Pergamon

www.neuroscience-ibro.com

PII: S0306-4522(01)00495-X

Neuroscience Vol. 109, No. 4, pp. 701–707, 2002

0306-4522/02 $22.00+0.00

PERCEPTUAL CHANGES IN ILLUSORY WRIST FLEXION ANGLES RESULTING FROM MOTOR IMAGERY OF THE SAME WRIST MOVEMENTS

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Abstract—Recent neuroimaging studies have suggested that similar cortical motor areas are recruited both by kinesthetic sensations elicited by tendon vibration and by voluntarily imaging one's own movements of the same joints. Little is known, however, as to whether kinesthetic motor imagery interacts with kinesthetic illusion. We examined such interaction by behavioral analysis in which 19 subjects imagined wrist flexion or extension, with or without illusory flexion induced by tendon vibration. Electromyograms were also recorded to monitor the peripheral modulations caused by the interaction.

The kinesthetic motor imagery had a psychophysical effect on kinesthetic illusion in the absence of overt movement. It was confirmed that the subjects could imagine wrist movements without facilitating muscle activities in the absence of vibration stimuli. The electromyogram activity of the vibrated extensor muscles was significantly higher than that of non-vibrated flexor muscles. Motor imagery of wrist extension, when illusory flexion was experienced, reduced the angle of illusory flexion while enhancing extensor muscle activities in comparison with the control. On the other hand, flexion motor imagery increased the angle of illusory flexion with or without enhancement of flexor muscle activities.

Our results indicate that motor imagery interacts with kinesthetic illusion with or without enhancement of activities of the related muscles. This suggests (1) that common neural substrates shared by imagery and by illusion exist and (2) that different physiological mechanisms contribute to the enhancement of muscle activities of vibrated muscles and their antagonists.

Key words: kinesthetic illusion, tonic vibration reflex, antagonist vibratory response, electromyograms.

Vibration stimuli applied to a tendon at around 80 Hz elicit a kinesthetic illusion (Goodwin et al., 1972; Roll and Vedel, 1982; Naito et al., 1999). Subjects ordinarily experience illusory movements towards the direction in which the vibrated muscle would be stretched (Roll and Vedel, 1982; Roll et al., 1989). The vibratory stimuli activate muscle spindles and tendon afferents, of which group Ia (GIa) afferents play the most important role in the kinesthetic illusion (Burke et al., 1976a,b; Roll et al., 1989).

Motor imagery, a mental rehearsal of body movements without overt movement, has two kinds of mental representations of motor acts: a kinesthetic motor imagery in which subjects feel themselves executing movements, and a visual motor imagery which is rather a third-person process (Mahoney and Avener, 1987; Jeannerod, 1994). During the kinesthetic motor imagery, subjects voluntarily imagine limb movements without making any actual movement or receiving any peripheral stimulus. While the kinesthetic illusion is a bottom-up information process in human sensory-motor systems, kinesthetic motor imagery can be classified as a top-down information process. These two streams of information flowing from opposite directions may merge somewhere within the CNS. Recent neuroimaging studies of motor imagery support this idea, suggesting that mental rehearsal may share similar motor-related cortical and cerebellar areas with those affected by kinesthetic illusion (Roland et al., 1980; Stephan et al., 1995; Porro et al., 1996; Naito et al., 1999). However, no objective quantification has been performed for motor imagery under kinesthetic illusion.

In this paper, we tested the hypothesis that motor imagery could influence a psychophysiological quantum of the kinesthetic illusion such as the illusory angle. Motor imagery of wrist flexion and extension was used to detect interaction with the illusory wrist flexion elicited by vibration of the wrist extensor muscles (represented by ECU, musculus extensor carpi ulnaris). Since vibration applied to muscle tendons is known to enhance muscle responses to top-down commands from the brain such as magnetic brain stimuli (Claus et al., 1988a,b), we also recorded surface electromyograms (EMG) from extensors and flexors (represented by FCU, musculus

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Abbreviations: ANOVA, analysis of variance; AVR, antagonist vibratory response; CMI test, controllability of motor imagery test; ECU, musculus extensor carpi ulnaris; EMG, electromyogram; FCU, musculus flexor carpi ulnaris; GIa, group Ia; IEMG, integrated EMG; TVR, tonic vibration reflex.

NSC 5336 1-2-02

flexor carpi ulnaris) in order to examine changes in muscle activities in more detail when the subjects imagined wrist movements during illusory wrist flexion.

