



## 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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## 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 (Pavlidis 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.

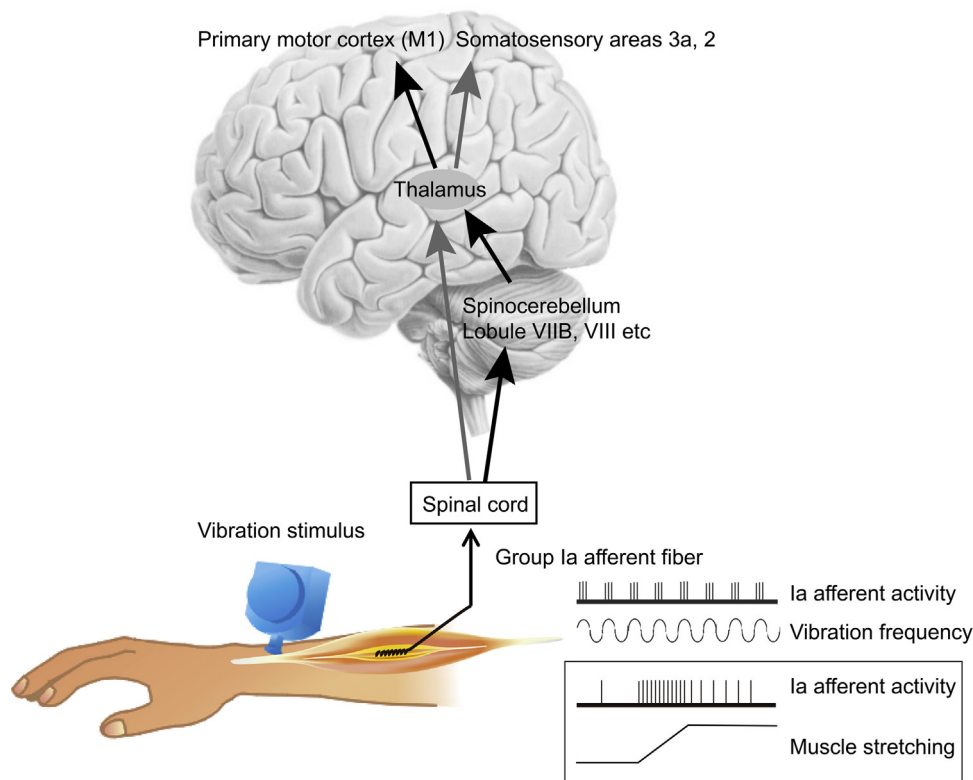
Recent neuroimaging studies dealing with kinesthetic illusions (see below) have unveiled the neuronal representation of the human body representation. In this chapter, we focus mainly on proprioception, and introduce the importance of three brain systems (the motor network, specialized parietal systems, 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



**Fig. 1.** Representative diagram of activity in the primary muscle spindle afferent fiber and two putative pathways of proprioceptive (kinesthetic) input to the central nervous system (CNS) when the tendon of the right wrist extensor muscle is vibrated. The afferent fiber, which normally increases in activity when the muscle is stretched, also exhibits harmonic activity reflecting the frequency of the vibration stimulus applied to the tendon. The brain receives this kinesthetic signal through two putative pathways (black and grey arrows) and the individual experiences stretching of the vibrated muscle (wrist extensor muscle) (i.e., illusory wrist flexion).

kinesthetic illusion studies, we conducted experiments in which participants closed their eyes.

Furthermore, it is important that the limbs being stimulated are relaxed for participants to experience the kinesthetic illusion. If they are not relaxed, then the tendon vibration can easily cause a tonic vibration reflex, which is an actual reflex that occurs in the opposite direction of the illusion.

In the following sections, we discuss the importance of three brain systems (the motor network, specialized parietal systems, and the right inferior fronto-parietal network) when the human brain builds up and updates the body representation during various types of proprioceptive bodily illusions.

### 2.1. Motor network activation during kinesthetic illusion

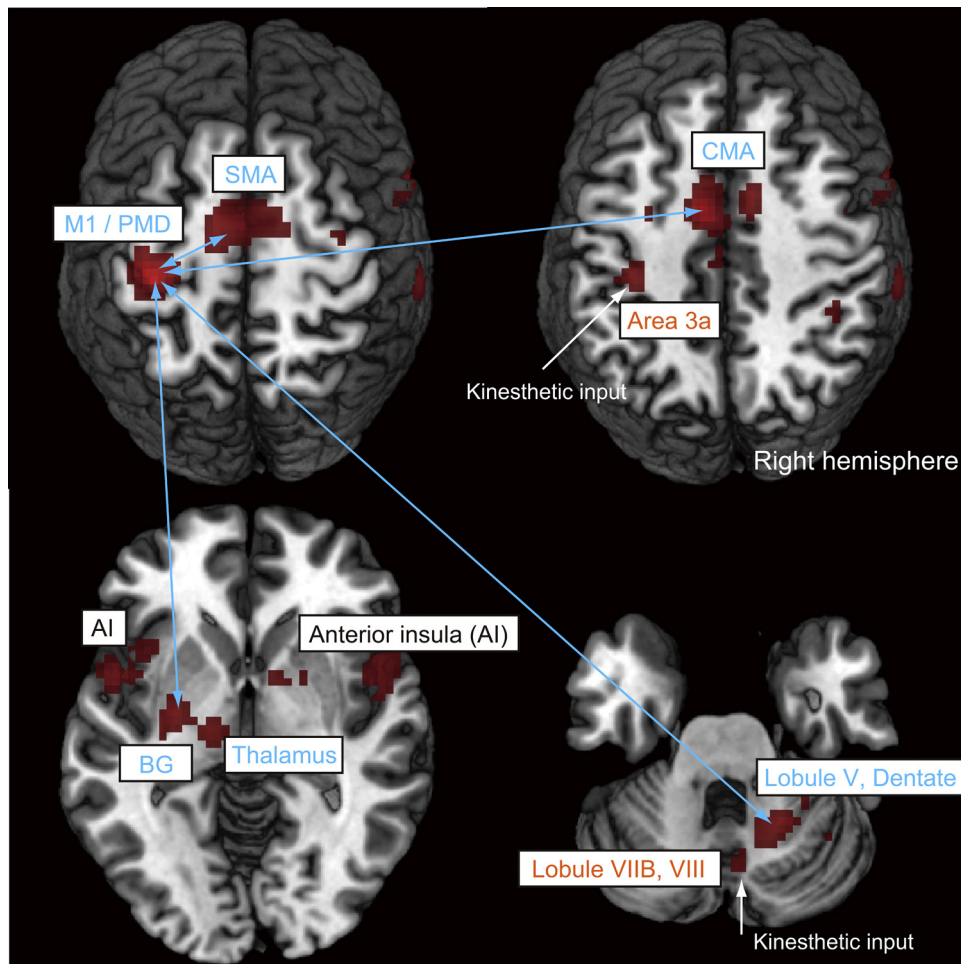
Functional magnetic resonance imaging (fMRI) of brain activity in right-handed healthy volunteers experiencing a kinesthetic illusion in the right hand (kinesthetic illusory wrist flexion) reveals activation in the motor network, including the M1, dorsal premotor cortex (PMD), supplementary motor area (SMA), cingulate motor area (CMA), sensorimotor territory of the basal ganglia (Lehéricy et al., 2004), and the motor cerebellar hemisphere (lobules V, VI; Strick et al., 2009). Activation can also be observed in somatosensory areas, such as area 3a of the SI and the spinocerebellum (vermis lobules VIII, VIIIB) (Fig. 2: Naito et al., 2002a,b, 2005, 2007). These motor areas are active when participants experience an illusory flexion of their hands in the total absence of actual movement and movement intention. Such activation is not seen in the control condition, in which we vibrate the skin surface beside the tendon, generating a stimulus that does not elicit any reliable illusions. Thus, the observed activity in the motor network during illusory flexion of the hand appears to reflect the central processing of

muscle spindle afferent input. A similar pattern of brain activity has also been observed in the motor network when people experience illusory movement of the arms (Naito et al., 1999) and feet (Naito et al., 2007; Fig. 3). These data support our view that the motor network participates in kinesthetic processing of muscle spindle afferent inputs from limbs.

