Sensing Limb Movements in the Motor Cortex: How Humans Sense Limb Movement

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We can precisely control only what we can sense. Sensing limb position or limb movement is essential when we precisely control our limb movements. It has been generally believed that somatic perception takes place in the neuronal network of somatosensory areas. Recent neuroimaging techniques (PET, fMRI, transcranial magnetic stimulation) have revealed in human brains that motor areas participate in somatic perception of limb movements during kinesthetic illusion in the absence of actual limb movement. In particular, the primary motor cortex, which is an executive locus of voluntary limb movements, is primarily responsible for kinesthetic perception of limb movements. This probably forms the most efficient circuits for voluntary limb movements between the controlled muscles and the motor areas. NEUROSCIENTIST (9)7:1–10 2004. DOI = 10.1177/1073858403259628

KEY WORDS *Motor cortex, Kinesthetic illusory limb movement, Somatic perception, Neuroimaging, Human*

Human beings are superbly moving animals. Sensing limb movements or limb position is essential when we precisely control our limb movements. Indeed, it is difficult for deafferented experimental animals or human patients lacking proprioceptive inputs to perform normal multijoint limb movements even though it is true that they can initiate limb movements (Bard and others 1995; Ghez and Sainburg 1995; Sainburg and others 1995). These evidences indicate that sensory afferent inputs conveying kinesthetic or proprioceptive information to the brain are important for the brain to archive precise and elaborate control of limb movements.

Furthermore, it also might be true that the kinesthetic feedback information during limb movements plays crucial roles when we acquire a motor skill. For example, healthy subjects can rotate two balls simultaneously on their palms (Kawashima and others 1998). When they try to rotate the balls as many times as possible within a restricted period (for 30 seconds) in one trial, the number of rotations significantly increases trial by trial. This skill improvement can be observed even in a situation in which subjects rotate the balls with their eyes closed. In this situation, because visual information of hand movements or ball movements is completely eliminated during the performance, kinesthetic information is the only available feedback information from the complex hand/finger movements. Thus, we may speculate that the kinesthetic feedback information updates motor programs so as to improve the motor performance trial by trial. The idea that kinesthetic information during limb movements plays crucial roles when we acquire a motor skill was supported by the fact that the deafferented patients showed a difficulty in acquiring new motor skills (Gordon and others 1995).

Sensory Afferents Signaling Limb Movements

The somatic sensation of limb movement is normally experienced when a limb is actually moved. This is because the sensory afferents from the muscle spindles, cutaneous receptors, and joint receptors increase their activities during passive and active limb movements (Vallbo 1974; Johansson and others 1982; Burke and others 1988; Edin and Vallbo 1988; Edin 1990, 1992; Edin and Abbs 1991; Edin and Johansson 1995), and the afferents convey the somatic information of limb movements to the brain. In particular, signals from the muscle spindles play very important roles in kinesthesia, the perception of limb movements (Burke and others 1976, 1988; Roll and Vedel 1982; Rogers and others 1985; Roll and others 1989; Edin and Vallbo 1990; Frederick and others 1990; Macefield and others 1990; Cordo and

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others 1995; Ribot-Ciscar and Roll 1998). It is shown that the frequency of action potentials in the Ia afferents from the muscle spindles increases during muscle lengthening, which tells the brain the direction and velocity of limb movement (Roll and Vedel 1982; Ribot-Ciscar and Roll 1998). Therefore, it is not the physical stretch of the muscles but rather the excitation of the afferents, which signals limb movements, that is most important for the brain to perceive limb movements.

Kinesthetic Illusory Limb Movements

When we vibrate the tendon of a limb at optimal frequencies (at around 80 Hz), subjects experience an illusion that the vibrated limb is moving even though the limb remains immobile (Goodwin and others 1972a, 1972b; Craske 1977; Roll and Vedel 1982; Roll and others 1989; Naito and others 1999; Naito and Ehrsson 2001; Naito and others 2002b, 2002c). Subjects experience that the vibrated muscles are being stretched. This kinesthetic illusion is elicited because the vibration of the tendon excites the muscle spindles in a similar manner to when the muscles are actually stretched (Burke and others 1976; Roll and Vedel 1982; Gandevia 1985; Roll and others 1989; Collins and Prochazka 1996) (Fig. 1). For example, when the tendon of the biceps (arm) muscles is vibrated, subjects feel that the arm is extending.

During kinesthetic illusions, the vibrated limbs are absolutely immobile. Therefore, the afferents from receptors signaling skin deformation or pressure to the joint tissues, which are normally excited when limbs actually move, should be silent during kinesthetic illusions. Thus, the afferent inputs from the muscle spindles are main contributors when the brain perceives the direction of illusory limb movements (Burke and others 1976; Roll and Vedel 1982; Gandevia 1985; Roll and others 1989; Collins and Prochazka 1996).