EXPERIMENTAL PROCEDURES

Subjects

Nineteen right-handed healthy male students, 18–22 years old, voluntarily participated in all of the following tasks. All subjects were fully informed and the experiments were performed in accordance with the Declaration of Helsinki.

Controllability of motor imagery (CMI) test

Prior to the experiment, we used the CMI test to evaluate the ability and accuracy of each subject to generate and manipulate vivid motor imagery. The controllability evaluated with this test was interpreted as the ability of subjects to transform and reconstruct their internal body schema (Nishida et al., 1986; Naito, 1994). The subjects answered 15 test questions and gained one point for each correct answer. The blindfolded subject was asked to manipulate his imagined body posture while sitting on a chair and listening to six verbal instructions for each question. After the sixth instruction, the subject was asked to actually assume with his body the final imagined body posture.

Vibration task

Experimental situation. The subject was comfortably lying on a bed in the supine position, with the right forearm restrained and resting horizontally on the bed. The more distal portion of the right wrist extended over the edge of the bed, and was hanging down freely without touching anything. The wrist angles were measured throughout the experiment with a pair of small bars placed on the lateral skin surface of the hand. The subject was instructed to close his eyes and not to move his hands or arms during the experiment.

Prior to the experiment, the subject's accuracy of evaluation and reproduction of a passively flexed wrist angle was tested. The relaxed right wrist was passively flexed by the experimenter. Immediately after each passive flexion, the subject was told to reproduce the perceived angle as precisely as possible with the same wrist. The angles tested ranged from 5 to 25° with increments of 2.5° (Clark et al., 1985). The angles were tested in random order.

Tendon vibration and data acquisition. Vibration stimuli were applied manually to the tendon of the extensor with an electromagnetic device (Handy Massager EV258, Matsushita Electronics Industrial, Osaka, Japan) at a displacement of about 2.0 mm and at a frequency of 83 Hz. Conventional methods were applied to recordings of EMGs of the ECU and FCU. The acquired data were further processed with Windows-based software (Acknowledge 3.5.3, Biopac Systems, Santa Barbara, CA, USA).

Experimental conditions. All subjects performed the tasks under four different conditions (Table 1). Each of the conditions was repeated five times in randomized order. With eyes closed, the subject naturally flexed his right wrist and completely relaxed it. Under three of the conditions, the tendon of the extensor muscles was vibrated for 55 s. During the 55 s of the vibration, onset and disappearance of the illusion was verbally signaled by the subject and event-marked within the software files by another experimenter. The 5 s prior to the vibration onset was defined as the control period (T1) for measurement of baseline EMG activities. The period of 55 s was further divided into three sections, namely T2, T3, and T4. T2 lasted from 0 to 15 s from the onset of the vibration stimuli, T3 from 15 to 40 s, and T4 from 40 to 55 s. The subject was asked to recall the maximum angle of perceived illusory flexion for each section. After each vibration trial, the subject flexed his right wrist to reproduce as exactly as possible the maximum angles experienced during the illusory stage. The subject was also asked to score the psychological ratings for the vividness and strength of the illusion (Naito et al., 1999) in order to confirm the validity of the angles produced. The angles experienced and the psychological ratings proved to be highly correlated, indicating that the former were valid and reliable.

With simple illusion (Vibration), the subject was only receiving vibratory stimuli during the 55 s of the task. With extension (Extension), he was receiving tendon vibration during the second section (T2), the same as during Vibration, but in the third section (T3), the subject imagined a very slow extension movement of his right wrist under continuous tendon vibration without actually moving his wrist. In the last section (T4), the subject was asked to stop imagining the wrist movement and continued to receive the vibratory stimuli without motor imagery. With flexion (Flexion), the procedure was almost identical to that for Extension, with the exception that, during T3, the subject imagined a flexion movement of the wrist. With motor imagery (Imagery), the subject was told to imagine a very slow motion alternating wrist extension and flexion for 40 s within a range between the natural maximum end points of each flexion and extension. The imagined movements were self-paced. Strict instructions not to move the wrist or activate EMG activity were given to the subject, who did not have to remember the maximum angles.

EMG data processing

A 25–220-Hz band pass filter, and 70–90-Hz and 160–180-Hz band stop filters were used for all EMG data to minimize EMG baseline fluctuations and anticipated harmonic noises at 83 Hz caused by vibration stimuli. Corrected and integrated values of EMG activities for T1, T2, T3, and T4 were calculated for each of the four conditions. The 5-s integrated EMG (IEMG) was used as an index of the muscle activities during each trial.