The motor areas in the brain are normally active when we actually move a limb. We argue here that merely processing kinesthetic afferent input from a limb can increase activity in motor areas. Indeed, when comparing the degree of M1 activity elicited by actual movement with that resulting from the illusory experience of right hand movement, the degree of M1 activity seen during the illusion is less than half that observed during actual movement. Additionally, overt muscle activity is not a prerequisite to the experience of the illusion (Amemiya and Naito, 2015). Thus, the muscle afferent processing that is essential for kinesthesia appears to generate sub-threshold motor activity in the motor network. As is the case during the actual execution of limb movement, activation occurs in the somatotopic sections of motor areas during illusions (Fig. 3). Hence, it is likely that the sub-threshold motor activity in the somatotopic sections for a particular limb may underlie movement sensation corresponding to that limb during kinesthetic illusion.

### 2.2. Roles of M1/PMD in kinesthetic illusion

Of the different motor areas involved in kinesthetic illusion, M1 is referred to as the executive locus of voluntary limb movement. This region is the major cortex that sends motor commands to the motoneurons in the spinal cord to generate and control movements. In non-human primates, cells in M1/PMD receive kinesthetic signals that likely originate from muscle spindles (Colebatch et al., 1990; Porter and Lemon, 1993), for instance, via



**Fig. 2.** M1-centered motor network activity during illusory flexion of the right hand. During the illusion, activation can be seen in the motor network, including the primary motor cortex (M1), dorsal premotor cortex (PMD), supplementary motor area (SMA), cingulate motor cortex (CMA), putamen/globus pallidus (BG), and motor cerebellar hemisphere (Lobule V, dentate). Activation also occurs in the somatosensory areas, such as putative somatosensory area 3a and the spinocerebellum (Lobule VIIIB, VIII). The light blue arrows represent functional and anatomical connections with M1. Note that the M1-BG circuit is formed by M1 → BG → thalamus → M1, and the M1-cerebellum circuit is formed by M1 → pontine nucleus → cerebellar hemisphere → dentate nucleus → thalamus → M1, which is simplified in the present diagram. The white arrows indicate kinesthetic input. Muscle afferent processing generates sub-threshold motor activity in the M1-centered motor network, which likely produces latent motor commands.

somatosensory area 3a (Phillips et al., 1971; Huerta and Pons, 1990; Fig. 2). Indeed, tendon vibration of triceps brachii muscles can elicit excitatory responses in M1/PMD cells at a mean latency of 21 ms (Colebatch et al., 1990). Thus, the M1 involves muscle afferent processing, which is essential for kinesthesia.

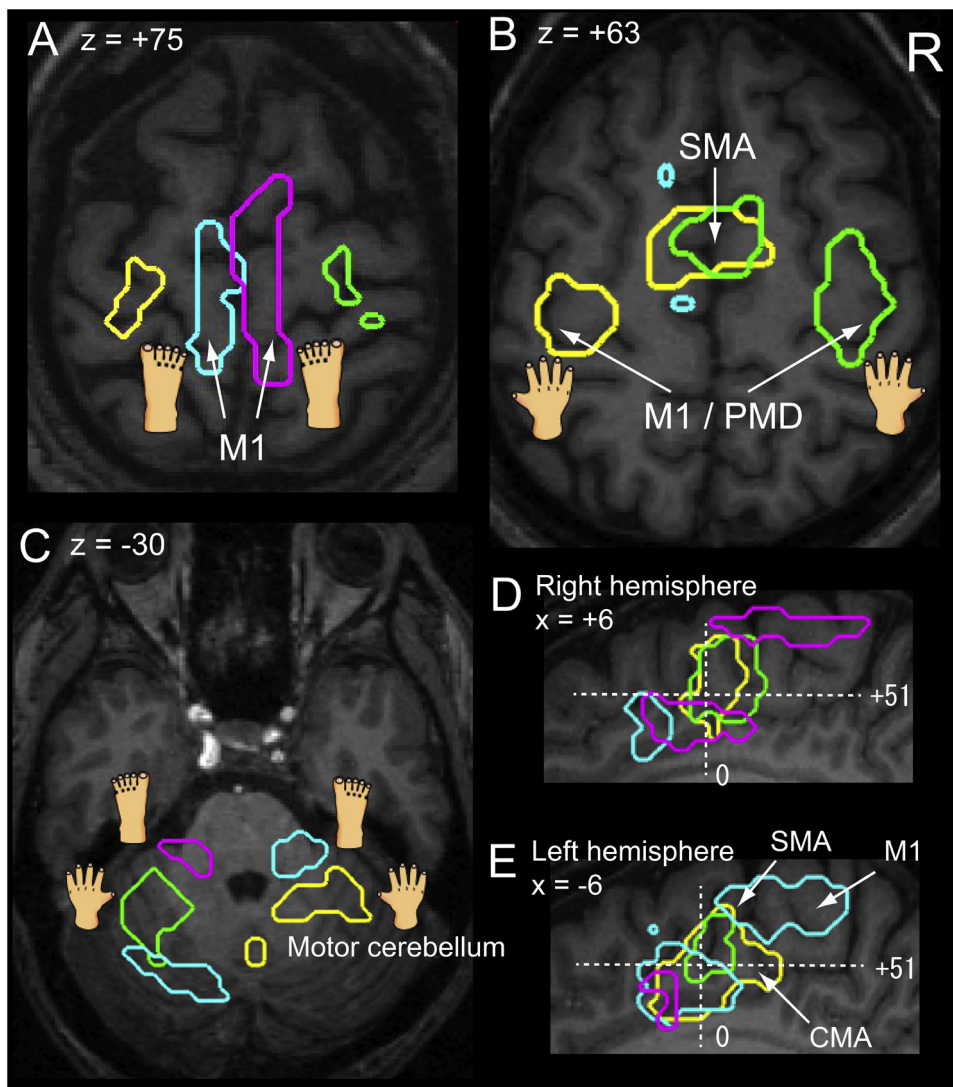
Considering that muscle spindle afferents are capable of signaling the direction and speed of limb movement (see above), it is likely that somatotopically organized M1/PMD activity during an illusion (Fig. 3) represents information about the direction and velocity of the illusory limb movement. [Additional parietal contribution is also suggested when the brain has to specify the direction and speed of illusory movement in an ambiguous situation when two antagonistic muscles are simultaneously vibrated (Romaiguere et al., 2003).] Thus, the fundamental information underlying kinesthesia is likely processed in the M1/PMD-centered motor network during an illusion.

The importance of the human M1/PMD in kinesthetic processing has been corroborated by several studies. First, the degree of motor-cortical (M1) excitability is correlated with the degree of illusion [the extent to which people experience an illusory hand movement (i.e., wrist angle) within a certain period of vibration time] (Naito et al., 2002b). Likewise, the degree of motor-cortical excitability also reflects the amount of illusory aftereffect [the extent to which

people experience movement sensation as if the vibrated hand is going back to its original position after the cessation of vibration stimulus] (Kito et al., 2006). Second, contralateral M1/PMD activity during an illusion has been found to decrease in proportion to the degree to which an illusion is attenuated by vision (i.e., the degree to which the experience of illusory movement is attenuated when participants look at their unmoving hand) (Hagura et al., 2007). Finally, focal damage in the hand section of M1/PMD can severely impair the experience of illusory movement of the contralateral hand (Naito et al., 2010). These findings strongly suggest that M1 is not simply a center for motor execution, but also an important node that may contribute to the somatic perception of limb movement (i.e., kinesthesia) by receiving and processing muscle afferent signals. Hence, the M1 could warrant its title as the primary motor-sensory cortex.

It is still under debate whether the human M1/PMD is purely involved in kinesthesia per se. Some studies have reported that transcranial magnetic stimulation (TMS) over M1 and PMD may produce movement sensations in the nerve blocked arm and leg (Christensen et al., 2010) and that TMS over M1 of traumatic amputees who report the presence of a phantom limb can evoke the movement sensation in the phantom limb (Cohen et al., 1991; Pascual-Leone et al., 1996; Mercier et al., 2006). On the other hand,



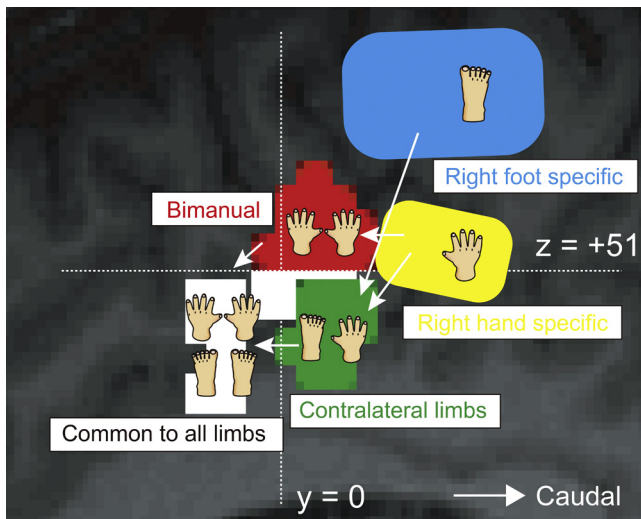


**Fig. 3.** Somatotopical sections of multiple motor areas active during illusory movement of the right hand (yellow), left hand (green), right foot (light blue), and left foot (pink). Clear somatotopy is seen in M1 and the motor cerebellar hemisphere (A–C). Somatotopical organization is less apparent in the medial-wall motor regions (D and E). Modified from Naito et al. (2007).

there is a report that M1 activity is not necessary when people experience visually induced illusory hand movement when they watch the video of their own moving hand (Kaneko et al., 2015).

