping hypothesis". Finally, they show how evidence from dysynchiric phenomena – in which touch is felt on the opposite side of the body – provide support for interhemispheric mechanisms involved in representing touch.

The location of tactile stimulation can be represented in a number of different reference frames. First, touch can be represented as a location on the skin surface (a skin-based, anatomical reference frame), irrespective of body position in space – e.g., a neuron can have a receptive field fixed to the left index fingertip regardless of the organism's body position. But to act on the world, one also needs representations of where that touch occurs in space relative to the organism, such that the location of touch on the same location of the skin surface is represented differently as the organism moves in space. This involves a remapping process from skin-based, anatomical representations to representations of touch in egocentrically defined external space. Some models propose that tactile information is first coded in an anatomical representation and then serially remapped and stored in an external representation. However, Badde and Heed (2016) provide evidence that information from both anatomical and external representations are integrated, with the relative contributions of each type of information flexibly weighted based on task relevance.

Tamè, Braun, Holmes, Farne, and Pavani (2016) note that, beginning with the initial mapping of somatosensory cortex by Penfield and Boldrey (1937), most studies have focused on contralateral activation in primary somatosensory cortex after touch. In their review, the authors examine ipsilateral tactile processing in depth. They review neurophysiological studies showing dense connections between somatosensory cortices in non-human primates and discuss other potential pathways that would allow for ipsilateral processing. They also review behavioural studies that have shown that stimulation of one hand influences perceived touch in the homologous location on the opposite hand, and neuroimaging studies demonstrating changes in ipsilateral activity after unilateral tactile stimulation. Evidence suggests that this ipsilateral activation occurs, not only in secondary somatosensory cortex, but even in primary somatosensory cortex. They provide evidence for different processes that could result in ipsilateral activation after touch. One is the existence of rapid, topographically homologous effects that are mediated either by direct ipsilateral thalamocortical projects or transcallosal connections between homologous regions of S1, with later bilateral processing in secondary somatosensory cortex.

Body representations are inherently multisensory, as there are clear contributions from visual, tactile, proprioceptive, and motor systems. However, relatively little research has been done on the contributions of the vestibular system to body representations. In their review, Ferrè and Haggard (2016) discuss three different aspects of body representation and how the vestibular system contributes at each representational level. First, the authors review results demonstrating improved tactile detection, both in brain-damaged individuals and in neurologically intact individuals, after caloric and galvanic vestibular stimulation. From these results, they propose that the vestibular system may improve tactile detection by modulating gain in the somatosensory system. Second, individuals who undergo vestibular stimulation, along with individuals with vestibular disorders, show consistent biases in both localizing touch on the body, localizing body position in external space, and changes in the perceived size and shape of the body, providing evidence for changes in somatoperception. Finally, they examine how vestibular changes influence an individual's sense of body ownership, reporting brain-damaged individuals who regain perceived ownership of their limb after vestibular stimulation. Overall, they note how the vestibular system influences body representation at a number of different levels, and the importance of studying this system in understanding body representations.

Our bodies are not only sensory gateways – they are also used to act on the world around us. When using a tool, it is necessary to integrate information from body representations with knowledge of tool use and configuration to effectively act on the environment. A number of studies have provided evidence for distinct, multimodal representations of peripersonal space – the area immediately around the body. Martel, Cardinali, Roy, and Farne (2016) examine how tool use influences body representations, first by reviewing studies on how tool use expands peripersonal representations in neurologically intact and brain-damaged individuals. Next, they review studies that examine whether tool use shapes different types of body representations. They find that individuals perceive their arm as lengthened when using a tool or a prosthetic, and they propose that tool use modifies the body schema itself, resulting in changes in perceived arm length. The authors also discuss whether the body image – defined as a lexico-semantic representation of body knowledge – is influenced by tool use, noting that this is one of many questions in the field of body representation for which we do not yet have a clear answer.

Models of motor control posit that information about the predicted position of the body (provided from copies of motor plans) is integrated with estimates of current body position using feedback from body representations to efficiently and accurately control movement. A great deal of research effort has been devoted to understanding the dynamics of these models from a motor perspective, with relatively little work on how different aspects of body representations contribute to the estimates of body position used in these models. The mirror box illusion, which can create conflicts between visual and tactile/proprioceptive information, has been used to examine how multisensory information is integrated into a representation of limb position. In their review, Soliman, Buxbaum, and Jax (2016) discuss how the mirror box illusion can be used to inform models of motor control. They propose that the mirror illusion primarily influences estimates of the desired and predicted state of body position, with less influence on estimates of the initial state of the body. Furthermore, they also speculate that area V6A is the brain region involved in developing these desired and/or predicted state estimates.

The subjective experience of ownership over our own bodies is easily taken for granted. However, studies of individuals with deficits in perceived body ownership have provided substantial information regarding how the brain constructs this sense of bodily self. A number of individuals have been reported who, subsequent to brain damage, feel loss of ownership of body part – for example, they experience their own hand as someone else's. Pia, Garbarini, Fossataro, Burin, and Berti (2016) describe a number of brain-damaged individuals who report the opposite pattern of performance – feeling that someone else's hand is their own hand. After "embodying" someone else's arm, they report increased pain (both via self-report and skin conductance response) when seeing the embodied arm pricked. Next, normal participants will tend to draw elliptical shapes when attempting to draw a circle with one hand and a straight line with the other. Interestingly, individuals who embody someone else's hand as their own (but not hemiplegic controls) demonstrated the same ovalization effect when the patients drew lines with their right hand and the experimenter drew circles with his/her left hand. The authors propose that viewing an arm in an anatomically plausible position can lead to ownership of the viewed hand. However, when visual information regarding the viewed, other hand does not match with sensory information from one's own body, neurologically intact individuals do not demonstrate such illusory ownership. The authors suggest that deficits in matching visual information regarding the viewed, other hand with sensory signals from one's own hand results in the perceived deficit.

Overall, the contributions in this special issue demonstrate the wide variety of different mental processes that are involved in representing the body, ranging from simple tactile detection to our sense of self. This collection of papers provides a timely review of different aspects of body representation from a variety of perspectives and illustrates that data from subjects with neurologic dysfunction provide a unique window into brain function. Although progress has been made in this domain, we hope that future work will continue to focus on developing testable models of how the brain represents the body.

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