Interestingly, perception of limb movements or limb position does not seem to be restricted by the physical constraints of actual position of the limb. Craske (1977) clearly showed that subjects can experience impossible limb position that cannot be experienced in normal situations. For example, when a hand is passively and maximally flexed at the wrist joint and the wrist position is completely fixed at this maximum joint angle, subjects cannot perform further flexion of the wrist due to the physical constraint of the wrist angle. But even in this situation when the tendon of the wrist extensor muscles is vibrated (this ordinarily elicits illusory flexion movements of the wrist), the subjects can experience that the hand is further flexing beyond the physical constraint of maximum joint angles. This evidence clearly shows that 1) the brain perceives limb movements by receiving and processing the muscle spindle afferent inputs and 2) limb movements or limb position is flexibly represented in the brain in a sense that their brain representations are not restricted by the physical constraints of actual position of the limb**.**
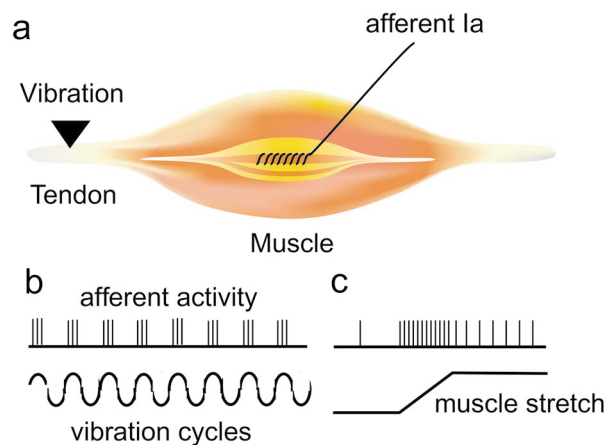

Fig. 1. Schematic diagrams of muscle spindle afferent activity. *a*, Vibration stimuli of the tendon of a muscle excite muscle spindle Ia afferent fibers. *b*, The muscle spindle afferents get excited in a cyclic manner that follows cycles of vibration stimuli when the tendon is vibrated at 80 Hz. The brain receives these afferent inputs aāÿnd illusions are elicited. c, The same muscle spindle afferents get excited when the muscle is being stretched even though the pattern of neural discharge is different from that during tendon vibration. Thus, during the tendon vibration, subjects experience an illusory limb movement that the vibrated muscles are being stretched.

Cortical Targets of the Afferent Inputs Signaling Limb Movements

It has been shown in animal (monkey) experiments that the primary somatosensory cortex (SI) is one of the cortical targets of the afferent inputs signaling limb movements. Neurons in the cytoarchitectonic area 3a (Phillips and others 1971; Schwarz and others 1973; Hore and others 1976; Iwamura and others 1983; Huerta and Pons 1990) and area 2 (Mountcastle and Powell 1959; Burchfiel and Duffy 1972; Schwarz and others 1973; Costanzo and Gardner 1981; Gardner and Costanzo 1981; Jennings and others 1983; Iwamura and others 1993, 1994) in nonhuman primates respond to passive or active limb movements by receiving the afferent inputs.

On the other hand, there is also electrophysiological evidence that neurons in the primary motor cortex (M1) respond to passive limb movements (Rosén and Asanuma 1972; Hore and others 1976; Lemon and others 1976; Lemon and Porter 1976; Wong and others 1978; Lemon and Van Der Burg 1979; Asanuma and others 1980; Fetz and others 1980; Lemon 1981a, 1981b; Strick and Preston 1982; Brinkman and others 1985; Colebatch and others 1990; Huerta and Pons 1990; Porter and Lemon 1993). Notably, Colebatch and others (1990) clearly demonstrated that the cells active during passive stretch of the wrist extensor muscles show tonic activity during tendon vibration of the muscles. This directly suggests that M1 cells respond to the muscle spindle afferent inputs during tendon vibration and that the activity in M1 may participate in perception of the vibrated muscles being stretched. However, even though

there are evidences that some M1 cells directly receive the afferent inputs from the thalamic nuclei (Lemon and Van Der Burg 1979), it is still uncertain what proportion of M1 cells receives the muscle spindle afferent inputs directly from the thalamic nuclei but not from the somatosensory cortex (area 3a).

Similarly, cells in the other cortical motor areas—premotor cortex (PM) (Fetz and others 1980), supplementary motor area (SMA), and the cingulate motor area (CMA) (Cadoret and Smith 1995)—also react to passive limb movements. If we remind ourselves that the cytoarchitectonic areas 3a and 2 in nonhuman primates are functionally strongly connected with M1, PM, SMA, and CMA (Ghosh and others 1987; Stepniewska and others 1993), we may expect that these cortical regions in humans would receive and process the afferent inputs signaling limb movements.

Functional Input-Output Relations in M1 Cells

M1 cells that respond to passive limb movement also react during active movement of the limb (Murphy and others 1978; Fetz and others 1980; Cheney and Fetz 1984; Colebatch and others 1990). Fetz and others (1980) clearly demonstrated that M1 cells, which respond to a passive movement of a wrist toward a particular direction (preferred direction), are also excited 1) during active movement toward the same direction with that of the passive movement, 2) during active movement toward the opposite direction, or 3) in both directions. The number of cells in these three groups was almost equal. Similarly, cortico-motoneuronal cells in M1 that are active during wrist movement toward a particular direction also respond 1) to passive movement toward the same direction, 2) to the opposite direction, or 3) to both directions (Cheney and Fetz 1984).

From these studies, it can be said that M1 cells that fired during active limb movements are associated with motor outputs (generation of muscle activities) (Fetz and others 1980; Cheney and Fetz 1984) and that cells active during passive limb movements are related to sensory inputs—the stretch of muscles (Colebatch and others 1990), skin deformation, and change of joint angle.