M1/PMD has been found to form efficient sensory-motor circuits with muscles (Fetz et al., 1980; Cheney and Fetz, 1984). Specifically, cortico-motoneuronal cells in M1/PMD that respond to passive movement of the elbow or wrist toward a particular direction (extension or flexion) also show excitatory activity (1) for active movement toward the same direction as that of the passive movement; Type 1, (2) for active movement toward the opposite direction; Type 2, or (3) in both directions. Importantly, the number of cells in these three groups is almost equal (Fetz et al., 1980; Cheney and Fetz, 1984). The cells that exhibit excitatory activity during active movements are associated with motor output (generation of muscle activity) and the cells that fire during passive movement likely respond to the stretching of muscles. This is because the muscle spindle is most sensitive to specify a direction of limb movement among various types of mechanoreceptors (joint, slow, and fast adapting cutaneous) that react to passive movement (Burke et al., 1988).

Some cells respond to both active wrist flexion and passive wrist flexion (Type 1: same preferred directions for active and passive movements). The activity of such cell is sent to motoneurons to facilitate wrist flexion during active flexion. On the other hand, the activity of the cell is induced by the afferent input from the stretching extensor muscle during the wrist flexion. Thus, these cells appear to be capable of facilitating wrist flexion while receiving muscle afferent input from the stretching extensor (antagonistic) muscle. It is likely that this circuit mediates kinesthetic illusory wrist flexion, because muscle spindle afferent input from a vibrated wrist extensor muscle elicits illusory wrist flexion movement (Fig. 1). Indeed, during illusory wrist flexion, motor-cortical excitability for the wrist flexor muscle is elevated compared with that for the extensor muscle (Kito et al., 2006). This pattern of motor-cortical excitation is similar to that observed during actual wrist flexion. Hence, this may support our view that *sub-threshold* motor activity is generated in the motor network when people experience kinesthetic illusory limb movement as if the movement is actually happening (veridical sensation of limb movement). The underlying neuronal operation seems to be the *generation of latent*



**Fig. 4.** Medial-wall activations in the left hemisphere ( $x = -6$ ; panel E in Fig. 3) during kinesthetic illusions in all limbs. Illusory movement of the right hand or foot activates the caudal part of the contralateral CMA (yellow section) and SMA (blue section), respectively. Activation is seen in the rostral section of the SMA regardless of whether participants experience an illusion in the right or left hand (bimanual section: red section). Activity in the rostral part of the CMA increases when participants experience illusory movement of the contralateral hand or foot (contralateral limb section: green section). In the more rostral section of the CMA, activation occurs regardless of whether participants experience illusory movement of the left or right hands and feet (common section: white section). Kinesthetic information specific to each limb appears to converge from the caudal to rostral direction (indicated by white arrows).

Modified from Naito et al. (2007).

*motor commands* to the agonistic muscles associated with the kinesthetic illusory movement (Naito, 2004b).

In contrast, cells that respond to both active wrist flexion and passive wrist extension (Type 2: opposite preferred directions) can activate the wrist flexor muscle when this muscle is stretched. This function is implemented in the transcortical long-loop reflex circuit (Cheney and Fetz, 1984). When a hand muscle is stretched, long-latency (50–90 ms from the stretch onset) EMG responses can be observed in the stretched muscle. We assume that this circuit is involved in the generation of the tonic vibration reflex, which is opposite to the kinesthetic illusion as a tendon vibration is applied to unrelaxed muscles as discussed above. This is an important biological defensive mechanism to prevent muscle damage caused by an unexpected and noxious stretch. While the spinal reflex circuit is automatic, the transcortical long-loop circuit may reflect some degree of voluntary action, as M1 (executive locus of voluntary movement) mediates this circuit. The greater contribution of the transcortical long-loop circuit to fast feedback control of limb movement has been demonstrated in a recent study (Pruszynski et al., 2011). M1 cells can integrate sensory information into motor commands within a very short time period (about 50 ms) in order to appropriately react to mechanical perturbations.

Finally, in addition to M1/PMD, medial-wall motor areas (SMA and CMA; Figs. 2–4) can also be considered executive loci of limb movement because these areas contain a considerable number of corticospinal neurons, both for distal and proximal muscles (He et al., 1995). Interestingly, CMA cells active during object manipulation also respond to perturbations applied to the object at the short latency of approximately 45 ms (Cadoret and Smith, 1995). This further implies that CMA may form transcortical circuits with its controlling muscles. Thus, several cortical motor areas appear to form efficient transcortical circuits with their associated

muscles where kinesthetic (muscle afferent) signals could be quickly converted and integrated into motor commands.

### 2.3. Convergence of kinesthetic information in medial-wall motor regions

As seen in M1 and the motor cerebellar hemisphere, illusory movement of a particular limb activates the corresponding somatotopical sections (Fig. 3A–C). However, kinesthetic information specific to each limb seems to be integrated in the medial-wall motor areas (Naito et al., 2007). As shown in Fig. 4, illusory movement of the hand or foot activates the caudal part of the contralateral CMA and SMA respectively (yellow and blue sections in Fig. 4). These sections are highly specific to contralateral hand or foot movement, as observed in the M1 and cerebellum. In contrast, topographical organization becomes less apparent in the more rostral sections of the SMA and CMA. For example, activation can be observed in the rostral section of the SMA regardless of whether participants experience illusory movement of the right or left hand (bimanual section: red section). Additionally, activation of the rostral part of the CMA, located just beneath the bimanual section of the SMA, is common when participants experience illusory movement of the contralateral hand or foot (contralateral limb section: green section). Finally, in the rostral CMA, neuronal activation increases regardless of whether participants experience illusory movement of the left or right hands and feet (common section: white section).

Although we are limited by the specific time course of neural information available when using fMRI, if we consider that kinesthetic information involves bottom-up processing, it is possible that kinesthetic information specific to each limb converges from the caudal to the rostral part of medial-wall motor areas (cf. Nachev et al., 2008). Interestingly, despite detailed investigation, no areas have been found that commonly activate during illusions of the right-hand and left-foot. Additionally, no areas have been found that activate in common during illusions of any three limbs. Considering that the SMA serves a bimanual function in motor control, the kinesthetic representation of multiple limbs in the medial-wall motor regions could be beneficial when coordinating movements between limbs.

### 2.4. Application of kinesthetic illusion for neuro-rehabilitation

As described, kinesthetic illusions elicit veridical somatic sensations of limb movement (as if the limb is actually moving) by activating the motor network that is normally involved in the voluntary control of limb movement (Fig. 2). Importantly, people can experience this illusion without accompanying actual limb movement. Thus, kinesthetic illusion has potential for use as a neuro-rehabilitation tool. There could be two main approaches to the therapeutic use of kinesthetic illusion: (1) the kinesthetic-guidance of limb movement in the restoration of its sensory-motor function and (2) the prevention of reduced cortical motor representation due to learned non-use.

In general, it is very difficult to verbally teach someone how to move his/her limbs because kinesthetic/motor experience is not linguistic in nature. Kinesthetic illusion can produce a very real and veridical somatic sensation of limb movement, and thus can be an intuitive way to provide kinesthetic guidance about limb movement. As mentioned above, the generation of overt muscle activity is not a prerequisite for illusory limb movement. However, muscle activity gradually emerges if the tendon is vibrated for a long period of time, as kinesthetic signals progressively spread to the motor network underlying voluntary limb movement (Fig. 2), thus increasing the likelihood of emergent muscle activity.