No overt wrist movement of the right wrist was observed throughout the study. The EMG of the wrist muscles showed far less activation under any of the four conditions than during actual wrist movement.

Statistic analysis

We calculated mean starting times, mean stopping times and mean durations of the illusory experience under the three vibratory conditions (Vibration, Extension and Flexion). Mean maximum angles and IEMGs were statistically evaluated by analysis of variance (ANOVA).

RESULTS

Although all subjects could imagine their body postures, the vividness and controllability of the motor imagery varied among subjects. During the accuracy test for reproducing passive wrist flexion, all subjects evaluated the flexion angles quite accurately. Figure 1A shows a strong positive correlation between the tested angles and reproduced angles for all trials in each subject. The subjects could discriminate a difference of 2.5° in tested angles, although most of the actually performed angles were underestimated. The slope of the least-square estimated regression line was 0.82.

During all the T2 periods except for Imagery, the vibration stimuli elicited an illusory flexion in all subjects in the absence of overt movement. In general, two types of illusory sensations were reported. In some trials sub-

Table 1. Task conditions

Condition	T1 (−5–0 s)	T2 (0–15 s)	T3 (15–40 s)	T4 (40–55 s)
VIB		○	○	○
EXT		○	○+↑	○
FLEX		○	○+↓	○
IMA		↑↓	↑↓	

There were four task conditions: T1 and T4 under Imagery (IMA) were controls. Under all conditions except Imagery, subjects experienced kinesthetic illusion for 55 s (T2, T3, T4). Under Extension (EXT), subjects imagined wrist extension during kinesthetic illusion in the T3 period. Under Flexion (FLEX), wrist flexion was imagined. Under Imagery (IMA), no vibratory stimulus (VIB) was given and the subjects imagined alternating extension and flexion during T2 and T3. ○: vibration, ↑: motor imagery of extension, ↓: motor imagery of flexion, ↑↓: motor imagery of alternating extension and flexion.

jects reported that the movements had stopped at certain angles seconds after their wrists began to move, which then maintained the angles until the end of the trial, in spite of a sensation of an urge to move. In other trials, however, subjects perceived repetitive wrist movements from the initial relaxed position to a certain flexion point. Sometimes, subjects reported both types of sensations within a single trial.

Table 2 shows the mean values of onset and duration of the illusion for all subjects under the three conditions. The average onset of illusion was 4.7 ± 0.3 s (mean ± S.E.M.) for Vibration. The average onsets and durations of the illusion were almost identical for the various conditions.

Effect of imagery on illusory angle

The maximum illusory angles perceived during each of the three sections gradually decreased as the time progressed for each Vibration trial. Compared with the Vibration during T3, motor imagery of wrist extension reduced the experienced flexion angles, while wrist flexion imagery increased them. Under either condition, no overt wrist movement was observed.

Figure 1B shows the mean maximum angles for the three sections under these three conditions. The average maximum angles were similar for T2 and T4 under all conditions, while the average maximum angles for T3 varied. Two-factorial [(3 time sections, T2, T3, and T4) × (3 conditions, Vibration, Extension, and Flexion)] ANOVA for the mean maximum illusory angles showed a significant interaction of both factors ($F_{4,72} = 18.0$, $P < 0.001$). Dunnett's correction for multiple comparisons among all three conditions showed that it was only during the T3 section that the maximum illusory flexion angle was significantly larger for Flexion ($12.3 \pm 1.2°$) and significantly smaller for Extension ($5.2 \pm 0.9°$) than for Vibration ($9.1 \pm 0.6°$).

Imagery controllability and effect of imagery on kinesthetic illusion

The subjects with higher scores in the CMI test perceived relatively larger illusory angles during T3 of Flexion. For normalization, the illusory flexion angle for T3 of Flexion was divided by the corresponding angle for Vibration, and this mean value for each subject was defined as the imagery effect of wrist flexion on the illusion. Figure 2A shows the correlation between CMI scores and the imagery effects for all subjects. The significantly positive correlation (df = 17, $r = 0.67$, $P < 0.01$) suggests that the motor imagery had a stronger influence on illusion in subjects who had more vivid motor images.