In the case that the preferred directions in an M1 cell are congruent between during active limb movements (motor outputs) and during passive limb movements (sensory inputs), it means that the activities of this cell related to muscle contraction are facilitated by the sensory afferent inputs during active limb movements. This seems to be an efficient motor circuit between M1 cells and its controlling limbs during active limb movements. In the case that the preferred directions in an M1 cell are opposite (active and passive incongruent), this means that the activities of the cell related to motor outputs are not facilitated by the sensory afferent inputs during active limb movements. These evidences suggest that the brain creates multiple motor circuits that functionally link between cells in M1 and its controlling limbs.

Brain Areas Active during Illusory Limb Movements

As described above, vibrating the tendon of a limb excites the muscle spindle afferents of the vibrated muscles and elicits an illusory limb movement. If we measure the brain activity while totally relaxed subjects experience illusory limb movements, we may detect brain areas that receive and process the kinesthetic afferent inputs. By taking advantage of kinesthetic illusions, one may depict brain areas that are related to human kinesthesia with neither overt limb movements nor intention of limb movements. Because there are no overt limb movements during illusions, cutaneous receptors that are normally excited by skin deformation during passive limb movements and joint receptors that are also recruited by joint angle displacement during passive limb movements must be silent during kinesthetic illusions.

One technical consideration is how to dissociate the brain activity related to the sensory processing of the kinesthetic afferent information from the activity related to the processing of vibration stimuli over the skin per se. In our series of neuroimaging experiments (Naito and others 1999, 2002b, 2002c; Naito and Ehrsson 2001), we adopted two approaches. 1) It has been demonstrated that vibrating the tendon at around 10 Hz or at more than 220 Hz does not elicit reliable and vivid illusions if any (Roll and Vedel 1982; see Fig. 1 in Naito and others 1999). If we directly compare brain activity when the tendon is vibrated at 80 Hz and subjects experience illusions with the activity when the identical skin surface over the tendon is vibrated at 10 Hz or 220 Hz and subjects experience no illusions, we may identify brain areas that are related to the sensory processing of the kinesthetic afferent inputs. 2) We found that vibrating the skin surface over the nearby bone to the tendon (e.g., the styloid process of ulna that is located 3–4 cm apart from the skin surface over the tendon of the wrist extensor muscles) at 80 Hz does not elicit strong sensations of illusory limb movements. If we directly compare brain activity when the tendon is vibrated at 80 Hz (subjects experience illusions) with the activity when the skin surface over the nearby bone is vibrated at the identical frequency (subjects experience no illusions), we may also detect brain areas that are related to kinesthesia.

First, Naito and others (1999) depicted brain areas active by PET when blindfolded subjects experienced illusory extension movements of their left arms that were elicited by the tendon vibration (80 Hz) of the biceps muscles. We found that the contralateral motor areas, that is, M1, dorsal premotor cortex (PMD), SMA, CMA, and the SI (most probably cytoarchitectonic area 1), are significantly active during illusory arm movements when compared with control conditions in which we vibrated the identical site at two different frequencies (10 Hz or 240 Hz), which does not elicit any illusion (see Fig. 1, 3 in Naito and others 1999). These results are in agreement with the findings that the contralateral SI/M1 was activated during passive limb movements (Weiller

and others 1996; Mima and others 1999) and that electrical stimulation in human SMA/CMA elicits the sensation of limb movements (Fried and others 1991; Lim and others 1994).

The activities in these motor areas are probably associated with neuronal processing of kinesthetic illusions because the main effect of skin vibration was to activate the contralateral SI and bilateral parietal operculums. None of these motor areas were significantly activated during skin vibration with no illusions.

The most interesting finding in this study was that the strongest activity during illusory arm movement was located in the contralateral M1 (cytoarchitectonic area 4) (Geyer and others 1996), even in situations in which 1) the subjects did not intend to move their arms, 2) the vibrated arm was not actually moving, and 3) there were no electromyogram activities from the triceps muscles that are agonist muscles for the illusory movements.

We further tested by PET if the contralateral motor areas active during kinesthetic illusory limb movements are also activated during actual limb movements (Naito and Ehrsson 2001). In this experiment, blindfolded subjects experienced illusory flexion movements of the right wrist when we vibrated the tendon of the wrist extensor muscles at 83 Hz. As a control condition in which no illusions are elicited, we vibrated the different skin surface over the styloid process of ulna (3–4 cm apart from the skin surface over the tendon) at the identical frequency. First, we depicted areas active during illusory wrist movements. Second, we compared locations of the activations during illusions with locations of activations during alternating flexion/extension movements of their wrists that were performed by an independent group of blindfolded subjects (Ehrsson and others 2000). The illusory wrist movements activated subregions in the contralateral M1, SI, and SMA/CMA that were also active during actual wrist movements. Again, the peak activity during illusions was located in the precentral gyrus (cytoarchitectonic area 4: M1). This result clearly showed that illusory limb movements activate motor areas that are normally engaged in the execution and control of limb movements.