This potential transition to voluntary movement is important, as kinesthetic illusions may be able to elicit urge-to-move sensations in limbs in a bottom-up manner. This outcome seems possible as kinesthetic illusions broadly activate the medial-wall motor regions where electrical stimulation is known to elicit the urge-to-move sensation (Fried et al., 1991; Lim et al., 1994). This, in combination with top-down approaches, i.e. motor intention and motor imagery, may represent an efficacious way to stimulate motor activity in a therapeutic setting (Naito et al., 2013). Indeed, motor imagery and kinesthetic illusion share neuronal substrates in the motor network (PMD, SMA, and cerebellum), and motor imagery has been found to augment kinesthetic illusory experience (Naito et al., 2002a; Thyron and Roll, 2009). Kinesthetic illusory experience may also be augmented by other approaches. For example, visual information about hand flexion makes kinesthetic illusory hand flexion seem more real and vivid (Hagura et al., 2009). Additionally, other types of somatosensory inputs, e.g. pressure and skin deformation, which are normally associated with hand flexion, may also augment the illusory experience.

If one remains completely immobile for a relatively long period of time, the brain will learn not to move the body. This phenomenon is generally referred to as learned non-use. Learned non-use has been found to reduce central motor representations in M1, PMD, and SMA (Liepert et al., 1995; Roll et al., 2012). However, if a person experiences kinesthetic illusions during the immobilization period (i.e., 5 days), the central representations in multiple motor areas may be preserved (Roll et al., 2012). Thus, kinesthetic illusion may be efficacious in preventing the disruption of cortical motor representations resulting from learned non-use. One advantage of the use of illusion is that it requires no actual movements; therefore, this technique can be used even when physical movements are completely restricted by a cast or other factors.

These perspectives are being introduced into current neuro-rehabilitation field (Naito et al., 2013), and we expect their potency in the restoration of sensory-motor functions after brain injuries.

### 2.5. Brief summary

During kinesthetic illusions, people experience changes in the position of their limbs, which is an important element of the body representation. Kinesthetic (muscle afferent) signals are widely distributed and processed in M1-centered cortical and sub-cortical motor networks. Information processed in these regions concerns the direction and extent of movement of individual limbs, and thus, M1 activity often corresponds well with the degree of the kinesthetic percept (i.e., illusory angle, strength of somatic sensation) during illusory limb movement. Accordingly, M1 could be an important brain node in kinesthesia (somatic perception of limb movement). In this way, the motor network likely contributes to the formation of the human body representation, and the body representation represented in this network is most likely a kinematic/dynamic postural model of a limb, which can be quickly utilized for fast feedback control (Scott, 2004). Common use of the motor network for voluntary control and somatic perception of limb movement implies an inseparable connection between action and perception (i.e., the duality of action and perception in the M1-centered motor control domain).

## 3. Specialized parietal systems

In the previous section, we described the importance of the motor network in the kinesthetic processing of a single limb. The motor network contributes to the formation of a limb position model, which is tightly coupled with motor control. In this section, we discuss several essential issues associated with the

formation of the body representation, such as (1) how the brain integrates somatic information from different body parts to compute a postural model (spatial configuration) of the body, (2) how the brain expands our body representation by incorporating external objects or tools, and (3) how the brain integrates visual and kinesthetic information to identify the exact position of a limb. We introduce the notion that distinct parietal regions play specialized roles in the transformation/integration of information across different coordinate systems (e.g., body-centered, body-parts-centered, eye/head-centered, object-centered), all of which may subservise the adaptability and flexibility of the body representation.

### 3.1. Integration of somatic information from multiple body parts in higher-order somatosensory areas

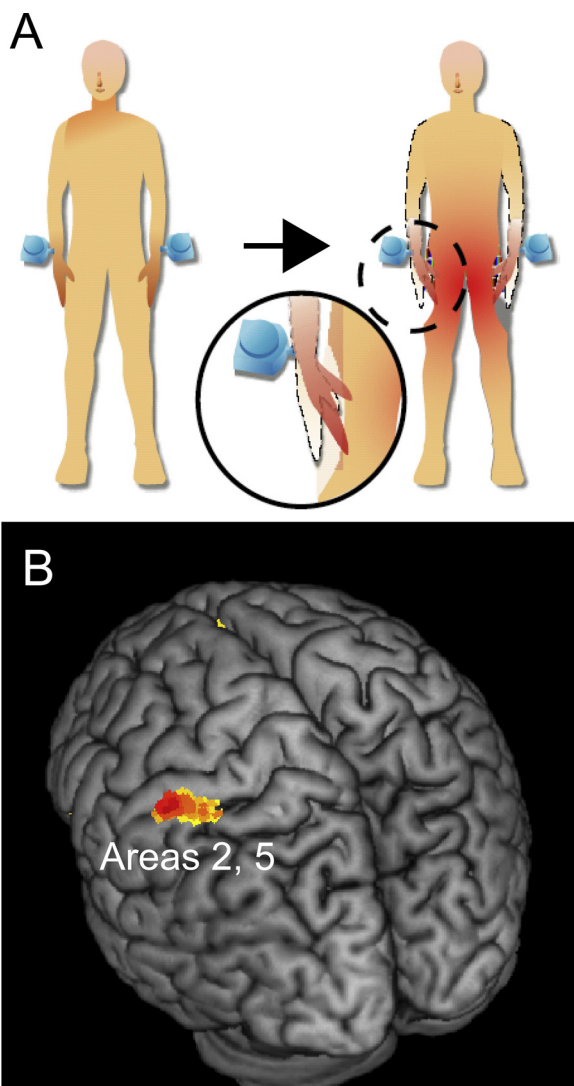
Somatosensory receptors are present in all parts of the body. However, no receptors are able to sense the positional relationship of multiple limbs or the entire body posture simultaneously. Hence, to generate such a body representation, the brain needs to integrate somatic information originating from each body part. This integration is performed by hierarchical information processing in the somatosensory areas of the brain (cf. Bodegard et al., 2001).

The Pinocchio illusion is the most famous bodily illusion showing that the formation of a body representation encompassing multiple parts of the body requires the integration of somatic information (Lackner, 1988). In the Pinocchio illusion, a person with their eyes closed touches their nose with his/her hand. The tendon of their biceps brachii muscle is then vibrated to elicit an illusory extension of the arm. The person may not only feel that their arm is extending, but also that their nose is elongating. Because the nose cannot physically elongate, this is a bodily illusion, experienced as a result of the neural integration of tactile information from the hand that is touching the nose with the proprioceptive (kinesthetic) information from the extended arm (i.e., the angle of the elbow joint feels as though it is increasing). As illustrated by this illusion, the body representation is very adaptable and flexibly represented in the brain. This is an important aspect of the body representation, as the brain must update the internal representation of the body, depending on various factors, such as development, aging, illness, accidents, or fatigue (de Vignemont et al., 2005).

We employed this bodily illusion in an fMRI experiment (Ehrsson et al., 2005). In this experiment, participants lay in an fMRI scanner with both hands at the sides of the body (around the waist/hip). We then vibrated the tendons of the wrist extensor muscles of both hands. In this situation, a person may feel not only that both hands are flexing but also that the waist is shrinking where the hands make contact with the body. This percept is in accordance with the perceptual logic of illusory hand movements (Fig. 5A). When we examined the brain regions specifically associated with this waist-shrinking illusion, we found activation in the cortices lining the postcentral sulcus (Fig. 5B) [the caudalmost part of the postcentral gyrus (cytoarchitectonic area 2) and the cortex rostral to the intraparietal cortex (putative area 5)]. The activities in these regions were basically bilateral and were well correlated with the degree of the waist-shrinking illusion.

Similar to the Pinocchio illusion, the waist-shrinking illusion is experienced as a result of the integration of tactile information from both hands as they touched the waist with proprioceptive information conveying the distance between the two hands, which was manipulated by the illusory flexion of both hands. In primates, areas 2 and 5 are higher-order somatosensory areas (Duffy and Burchfiel, 1971; Sakata et al., 1973; Iwamura, 1998). And these areas can also be considered as anterior parietal association areas





**Fig. 5.** Waist-shrinking illusion (A) and brain activity specific to waist-shrinking illusion (B). (A) When both hands are at the sides of the body (around the waist/hip) and the tendons of the wrist extensor muscles of both hands are vibrated, a person may not only feel that both hands are flexing, but also that their waist is shrinking where their hands make contact with their body. This experience is in accordance with the perceptual logic of illusory hand movements. (B) During the waist-shrinking illusion, activation is seen in the cortices lining the postcentral sulcus [the caudalmost part of the postcentral gyrus (cytoarchitectonic area 2) and the cortex rostral to the intraparietal cortex (putative area 5)]. The amount of activity in these regions is correlated with the degree of the waist-shrinking illusion (see Ehrsson et al., 2005).

since human area 2 becomes activated by merely viewing hand movements in the context of imitation (Oouchida et al., 2004). Cells in these areas are active when different limbs and other parts of the body are touched or moved, i.e., they have complex receptive fields that include several body parts. For example, some cells discharge when the hand, arm, or torso is touched (Taoka et al., 1998), and many cells have bilateral hand receptive fields (Iwamura et al., 1994). Importantly, such cells are not found in primary somatosensory areas 3a, 3b, or 1. Thus, the neuronal populations in such brain areas have the capacity to integrate tactile and proprioceptive information from different body parts, and contribute to the formation of a postural model encompassing multiple body parts. Hence, human areas 2 and 5 seem to integrate information between body-centered and body-parts-centered coordinate systems (see also Naito et al., 2008).

