Neuroscience Research 104 (2016) 16–30

Contents lists available at ScienceDirect

Neuroscience Research

journal homepage: www.elsevier.com/locate/neures

Review article

Body representations in the human brain revealed by kinesthetic illusions and their essential contributions to motor control and corporeal awareness

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ARTICLE INFO

Article history:
Received 1 September 2015
Received in revised form 22 October 2015
Accepted 23 October 2015
Available online 10 November 2015

Keywords:
Muscle spindle
Kinesthesia
Body representation
Motor control
Sensory-motor association
Corporeal awareness
Self-consciousness
Functional magnetic resonance imaging

ABSTRACT

The human brain can generate a continuously changing postural model of our body. Somatic (proprioceptive) signals from skeletal muscles and joints contribute to the formation of the body representation. Recent neuroimaging studies of proprioceptive bodily illusions have elucidated the importance of three brain systems (motor network, specialized parietal systems, right inferior fronto-parietal network) in the formation of the human body representation.

The motor network, especially the primary motor cortex, processes afferent input from skeletal muscles. Such information may contribute to the formation of kinematic/dynamic postural models of limbs, thereby enabling fast online feedback control. Distinct parietal regions appear to play specialized roles in the transformation/integration of information across different coordinate systems, which may subserve the adaptability and flexibility of the body representation. Finally, the right inferior fronto-parietal network, connected by the inferior branch of the superior longitudinal fasciculus, is consistently recruited when an individual experiences various types of bodily illusions and its possible roles relate to corporeal awareness, which is likely elicited through a series of neuronal processes of monitoring and accumulating bodily information and updating the body representation. Because this network is also recruited when identifying one's own features, the network activity could be a neuronal basis for self-consciousness.

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http://dx.doi.org/10.1016/j.neures.2015.10.013
0168-0102/

1. Introduction

The human brain creates an internal representation of the body that assists in controlling physical movement. The presence of anatomical and functional somatotopy, which is referred to as a homunculus, is the most vivid example of this, and can be seen in the primary somatosensory cortex (SI) and in the primary motor cortex (M1). Somatosensory information originating from one's own body plays a very important role in motor control. For example, patients with impaired proprioceptive input (somatic signals about spatial position and movement of limbs) may not be able to accurately perform a reaching movement toward a target located just 10 cm away (Ghez et al., 1995). When such patients have visual input about the movement of their hands and arms, only then will they be capable of performing an accurate reaching movement. However, removal of this visual information will result in impairment of reaching performance again. Similar behavior has been reported when such patients were made to perform a thumb-to-finger opposition task (Rothwell et al., 1982). These lines of evidence indicate that somatic signals are extremely important in the control of movement and motor learning. Indeed, non-human primates with a disrupted SI, and thus, impaired somatosensory inputs to the M1, have difficulty in learning new movements (Pavlides et al., 1993).

Somatic signals are also essential for recognizing one's own body. Humans normally recognize their own bodies mainly through visual and somatic sensations. The visual system can be used to acquire information about distant areas that have no direct relationship to the individual. In contrast, somatic sensations are induced by various sensory receptors that are present in the skin, muscles, and joints, and they normally originate from one's own body. Hence, somatic sensations allow us to conceive of ourselves as the source of incoming sensations and as separate entities from other agents and the external world. Somatic sensations that originate from sensory receptors in the muscles and joints are referred to as proprioception, and these sensations are qualitatively different from skin (cutaneous/tactile) sensations. Proprioception is involved in the perception of positional changes and movements of body parts, such as the hands and feet, while the main function of skin sensations is to extract the feel of materials and objects, such as those touched by our hand (Naito, 2004a).

Although it has yet to be clearly defined, the concept of body image refers to the image of oneself, and generally encompasses both mental and psychological factors. In contrast, the body schema refers to a model of one's posture (body configuration) that is updated constantly with new sensory information elicited by postural changes (Head and Holmes, 1911). Consequently, the body schema is a neural representation of the body that involves motor and posture control. As described, proprioception largely encompasses the perception of positional changes and movements of body parts; thus, it is the most essential sensory modality for the formation of the body representation. Proprioception is Latin for 'one's own perception', and this sensation has long conceived of as the source of physical self-perception. Hence, we believe that this sensation must be deeply involved in corporeal awareness, which could be the basis of self-consciousness.

Recent neuroimaging studies dealing with kinesthetic illusions (see below) have unveiled the neuronal representation of the human body representation. In this chapter, we focus mainly on proprioception, and introduce the importance of three brain systems (the motor network, specialized parietal systems, and the right inferior fronto-parietal network) in the formation of the human body representation, which has been revealed by a series of our kinesthetic illusion studies. We also discuss and speculate how proprioceptive input could lead to corporeal awareness and self-consciousness.

2. Kinesthetic illusion as a useful tool to elucidate neuronal representation of the human body

Muscles and joints contain proprioceptors that sense the movement and position of limbs (the hands and feet). Among these, the receptors in the (intrafusal) muscles are called muscle spindles, and the signals are transmitted to the central nervous system (CNS), mainly through group Ia primary muscle spindle afferent fibers (Fig. 1). When the muscles are stretched, the activity of muscle spindle afferents normally increases (Fig. 1), and this activity can carry information about the direction and speed of limb movement (Burke et al., 1976, 1988; Edin and Vallbo, 1988, 1990; Ribot-Ciscar and Roll, 1988). Thus, movement sensations that largely depend on muscle spindle afferent input are called *kinesthesia*. Proprioceptive input to the CNS is generally known to comprise the following two main pathways: the spinal cord-thalamus-cerebral cortex pathway and the spinal cord-cerebellum-thalamus-cerebral cortex pathway (Fig. 1). Hence, the brain can receive kinesthetic information about the direction and speed of limb movement through Ia muscle afferent fibers.

Interestingly, the activity of muscle spindle afferents also increases in response to vibration stimuli of specific frequencies (around 80 Hz) (Fig. 1). Thus, it is possible to employ this property to elicit a clear illusory movement sensation, such that vibrated limbs (hands and feet) feel as though they are moving when they are not (kinesthetic illusion: Goodwin et al., 1972; Roll and Vedel, 1982; Roll et al., 1989). For example, when a vibration stimulus is applied to the tendon of the wrist *extensor* muscle, an illusory wrist *flexion* is elicited (Fig. 1). This involves no movement of the hand and no intention to move their hand, but it is possible to experience a clear movement sensation as if their hand is moving. In other words, during kinesthetic illusion, people can experience postural change of a limb, which is an indispensable element in the formation of the body representation (body schema). Further importantly, this method enables the experience of not only simple limb movements but also various types of bodily illusions (see below). Hence, this illusion is a useful tool to experimentally manipulate and elucidate the neuronal basis of the human body representation.

Because vision normally supersedes proprioception, the visual information about the unmoving limbs significantly attenuates the illusions (Hagura et al., 2007). Thus, in the majority of our