These cortical motor areas were consistently active when we identified brain activity related to kinesthetic illusions, no matter when we used two different control conditions: vibrating the tendon at nonoptimal frequency or vibrating the skin surface over the nearby bone at the optimal frequency. The peak of the activations during kinesthetic illusory movements of left arm or right wrist was located in the contralateral M1 with no intention of limb movements, with no actual limb movements, and with no significant surface electromyogram activity from the agonist muscles to the illusory movements.

Kinesthetic Illusions Activate Somatotopical Section of M1

Naito and Ehrsson (2001) showed that motor areas active during illusory wrist movements are also activated during actual wrist movements. This result suggests that illusory limb movements activate somatotopical sections of motor areas. We address this question by using fMRI (unpublished observation) to increase the sensitivity to detect brain signals. In this study, we vibrated the tendon of the wrist extensor muscles of right or left hand so as for 13 blindfolded subjects to experience illusory flexion movements, and as a control we vibrated the skin surface over the nearby bone. In other conditions, we vibrated the tendon of the anterior tibialis of right or left foot so as to elicit illusory palmar flexion of the foot, and as a control we vibrated the skin surface over the nearby bone (the lateral malleolus).

We found that the somatotopical sections in the contralateral M1 were significantly and consistently activated across all subjects, no matter when the subjects experienced illusions of right wrist, left wrist, right foot, or left foot (Fig. 2a, c, e, f). In this study, we also found the contralateral activity that was clearly located at the fundus of the central sulcus (most probably cytoarchitectonic area 3a) when subjects experienced illusory movements of right or left wrist (see Fig. 2b, d).

This fMRI result, together with the results from the two previous PET studies, clearly showed that the neuronal activities in the somatotopical sections in the contralateral M1 are robust during illusory limb movements. Because the illusions are elicited in the brain that receives and processes the muscle spindle afferent inputs, the activity in the somatotopical sections in the contralateral M1 may reflect sensory processing of the kinesthetic afferent inputs.

Receiving Afferent Inputs and Perceiving Sensory Events

Human subjects can sense a sensory component that is not physically present in the provided stimuli. When we experience a color, it is not always necessary for the brain to receive color compositions (wavelength compositions of the light) that normally elicit color perception. We can vividly experience a color even while we are simply viewing achromatic visual stimuli after visual training (a color aftereffect, i.e., McCollough effect) (McCollough 1965). Similarly, we can experience visual motions (visual motion aftereffect) even when we are viewing absolutely static visual images (Zeki and others 1993; Tootell and others 1995).

Even though these two visual experiences are elicited as aftereffects that are induced by previously presented visual stimuli, these psychophysical experiences suggest that sensory information (e.g., a static visual image) can elicit a sensory experience (e.g., motion perception) that is not elicited by the nature of the provided information (e.g., a static visual image). This means that receiving sensory inputs is not entirely equal to experiencing sensory events (= perception). Thus, perception may occur after the brain computes sensory inputs and may reflect how the brain interprets the currently provided sensory information.

Most important, the brain areas (V4 for color perception and MT for visual motion perception) that normal-
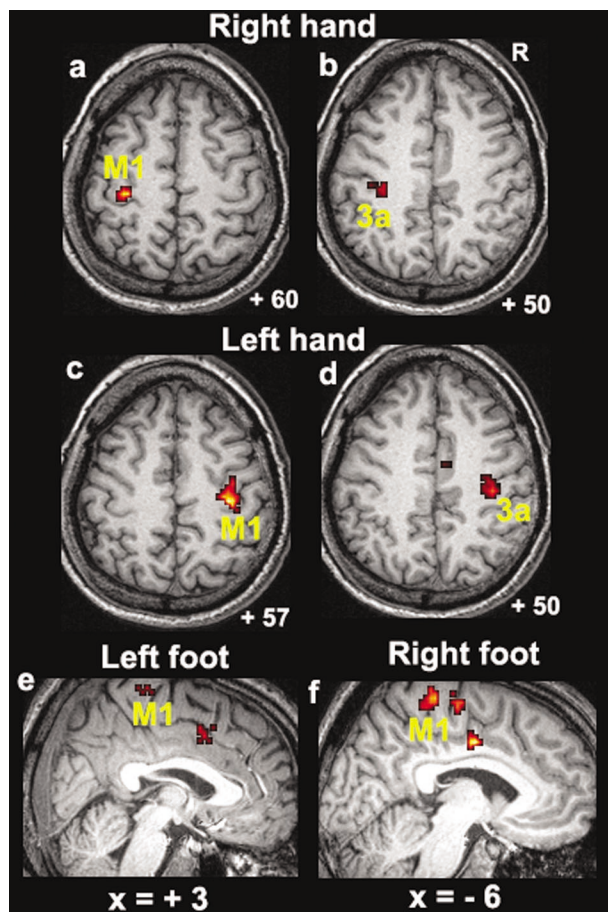
Fig. 2. Illusions of right wrist, left wrist, right foot, or left foot consistently engage corresponding somatotopical sections of the primary motor cortex (M1). The somatotopical sections in the contralateral M1 were consistently activated across all 13 subjects, no matter when the subjects experienced illusions of right wrist, left wrist, right foot, or left foot (a, c, e, f). The fundus of the central sulcus (most probably cytoarchitectonic area 3a) was also activated when subjects experienced illusory movements of right or left wrist (b, d). The right hemisphere is shown to right.

ly participate in the processing of the visual compositions that directly elicit corresponding perceptions are also activated even when the subjects experience those visual aftereffects (Tootell and others 1995; Barnes and others 1999). These observations suggest that perception may take place in the brain areas that are crucially responsible for neuronal processing of sensory inputs. If this idea is true, because our PET and fMRI data suggest that M1 is primarily responsible for the processing of kinesthetic afferent inputs, we may expect that M1 would be activated when we experience our limbs are moving even in a situation in which the muscle spindle afferent information does not directly reach the contralateral M1.