### 3.2. Expansion of the body representation by incorporating external objects in the left inferior parietal lobule

The expansion of the body representation by the incorporation of external objects is a fascinating issue in body representation research. Accordingly, this issue has been addressed by many researchers in both monkey (Iriki et al., 1996; Maravita and Iriki, 2004) and human (Ganesh et al., 2014) studies focused on object manipulation and tool-use.

We are constantly surrounded by various external objects. As long as we do not directly interact with these objects, they are considered to have no relationship to us. However, once we approach an external object such that it relates to our body, we incorporate the object into our own body-centered/body-parts-centered coordinate systems through proprioception of our body positions and movements. Through this process, the brain incorporates the object into our body representation (Object embodiment) as an extension of the body.

Recently, our research team discovered a new type of bodily illusion wherein individuals are able to experience the real somatic sensation of moving an external object by the hand in the complete absence of actual movements. When a person with their eyes closed places his/her hand around a ball, and the tendon of the wrist extensor muscle is vibrated (Fig. 6A), the person has the experience of the touched ball moving together with their hand, which is undergoing illusory flexion (hand-object illusion; Naito and Ehrsson, 2006). This is an example of a perceptual illusion resulting from the integration of kinesthetic information about the hand movement with information about the object touched by the hand.

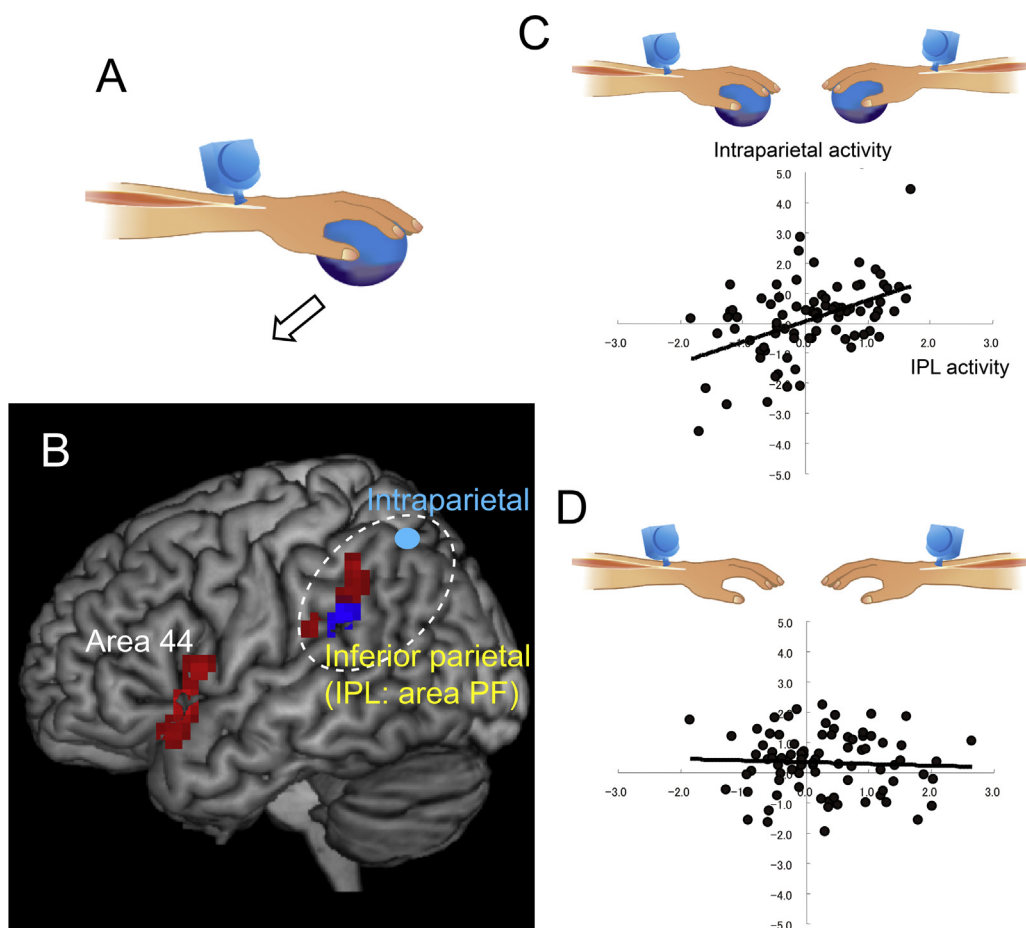
When we examined the specific brain activity underlying the hand-object illusion, we found activity in the inferior frontal cortex (IFG; cytoarchitectonic area 44) and the inferior parietal lobule (IPL; area PF) of the left hemisphere (Fig. 6B). In particular, left IPL activity appears to be common to both the left and right hands, and this region does not usually show robust activity when people merely experience simple illusory hand movement. Thus, the left IPL seems to play a key role in integrating kinesthetic information about the movement of the hand with information about the object touched by the hand (i.e., integrating information from the body-parts-centered and object-centered coordinate systems). The left IPL region (area PF) could be distinct from the human-specific anterior supramarginal region, which is active during the observation of tool use (Peeters et al., 2009). Thus, the IPL could have a more general function when the hand interacts with a variety of objects, rather than with tools used for specific purposes.

When we further analyzed the data, we found enhanced functional coupling of IPL activity with intraparietal cortex activity within the same hemisphere during the hand-object illusion (Fig. 6C). This is not observed during simple illusory movements in which the hand touches nothing (Fig. 6D). In non-human primates, many object manipulation-related neurons are known to exist in area AIP in the intraparietal cortex, and some of these neurons appear to represent objects to be manipulated (Murata et al., 2000). The human brain is known to have an anterior intraparietal region that is homologous to the AIP in monkeys (Binkofski et al., 1999; Culham et al., 2003). Thus, we speculate that, to facilitate the abovementioned sensory integration during the hand-object illusion, the IPL needs to communicate with the intraparietal area that can represent objects.

Importantly, the activity specific to the hand-object illusion is greater in the left IPL than in the right corresponding region, regardless of which hand is the focus of the hand-object illusion. Thus, the IPL activity specific to the hand-object illusion appears to be left-side dominant.

Interestingly, the left IPL region specific to the hand-object illusion corresponds well with the brain regions in which damage





**Fig. 6.** Hand-object illusion (A) and brain activity specific to the hand-object illusion (B). (A) When a person with eyes closed places his/her hand around the sides of a ball, and the tendon of the wrist extensor muscle is vibrated, this person can have the experience that the touched ball is moving together with the hand experiencing the illusory flexion. (B) Brain activities specific to the hand-object illusion are observed in the inferior frontal cortex (cytoarchitectonic area 44) and in the inferior parietal lobule (IPL; area PF) of the left hemisphere. Left IPL activity is common to both the left (red section) and right (blue section) hands. Left hemisphere damage, as indicated by the dotted-line region, often causes (ideomotor) apraxia. C, D: Activity in the IPL is functionally coupled with activity in the intraparietal cortex in the same hemisphere (light blue section in panel B) during the hand-object illusion (panel C). This is not observed during simple illusory movement of a hand that is touching nothing (panel D).

often causes (ideomotor) apraxia (Fig. 6B; Johnson-Frey, 2004). Apraxia, which often coexists with aphasia, is a disorder affecting higher-order cognitive-motor functions. Patients exhibit difficulty in imitating gestures and pantomiming tool-use despite lack of deficits in basic motor functions (Goldenberg and Randerath, 2015). Apraxia patients may not be able to associate a repertoire of appropriate motor behaviors (e.g., those involved in brushing teeth) with a presented tool (e.g., toothbrush). Thus, the human left IPL seems to implement a function of *association* between kinesthetic-motor representations of one's own body and internal representations generated as a result of interactions with external objects and tools.