Muscle activities during Imagery

Imagery itself did not significantly activate either the extensor or flexor muscles, but the other conditions did (Fig. 2B). One-factorial (4 conditions, Vibration, Extension, Flexion, and Imagery) ANOVA for the average IEMGs of the ECU and the FCU of T2, T3, and T4 showed that there were significant differences among all conditions in the ECU ($F_{3,54} = 28.5$; $P < 0.01$) and in the FCU ($F_{3,54} = 6.16$, $P < 0.05$). Dunnett's correction for multiple comparisons showed that the mean IEMG of the ECU and FCU during Imagery was significantly smaller under all conditions.

Changes in muscle activities caused by vibration stimuli during Vibration, Extension and Flexion

When vibration was applied to the tendons, the extensor and flexor muscles were both activated, although much more activation was observed in the extensor than in the flexor muscles. These activities in the muscles still remained far below the level of the actual movement (less than one tenth). Two-factorial ANOVA [(2 sections, T1 and T2) × (2 muscles, ECU and FCU)] for IEMGs in each condition showed a significant interaction

Table 2. Onset time of illusion

Condition	Mean onset time (s)	Mean duration (s)
VIB	4.7 (0.3)	44.1 (1.1)
EXT	4.7 (0.3)	41.9 (1.3)
FLEX	4.6 (0.3)	45.2 (1.0)

Mean (± S.E.M.) onset time and duration of the kinesthetic illusion. Neither Extension (EXT) nor Flexion (FLEX) showed a significant difference from Vibration (VIB). $N = 95$ for each condition.

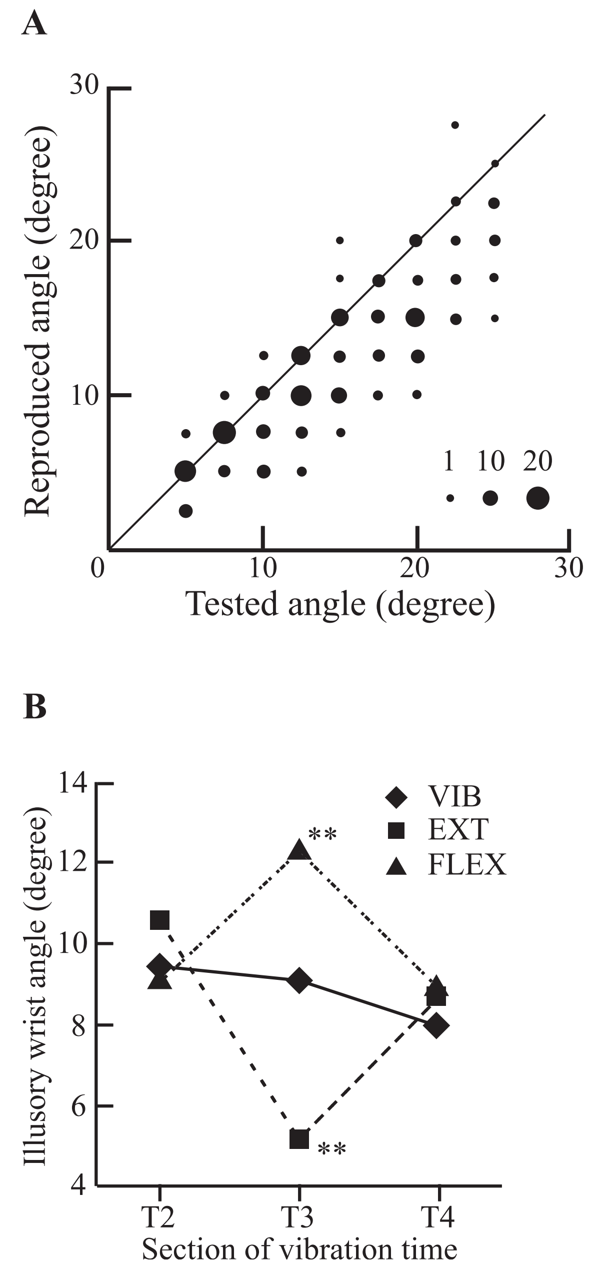

Fig. 1. Behavioral data (angle) of the tasks. (A) Accuracy of the reproduced wrist angle. All trials plotted on the graph imply that subjects could reproduce the tested angles but slightly underestimated them (below the 45° line). The slope of the least-square estimated regression line was 0.82 ($n = 251$, $r = 0.89$). Dot size reflects the number of samples. (B) Effect of motor imagery on kinesthetic illusion. Experienced illusory angles (vertical axis) in three time sections (T2, T3, T4) show a greater maximum illusory flexion angle under Flexion (FLEX) and a smaller illusory angle under Extension (EXT) than under Vibration (VIB) during T3. $N = 19$ for each data point (**$P < 0.001$).