Kinesthetic Illusions of Nonvibrated Limbs

When the tendon of the right biceps muscle is vibrated at the same time as a subject holds her nose between the

right thumb and index finger, she feels the nose becoming increasingly elongated (Lackner 1988; Lackner and Taublieb 1983). In this case, the brain receives the sensory information about the skin contact between the hand and the nose and gets the information from the muscle spindles that the arm is stretching. The brain interprets these multiple sensory inputs as the nose becoming increasingly longer. We experimentally modified this illusion that is transferred from the vibrated limb (which is subject to illusory movements) to nonvibrated body parts.

We vibrated the tendon of wrist extensor muscles of either the right or the left hand while both hands passively had mutual skin contact palm to palm (Fig. 3b). In this situation, the illusions seem to transfer from the vibrated hand to the nonvibrated hand, and the blindfolded subjects feel that the nonvibrated hand is also moving in the same direction as the vibrated hand. For example, when the right extensor tendon is vibrated, all subjects feel both hands bending leftward as if the illusion of the right hand bending is transferred to the left hand ("transferred kinesthetic illusion") (Fig. 3b). Usually, it takes several seconds for the subjects to experience the transfer of illusions from the onset of vibration stimuli. The skin inputs from the palms, verifying the contact between the hands, and the muscle spindle afferents informing that the hand is flexing at the wrist are interpreted by the brain as both hands being bent in the direction of the vibrated hand.

If the neuronal activity in M1 is involved in kinesthetic perception, M1 that is contralateral to the nonvibrated hand must be activated when subjects experience the nonvibrated hand is moving even in a situation in which M1 does not directly receive the muscle spindle afferent inputs.

Psychophysical Features of Transfer of Illusions

The illusory experiences on the nonvibrated hand are not as strong as those in the vibrated hand. The velocity or maximum angle of the illusory movements of the nonvibrated hand is approximately half of that of the vibrated hand. And the illusory experiences of the vibrated hand and those of the nonvibrated hand are well correlated (r = 0.73) (see Fig. 4 in Naito and others 2002c). This means that there is a tight relationship between the illusory movement of the vibrated hand and the transferred illusory movement. This also indicates that the transfer of illusion is a passive sensory process that is somehow regulated by the amount of illusion of the vibrated hand. This is indeed true because some subjects, who feel relatively weak illusory movements in the vibrated hand, are not able to experience vivid transfer of illusions.

Brain Areas Active during Transfer of Illusion

We measured the brain activity with fMRI to test whether activation of the M1 controlling the nonvibrated hand is necessary to experience the transfer of kines-

thetic illusions. First, we depicted brain areas active when hands were separated and subjects only experienced kinesthetic illusory flexion of the vibrated hand (Fig. 3a). Second, we identified brain areas active when hands were in contact and subjects experienced movement of both the vibrated and the nonvibrated hand (Fig. 3b). The control condition was vibrating the skin surface over the nearby bone. We vibrated the tendon of the wrist extensor muscles of the right or left hand.

When the hands were separated and the tendon on the right muscle was vibrated, the left M1 was activated when compared with a control of vibrating the nearby bone, and all subjects felt the unilateral illusion of a flexion of the right wrist (Fig. 3c). Similarly, when the tendon on the left muscle was vibrated, the right M1 was activated, and all subjects felt the illusion of a flexion of the left wrist (Fig. 3f). During unilateral illusions, M1 that is ipsilateral to the vibrated hand was not activated (Fig. 3c, f).

In contrast, when the hands were in contact and the illusion of the vibrated right hand transferred to the nonvibrated left hand, not only the left M1 but also the right M1 were significantly activated (Fig. 3d). Similarly, when the illusion of the vibrated left hand transferred to the nonvibrated right hand, not only the right M1 but also the left M1 were significantly activated (Fig. 3g). During transfer of illusions, M1 that is ipsilateral to the vibrated hand was activated.

When we directly compared activations during transfer of illusions with those during unilateral illusions, the ipsilateral M1 to the vibrated hand equal to the contralateral M1 to the nonvibrated hand (most probably cytoarchitectonic areas 4a and 4p) (see Fig. 2 in Naito and others 2002c) was exclusively activated when the hands were in contact, and the subjects experienced that the nonvibrated hand was moving (Fig. 3e, h). The ipsilateral M1 activations were the only consistent activations no matter whether the illusions transferred from right hand to left hand or from left hand to right hand.