Strong anatomical and functional connections exist between the inferior parietal and inferior frontal cortices in primates (Averbeck et al., 2009). As described in detail in the next section, it is highly likely that the IPL and IFG, which are specifically activated during the hand-object illusion, are anatomically connected by the fiber tracts of the arcuate fasciculus (Catani et al., 2007) and by the inferior branch of the superior longitudinal fasciculus (SLF III; Thiebaut de Schotten et al., 2012). Both tracts likely connect these regions, but a chief difference is that the former mainly connects only these regions, while the latter connects a much broader range of frontoparietal cortices, including the prefrontal cortices and higher-order somatosensory and visual association cortices. In contrast to the SLF III (see below), the arcuate fasciculus bears language function, and

was found to have left hemisphere dominance in approximately 80% of 50 right-handed people (Catani et al., 2007).

Despite the strong connections between the inferior parietal and the inferior frontal cortices (Matsumoto et al., 2012), hierarchical cluster analyses based on patterns of cortical input (Averbeck et al., 2009) and on those of receptor distribution (Caspers et al., 2013) have indicated that these cortices have relatively independent regional networks; thus, these cortical regions may have somewhat specialized functions. This view seems to be supported by a recent apraxia study. Goldenberg and Karnath (2006) reported that apraxic patients with primary damage in the left IPL exhibited difficulty in imitating relatively large hand motions, while those with predominant damage in the left IFG had difficulty imitating more detailed finger motions. These data suggest that information processing in the IPL and IFG is specialized, e.g. the former handles relatively gross and abstract information, while the latter deals with more specific information. Area 44 is commonly referred to as Broca's area, and this area appears to hold information not only about repertoires of detailed finger movements (Murata et al., 1997), but also about the generation of language, in which elaborate motor control is required (Nishitani et al., 2005). Thus, area 44 might play a role in the selection of appropriate detailed information among multiple competing sources (e.g., the selection of a specific motor repertoire for the fine control of language and finger

movements, specifying the current status of limb position among possible options and so on).

### 3.3. Visual dominance over kinesthesia is computed in the posterior parietal cortex

To experience the abovementioned illusions, participants must close their eyes during the stimulation. This is because the visual information about the unmoving limbs significantly attenuates the illusions (Hagura et al., 2007). In this way, the primate brain relies most heavily on visual information when identifying exact location of a limb.

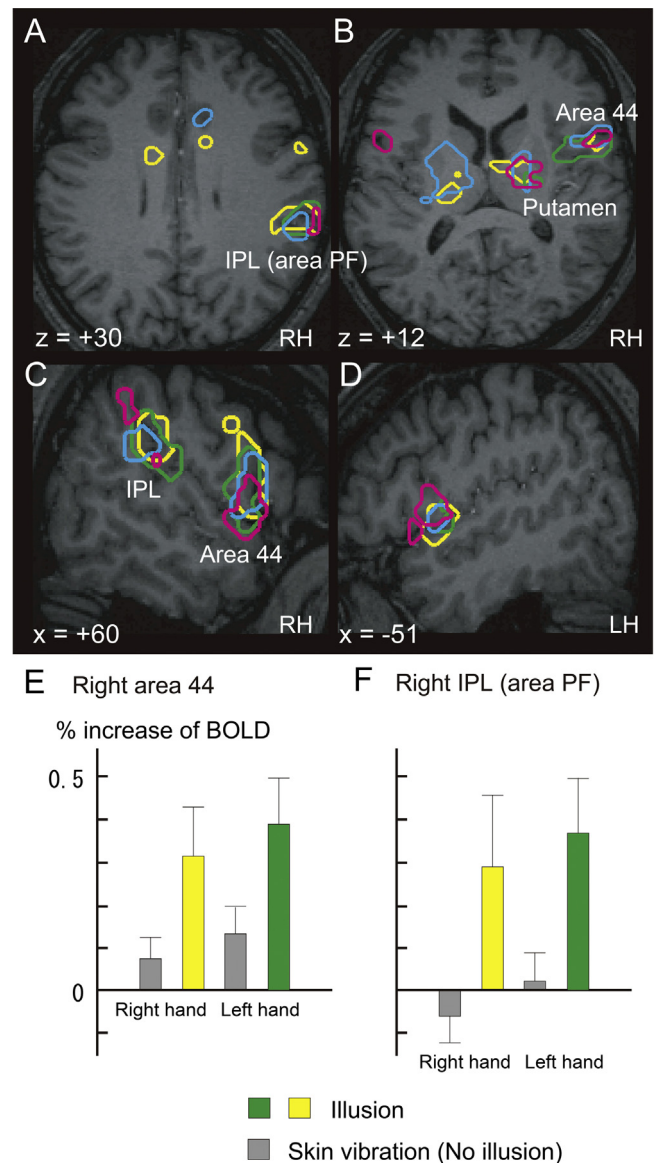
We conducted an experiment wherein people experiencing illusory hand movement viewed either their vibrated hand or the opposite, non-vibrated hand. Importantly, both hands were stationary during the illusion. We tested both the left and right hands. We found that the illusory experience was significantly attenuated only when the participants viewed the vibrated hand. When we examined the brain regions that were activated when the illusion was attenuated by the visual information about the static hand, we found that activity in the bilateral posterior parietal cortices (PPC; area 7) increased in proportion to the degree of attenuation (Hagura et al., 2007). This modulation of PPC activity was in clear contrast with the finding that contralateral M1/PMD activity decreased in proportion to the degree of attenuation of the illusion by visual input (see section 3.2). Thus, visual dominance over kinesthesia appears to be computed in the posterior parietal cortex, and the associated neuronal computation likely comprises the integration of information between body-centered/body-parts-centered and eye/head-centered coordinate systems.

### 3.4. Brief summery

Distinct parietal regions play specialized roles in the transformation/integration of information across different coordinate systems involved in the formation of the body representation. Anterior parietal somatosensory association areas (areas 2 and 5) are capable of integrating somatic information from different body parts to compute a postural model of the entire body. The left IPL (area PF and its sub-regions), in concert with the intraparietal cortex and area 44, appears to integrate information from body-parts-centered and object-centered coordinate systems to incorporate an external object into the body representation. Finally, the PPC seems to integrate information from the body-parts-centered and eye/head-centered coordinate systems to compute visual dominance over kinesthesia, enabling identification of the exact position of a limb. All of the abovementioned functions may subserve the adaptability and flexibility of our body representation.

## 4. Activation of the right inferior frontoparietal cortices during a kinesthetic illusion

In addition to the regions discussed in the above sections, the right inferior fronto-parietal cortices are also active during kinesthetic illusions (Naito et al., 2005, 2007; Amemiya and Naito, 2015). These brain regions include the ventrolateral prefrontal cortices (middle orbital gyrus), the inferior frontal gyrus (IFG: cytoarchitectonic areas 44 and 45), the anterior insular cortex, the inferior parietal lobule (IPL: cytoarchitectonic areas IP1, OP1, PF and its sub-regions; Caspers et al., 2013) and the putamen (Fig. 7A–D). Among these regions, we have consistently observed activity in the IFG and IPL during kinesthetic illusions (Fig. 7A–D). These brain regions are significantly activated when participants experience illusions during tendon vibration, and are not activated in control conditions, where participants merely feel a skin vibration (Fig. 7E and F). Furthermore, we have observed activation in these regions regardless