More important, the M1 activations related to the illusions of nonvibrated hands were located in the same wrist sections of the M1 (Ehrsson and others 2000). And the illusions of the nonvibrated hand activated a quite similar section of M1 that was activated when the nonvibrated hand was actually vibrated (see Fig. 2 in Naito and others 2002c). This strongly suggests that kinesthetic perception may take place in the sections of M1 that receive and process the muscle spindle afferent inputs. This supports the general idea that the brain areas that are responsible for the processing of the sensory afferent inputs are also primarily involved in perceptual experiences.

Neuronal Excitability in M1 during Illusory Movements of the Nonvibrated Hand

The increase in the BOLD signal in the M1 when the subjects experienced the illusions of the nonvibrated hand indicates that the neuronal excitability representing the nonvibrated hand movements increased (Logothetis
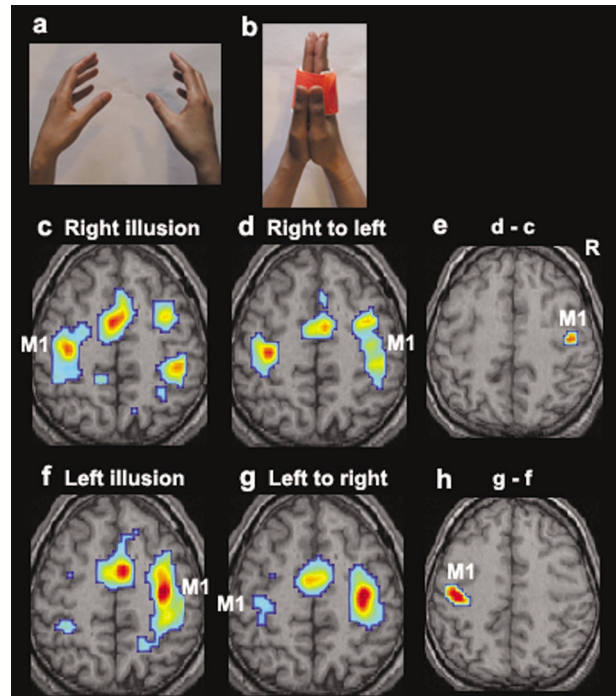

Fig. 3. Activations during transfer of illusion. a, When the hands were separated and the tendon on the right or the left wrist extensor muscles was vibrated, this only elicits illusory flexion movements of the vibrated hand. b, When the hands were in contact and the tendon on the right or the left wrist extensor muscles was vibrated: When the right extensor tendon is vibrated, subjects feel both hands bending leftward as if the illusion of the right hand bending is transferred to the left hand. When the left tendon is vibrated, subjects feel both hands bending rightward. c, The left primary motor cortex (M1) as well as bilateral supplementary motor area, right areas 2 and 8, were activated when subjects felt the unilateral illusion of a flexion of the right wrist. d, Not only the left M1 but also the right M1 were activated when the hands were in contact, and the illusion of the vibrated right hand transferred to the nonvibrated left hand. e, The right M1 was only activated when we directly compared the activations during transfer (right wrist to left wrist) of illusions with activations during unilateral illusions of right wrist. f, The right M1 was activated when subjects felt the unilateral illusion of left wrist. g, Not only the right M1 but also the left M1 were activated when the illusions transferred from the vibrated left hand to the nonvibrated right hand. h, The left M1 was only activated when we directly compared the activations during transfer (left wrist to right wrist) of illusions with activations during unilateral illusions of left wrist.

and others 2001). We further investigated the neuronal excitability in M1 by transcranial magnetic stimulation (TMS) during the transfer of illusions. Single-pulse TMS (0.67 T at maximum) was delivered to the M1 that is contralateral to the nonvibrated hand when the subjects experienced illusory movements of the nonvibrated hand. The motor evoked potential (MEP), which is evoked on the target muscles (wrist flexor muscles) of the nonvibrated hand, was recorded as an index to evaluate neuronal excitability in M1 (Rossini and others 1994).

In this experiment, we again vibrated the tendon of the wrist extensor muscles of the right or left hand. This

time, we changed the hand positions (the vibrated hand was placed on the dorsal surface of the nonvibrated hand) to verify that illusions transfer even in this different hand position (Fig. 4a). In this hand position, as we expected, illusory flexion movements of the vibrated hand transferred to the nonvibrated hand so as to elicit illusory flexion of the nonvibrated hand. When the hands were separated, illusions never transferred.

By TMS stimulating the motor cortex contralateral to the nonvibrated hand during illusory flexion of the nonvibrated hand (transfer of illusion), we found a strong facilitation of the MEPs in the muscle flexing of the wrist of the nonvibrated hand in the same direction as the illusory flexion of the vibrated hand when compared with control conditions (Fig. 4b and c; see "Methods" in Naito and others 2002c). The MEP was never enhanced when the hands were separated (s; Fig. 4a) and the motor cortex contralateral to the nonvibrated hand was TMS stimulated. These results show that the M1 excitability for the wrist flexor muscles was enhanced during illusions of the nonvibrated hand.

When hands were in contact (c; Fig. 4a) and the tendon of one hand was vibrated, it is true that vibration stimuli transmit from the vibrated hand to the nonvibrated hand. Therefore, one may speculate that the spread of the vibration to the nonvibrated hand may activate the contralateral M1 and increase the neuronal excitability. If this is the case, vibrating the skin surface over the nearby bone could also increase the neuronal excitability in M1. But this was not the case.