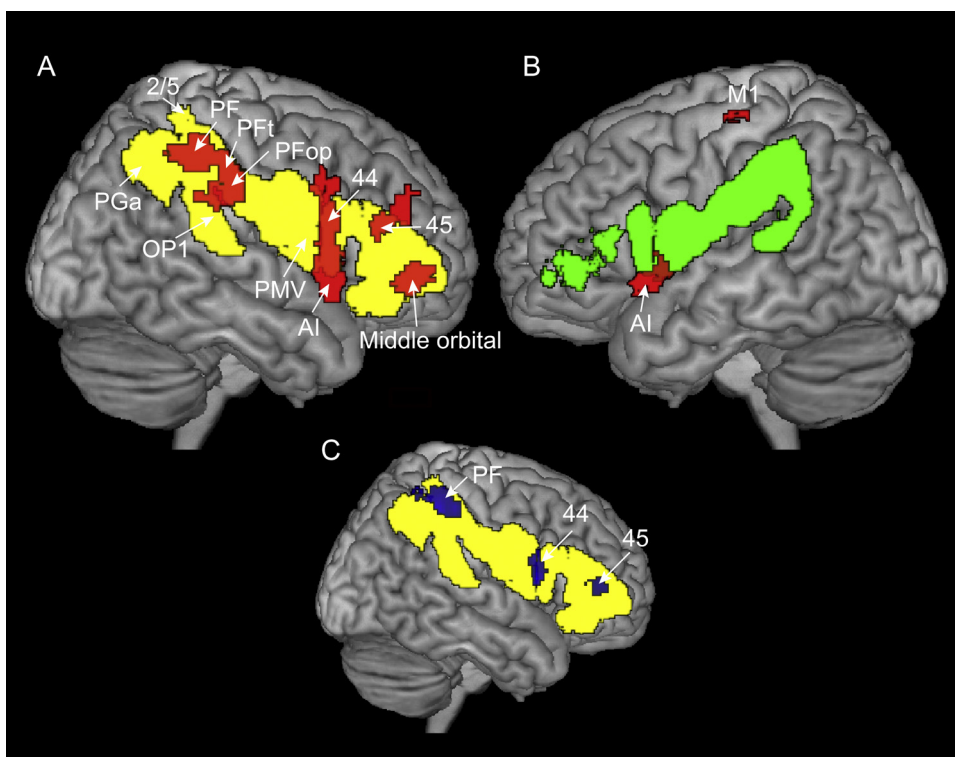


**Fig. 7.** Right inferior fronto-parietal cortices commonly active during illusory movements of all limbs (A–C) (see Fig. 3 for colors). Activation is commonly observed in the inferior parietal lobule (IPL; area PF), area 44, and the putamen (A–C). Activity in area 44 extending into the anterior insula is also observed in the left hemisphere (D), but right-side activity is often dominant. Modified from Naito et al. (2007). E, F: Activity in the right area 44 (E) and in the right IPL (F) significantly increases when people experience illusory movements, irrespective of whether the illusion takes place in the right or left hand, but not in the control condition wherein people merely feel a skin vibration.

Modified from Naito et al. (2005).

of whether participants experience illusory movement in the right or left hands or feet (Fig. 7A–D). Thus, somatotopical organization is less apparent in these regions. As these regions are always active during kinesthetic illusory hand movement, regardless of with or without vision, they are consistently involved all of the bodily illusions described in Section 4.

Importantly, as seen in Fig. 7A–D, activity in these regions is right-hemisphere dominant (Naito et al., 2007). Indeed, right-side dominance of IFG and IPL activity, when compared with the corresponding regions in the left hemisphere, has been repeatedly confirmed when participants experience kinesthetic illusion in the right hand (Naito et al., 2005; Amemiya and Naito, 2015). This evidence supports the fundamental importance of the right inferior



**Fig. 8.** (A) Right inferior fronto-parietal cortices active during illusory movement of the right hand (red sections) superimposed onto the brain regions connected by the SLF III (yellow sections). Brain activation (red) was obtained from Amemiya and Naito (2015) and the SLF III map (yellow) indicates connected cortical regions in over 50% of 47 participants (<http://sourceforge.net/projects/tractotron/files/>). Activity in the IFG (area 44) and IPL (area PF and its sub-regions) was consistently observed across our studies (Naito et al., 2005, 2007). In this particular experiment (Amemiya and Naito, 2015), participants were asked to remember the illusory wrist angle and replicate it after scanning. Robust activation in area 45 and the middle orbital gyrus emerged as a result of this extra cognitive demand. (B) Brain activation in the left hemisphere during illusory right hand (red) movement superimposed onto brain regions connected by the SLF III (green). The human SLF III appears to connect a broader range of fronto-parietal cortices, including the prefrontal cortices and higher-order somatosensory and visual association cortices, and the volume of the right SLF III (A) is greater than that of the left SLF III (B). (C) The right inferior fronto-parietal cortices (areas 44, 45 and PF; blue sections) connected by the SLF III (yellow sections) are commonly activated when people view their own faces (in comparison with the faces of others; self-identification) and when they experience illusory movement of the right hand with their eyes closed (corporeal awareness) (Morita et al., 2015).

fronto-parietal cortices in the formation of the human body representation (cf. Berlucchi and Aglioti, 1997; Daprati et al., 2010).

The right inferior fronto-parietal cortices active during a kinesthetic illusion is most likely connected by the inferior branch of the superior longitudinal fasciculus (SLF III; Thiebaut de Schotten et al., 2012; Fig. 8A). As shown in Fig. 8A, the human SLF III appears to connect the IPL and the IFG with the anterior parietal (higher-order somatic) cortices and the posterior parietal (visual association) cortices. Thus, the SLF III network is likely involved in multisensory (somatic and visual) information processing. Indeed, core brain regions bearing mirror neuron function in primates [i.e., the ventral premotor cortex (PMV), area 44, and the IPL] likely belong to the SLF III network. In addition, it is shown that some of brain regions in the human SLF III network, e.g. human PMV/area 44, play essential roles when people feel ownership for a rubber hand (Ehrsson et al., 2004) and for their experimentally manipulated hands (Gentile et al., 2013) through multisensory integration.

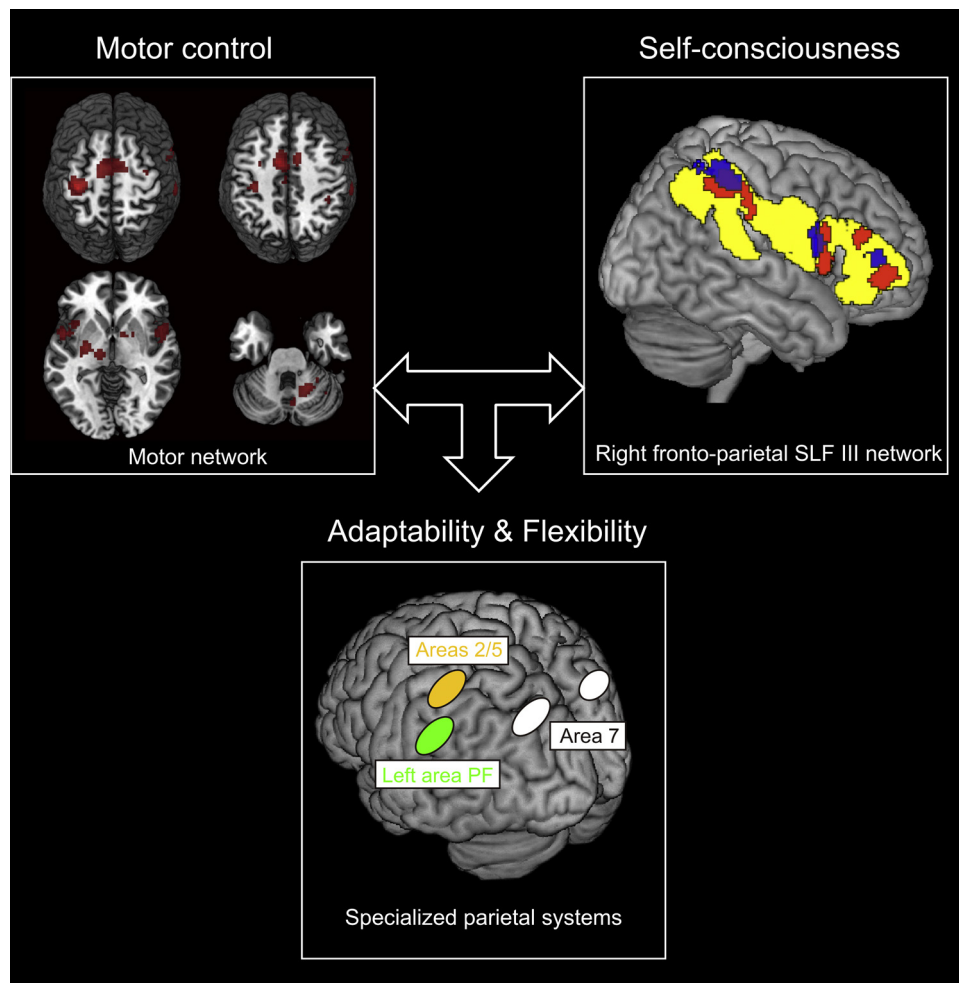
It is reported that the volume of the SLF III in the right hemisphere is significantly greater than that in the left hemisphere (Thiebaut de Schotten et al., 2011; see also Fig. 8A and B). This could be explained by several factors; for example, the right SLF III may contain a greater number of axons, axons with a thicker diameter, or richer myelinated axons. However, all of these possibilities imply rapid neuronal processing in the right SLF III. This is advantageous when the brain monitors the bodily information and updates the postural model of our body, which momentarily changes, by accumulating each new piece of sensory information. These series of neuronal processes may underlie the experience of

a kinesthetic illusion. Thus, the kinesthetic experience during an illusion (kinesthetic awareness) is likely supported by a large-scale brain network, which appears to be connected by the right SLF III.