As described above, it takes several seconds for the subjects to experience the transfer of illusions from the onset of vibration stimuli. In view of this, we provided TMS to the motor cortex at two different vibration periods: One is before the illusions transferred after tendon vibration initiated, and the other is after the illusions transferred. If the increase of the neuronal excitability in M1 is confined to the period when subjects experience illusory movements of the nonvibrated hand, the neuronal excitability should only increase in the latter period. This was indeed so. The MEP of the flexor muscles was facilitated with concomitant reduction of MEP of the extensor muscles only after the illusion transferred (Fig. 4d; see also Figure 6A and B in Naito and others 2002c). These results clearly demonstrated that the MEP changes were specifically confined to the period when the subjects experienced that the nonvibrated hand was moving (transfer of illusions). Thus, one may speculate that the neuronal excitability in M1 that is contralateral to the nonvibrated hand during transfer of illusions would reflect the neuronal processes for kinesthetic perception.

We finally addressed the question that if the neuronal excitability in M1 reflects kinesthetic perception, the amplitude of neuronal excitability might be correlated with the amplitude of illusory experiences. The MEP amplitudes from the nonvibrated flexor muscles were well correlated with the experienced angles of illusory movement of the nonvibrated hand (r = 0.52, P < 0.05)
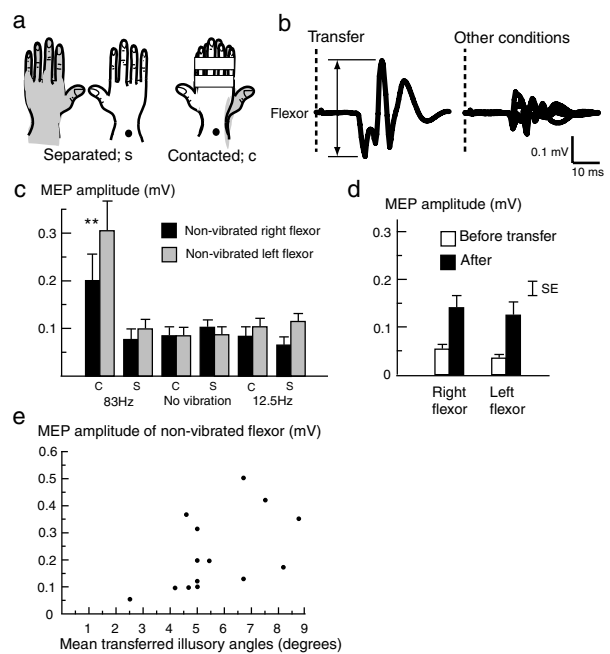

Fig. 4. Results from transcranial magnetic stimulation experiment. a, Hand position. In the hand contact condition, the vibrated hand was placed on the dorsal surface of the nonvibrated hand. b, The motor evoked potentials (MEPs) in the nonvibrated flexor muscles were strongly facilitated during transfer of illusions when compared with other control conditions (see details in "Methods" in Naito and others 2002c). (?) indicates amplitude of MEP. c, MEP amplitude in the nonvibrated flexor muscles was significantly greater during transfer of illusions when compared with other five control conditions, no matter when the illusions transferred from right hand to left hand (gray bars) or from left hand to right hand (black bars). d, The MEP of the flexor muscles of the nonvibrated right or left hand was only facilitated after the illusion transferred (black bars) but not before (white bars) the tendon vibration started. e, The MEP amplitudes from the nonvibrated flexor muscles were well correlated with the experienced angles of illusory movement of the nonvibrated hand (r = 0.52, P < 0.05).

(Fig. 4e). This means that the amplitudes of neuronal excitability in M1 are well correlated with amplitudes of illusory experiences of the nonvibrated hand, strongly suggesting that the neuronal activity in M1 reflects kinesthetic perception per se, even in a situation that M1 does not receive the afferent information from the muscle spindles.

These observations, together with the fMRI results, clearly show that the neuronal excitability in the somatotopical sections of M1 may reflect somatic perception of limb movements.

M1 Activity That Reflects Perceptual Changes of One's Own Limb Movements

Our fMRI and TMS results suggest that the neuronal activity in M1 reflects somatic perception of one's own limb movements. We further tested this by using another experimental approach (Naito and others 2002a).

Visual information of limb position or limb movements gives perceptual influences to kinesthetic experience of limb movements. Lackner and Taublieb (1984) showed that visual information of a "static" arm position perceptually attenuates the kinesthetic experiences of illusory arm movements. In this situation, the brain receives somatic inputs signaling that the arm is moving, and simultaneously it receives visual inputs telling that the arm is not moving. This may cause sensory conflicts in the brain. The brain has to compute the mismatched information that is simultaneously provided by two independent sensory systems and interprets as attenuation of kinesthetic experience of arm movements.

Building on this, we might expect that kinesthetic illusory experience of wrist flexion would be perceptually attenuated when subjects simultaneously view their own hands that are extending (toward incongruent direction) when compared with a situation in which they are viewing their hands flexing (toward congruent direction). If the activity in M1 reflects the perception of one's own limb movements, its activity would be affected by the visual information of hand movements in a way that the activity reflects these perceptual changes.