#### 4.1. Roles of the right inferior frontoparietal cortices in the formation of the body representation

Although the SLF III network likely has multiple functions, here we discuss the possible roles of the right inferior frontoparietal cortices in the formation of the body representation. First, we argue that the right inferior frontoparietal cortices bear important roles more than attention. This view is corroborated by the following findings. First, these regions are active when people experience illusions, but not when people merely feel skin vibrations, which should also attract attention to the vibrated body parts. Second, the temporoparietal junction, which is a core member of the ventral attentional network (stimulus-driven attention: Corbetta and Shulman, 2002), does not appear to be activated either during tendon vibration or during skin vibration. Finally, recent resting-state connectivity analysis suggests the independence of the inferior fronto-parietal network most likely connected by SLF III from the ventral attentional network (Mantini et al., 2013). Instead of an attentional function, we propose *monitoring* function, especially for the right inferior frontal cortices. We suggest this possibility because right inferior frontal damage can disrupt self-monitoring function in humans, impairing the appropriate evaluation of the current status of the musculoskeletal system (Berti et al., 2005).





**Fig. 9.** Contribution of multiple brain systems (the motor network, specialized parietal systems, and the right inferior fronto-parietal SLF III network) in the formation of the human body representation.

In the non-human primate literature, cells in the inferior frontal and inferior parietal cortices are characterized according to whether they process body-centered or body-part-centered information (Graziano et al., 1997; Ishida et al., 2010). This is also the case for cells in the putamen (Graziano and Gross, 1993). These cells represent sensory stimuli in a coordinate system that is anchored to a particular body part, and thus can strongly contribute to multi-sensory (somatic and visual) integration associated with the body part and the adjacent space. In favor of this view, we have shown that the right inferior fronto-parietal cortices, in concert with the left cerebellar hemisphere (Lobule VI and Crus I; Kipping et al., 2013), engage in visuokinesthetic processing when participants are asked to identify the spatial location of their moving right hands by combining visual and kinesthetic information (Hagura et al., 2009). Given that the right inferior fronto-parietal cortices are also activated when individuals experience illusory limb movements with their eyes closed (Fig. 7A–C), it is conceivable that the right inferior fronto-parietal network may also function to build and update the postural model of the body. These actions likely occur in concert with the right putamen (Fig. 7B) and the left cerebellar hemisphere (Lobule VI and Crus I; see above). Indeed, damage to right SLF III fibers and also to the right putamen may cause a supernumerary phantom limb (third arm) experience (Halligan et al., 1993). This could be attributed to a miscalculation in the formation (*building-up and updating*) of the body representation, as mediated by the right SLF III network and its associated subcortical structures.

An important aspect of supernumerary phantom limb syndrome is that the patient feels the subjective reality of this “third arm” (i.e., a conscious experience of owning the arm). We assume that corporeal awareness, including kinesthetic illusory awareness, is an attribute of the neuronal activities in the right SLF III network that occurs while the brain constructs and updates the postural model of our body (cf. Kinsbourne, 2006). This claim is supported by several findings. First, we have recently shown that activity in the right inferior fronto-parietal (areas 45 and PF) cortices changes according to the amount of illusory right hand movement reported by blindfolded participants (Amemiya and Naito, 2015). This is in accordance with another recent finding that a certain amount of brain activity in the right fronto-parietal network is required to experience illusory foot movement (Cignetti et al., 2014). Second, high-intensity electrical stimulation of the human right IPL causes the illusory sensation of limb movement (Desmurget et al., 2009). This is direct evidence that right IPL activity is capable of eliciting corporeal awareness of limb movement.

#### 4.2. The right SLF III network, self-identification, and self-consciousness

In general, corporeal awareness allows us to conceive of ourselves as the source of incoming sensations and as an independent functional entity separate from other agents and the external world. Thus, we speculate that corporeal awareness could be a basis for self-identification and self-consciousness. As with the

dominance of the right-hemisphere in corporeal awareness (kinesthetic illusory awareness), the right hemisphere has also been implicated as playing a stronger role in self-face recognition (Devue and Brédart, 2011) and in the sense of the physical and emotional self (Devinsky, 2000).

This concept is upheld by our recent finding that the right inferior fronto-parietal cortices (areas 44, 45, and the PF), connected by SLF III, were commonly activated when participants viewed their own faces compared with the faces of others (self-identification) and when they experienced kinesthetic illusory movement of the right hand with their eyes closed (corporeal awareness; Fig. 8C; Morita et al., 2015). The importance of the right fronto-parietal cortices (ventrolateral prefrontal cortices and IPL) in self-other face discrimination has also been reported by previous studies (Uddin et al., 2005, 2006), and the right inferior fronto-parietal cortices have been found to be predominantly activated when participants visually discriminate their own faces and bodies from those of others (Sugiura et al., 2006). These lines of evidence seem to indicate that the right inferior fronto-parietal SLF III network may bear higher-order functions for self-identification and self-consciousness, presumably by extending the basic role that this region plays in corporeal awareness.

A recent resting-state connectivity analysis revealed human-specific fronto-parietal networks that represent our greatest evolutionary divergence from monkeys, as these regions do not have topological or functional correspondents in monkey brains (Mantini et al., 2013). These brain regions seem to include the intraparietal cortex, frontal operculum, and the middle frontal gyrus, all of which are likely core constituents of the SLF III network in the left and right hemispheres. Thus, we speculate that right inferior fronto-parietal SLF III activity in the human brain could subserve the human-specific conscious experience of the self.

In this paper, we could not cover the roles of much higher-order brain regions (e.g. insula; Craig, 2009; Tsakiris, 2010). However, the right ventrolateral prefrontal cortices seem to be involved in the processing of both physical and metaphysical concepts associated with the self, such as the evaluation of the appearance of one's own face (Morita et al., 2008), the discrimination of one's own voice (Nakamura et al., 2001), the appraisal of one's own personal traits (Ochsner et al., 2005) and the retrieval of autobiographical memories (Fink et al., 1996). Further studies are definitely needed to ascertain the roles of much higher-order brain regions.

#### 4.3. Brief summary

The right inferior fronto-parietal SLF III network might bear a series of functions including monitoring and accumulating the bodily information and updating the postural model of our body (body representation). It is likely able to perform these functions due to its high capacity for rapid multisensory processing of neuronal information represented in body-centered/body-parts-centered coordinate systems. To monitor the current status of the musculoskeletal system, the network most likely communicates with the motor network (e.g., through the frontal aslant tract; cf. Naito et al., 2005) that processes the fundamental elements of kinesthesia (e.g., which limb is moving toward which direction to what extent). The anatomical connection features of the SLF III network allow good access to specialized parietal systems, which can subserve the adaptability and flexibility of the body representation by transforming and integrating the information in different coordinate systems (see Section 3). Finally, we presume that corporeal awareness might emerge from the series of neuronal processes in the right SLF III network, which could underlie self-identification and self-consciousness.

## 5. Conclusions

We have described how the human brain represents the body representation using examples about a variety of kinesthetic illusions, such as those where people experience changes of limb position or body configuration. It appears that multiple brain systems, namely, the motor network, specialized parietal systems, and the right inferior fronto-parietal SLF III network, work together to form the body representation (Fig. 9). Thus, the series of our studies have elucidated more specified sets of brain systems than previously proposed (Melzack, 1990; Berlucchi and Aglioti, 1997; Daprati et al., 2010).

The direct involvement of the M1-centred motor network in the formation of the body representation indicates tight coupling between the body representation (body schema) and motor control. Activity in the motor control network is a strong gauge of the current status of the musculoskeletal system, enabling fast online feedback control. The involvement of specialized parietal systems demonstrates the importance of goal-directed 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 SLF III network might play essential roles in the monitoring of bodily states and the updating of body representation, which leads to corporeal awareness, probably one of the origins of self-consciousness.

In this review, we described the neuronal representation of the human body representation, which is highly adaptive, flexible and plastic. However, many questions remain about, for example, how a relatively constant self-body image is formed from this changeable body representation, and how mental and emotional self-consciousness develop with corporeal self-consciousness. Despite these questions, the present findings strongly indicate that the neuronal representation of the body representation is fundamental for motor control and corporeal awareness, which form the basis of human life.

## Acknowledgements

This work was supported by Scientific Research on Innovative Areas "Understanding brain plasticity on body representations to promote their adaptive functions" (JSPS KAKENHI No. 26120003), and partially supported by a Grant-in-Aid for Specially Promoted Research (No. 24000012). We would like to thank Dr Thiebaut de Schotten for providing the diffusion tensor imaging data. Finally, we appreciate invaluable comments from Dr. H. Henrik Ehrsson.

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