We vibrated the tendon of the right wrist extensor muscles at 83 Hz, which elicits illusory palmar flexion when the eyes are closed (Naito and Ehrsson 2001). Visual motions of the subject's own wrist movements (palmar flexion: $0.9 \pm 0.2°/\text{sec}$ or dorsiflexion: $0.7 \pm 0.2°/\text{sec}$) were video recorded in advance and passively provided through a face-mounted display during experiment. When the 17 subjects experienced illusory palmar flexion while 1) they closed their eyes, or 2) they were passively viewing their wrists flexing (congruent), or 3) they were extending (incongruent), we measured regional cerebral blood flow by PET (Fig. 5a).

When the directions of the movement sensed by kinesthesia and by vision were incongruent, the amount of illusory experiences significantly decreased when compared with the congruent condition (Fig. 5b). The neuronal activity in the contralateral M1 was affected by the visual information of one's own hand movements so as to reflect the perceptual changes (Fig. 5c), even though the wrist tendon was vibrated by the identical stimuli (= M1 receives same amount of the kinesthetic afferent inputs). This result also supported the idea that the neuronal activity in M1 reflects somatic perception of one's own limb movements.

Conclusions

All mammals have motor cortices. The motor cortex (M1) has been regarded as the executive locus of voluntary limb movements. Even though electrophysiological animal studies have shown that M1 neurons react to sensory stimuli, the functional roles of these M1 neurons only have been attributed to sensory guidance of voluntary movements or generation of transcortical reflexive movements.

However, recently our neuroimaging studies (PET, fMRI, TMS) have clearly demonstrated that somatic per-
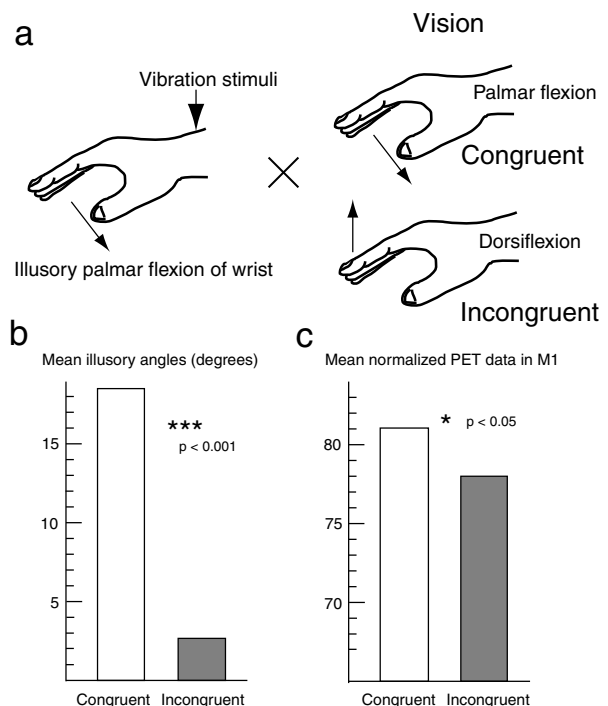

Fig. 5. Kinesthetic experiences and primary motor cortex (M1) activity during illusions are affected visual information of one's own limb movements. a, Tasks. Subjects experienced illusory palmar flexion of the right hand simultaneously while they were passively viewing their video-recorded wrists flexing (congruent) or extending (incongruent). We measured regional cerebral blood flow by PET during these tasks. b, When the directions of the movement sensed by kinesthesia and by vision were incongruent (dark bar), the amount of illusory flexion angles significantly decreased when compared with the congruent condition (white bar). c, The neuronal activity (mean normalized PET data) in the contralateral (left) M1 (–36, –18, 56) was significantly more attenuated in the incongruent condition (dark bar) than in the congruent condition (white bar). This behavior of M1 activity reflects the perceptual changes shown *in* b.

ception of limb movements engages the human motor cortex (cytoarchitectonic area 4) with neither overt limb movements nor intention of movements.

Vibrating the tendon of a limb at an optimal frequency elicits illusory sensation of limb movements by exciting muscle spindle afferents, despite the limb remaining absolutely immobile. Our PET and fMRI studies consistently showed that the illusory limb movements engage the contralateral motor areas (M1, SI, PMD, SMA, CMA), especially the somatotopical section of M1 (which normally participates in the control of actual movements of a limb) that is primarily activated during illusory limb movements. This means that M1 has sensory functions in a sense that its neurons receive and process sensory afferent inputs from the muscle spindles without generating any actual movements.

Furthermore, the activity in M1 is necessary when subjects perceive their limb movements even in a situation in which M1 does not receive the kinesthetic afferent inputs during transfer of illusions. The amplitude of

neuronal excitability in M1 correlates well with the amplitude of kinesthetic perception. This result is also supported by the finding that the M1 activity reflects the perceptual changes of kinesthetic illusion that are affected by the visual information of one's own limb movements. These observations show that M1 has a perceptual function for one's own limb movements that seems to be independent from the sensory afferent processing.

These neuroimaging experiments reveal hidden sensory and perceptual functions in the human motor cortex and demonstrate clear contrasts to its traditional role as the executive locus of voluntary limb movements. These studies raise the possibility that the motor cortex could be a part of a network whose neurons update and represent limb configuration. These neuronal activities may partly form a neuronal representation of one's "body schema" in the brain.

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