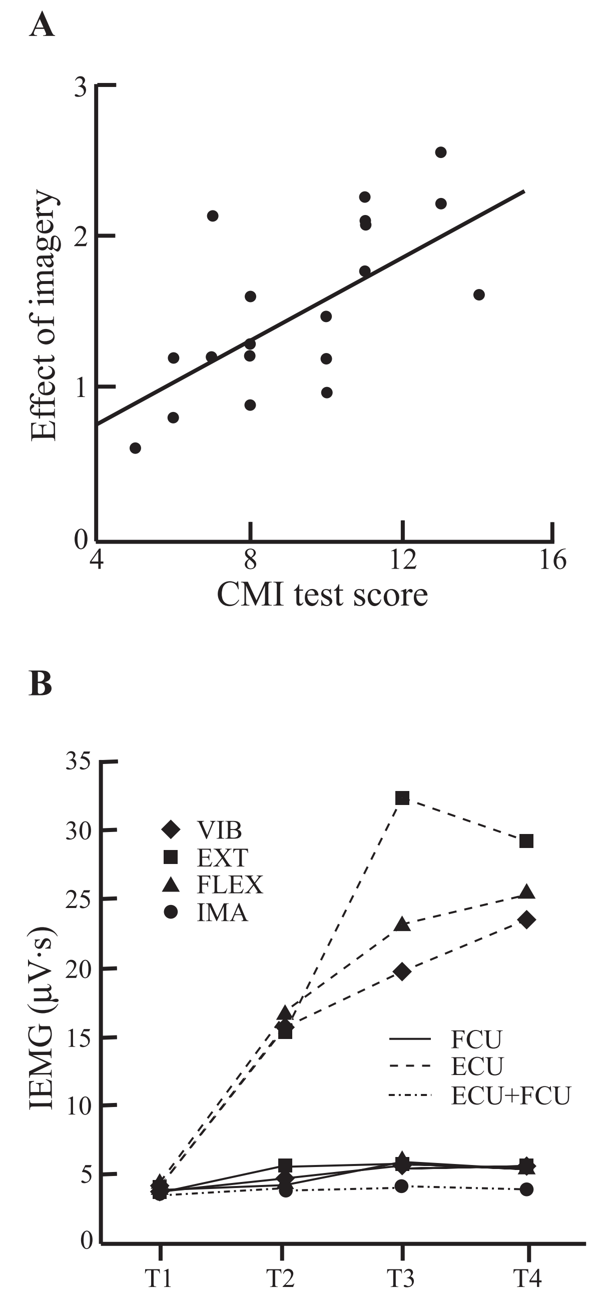

Fig. 2. Behavioral data (angle and EMG) of the vibration task. (A) Positive correlation between CMI scores and the effect of imagery on kinesthetic illusion. The line represents a regression line (df = 17, $r = 0.67$, $P < 0.01$). Imagery effects: Illusory flexion angles during T3 under Flexion divided by those under Vibration. (B) EMG activities of the ECU and FCU during each time section under Vibration (VIB), Extension (EXT), and Flexion (FLEX). IEMGs of both ECU and FCU are combined and averaged for Imagery (IMA), because IEMGs were very similar and low. $N = 19$ for each data point.

for Vibration ($F_{1,18} = 19.8$, $P < 0.0001$), Extension ($F_{1,18} = 10.5$, $P < 0.01$) and Flexion ($F_{1,18} = 17.9$, $P < 0.001$). During T2, IEMG of ECU was significantly higher than that of FCU under three conditions (Vibration, df = 18, $t = 4.5$, $P < 0.001$; Extension, df = 18, $t = 3.4$, $P < 0.01$; Flexion, df = 18, $t = 4.3$, $P < 0.001$).

Effect of imagery on muscle activities under vibration stimuli

The Extension activated the extensor muscles during T3, while the subjects experienced illusory flexion movement, more than did Vibration or Flexion in all subjects, implying a directional influence of motor imagery on the extensor muscles. Two-factorial [(2 sections, T2 and T3)×(3 conditions, Vibration, Extension and Flexion)] ANOVA for IEMGs of the ECU, for more detailed analysis, showed a significant interaction ($F_{2,36} = 14.3$, $P < 0.001$). For T3, the multiple comparisons showed IEMGs for Extension were significantly higher than for Vibration, while there was no significant difference between Flexion and Vibration (Fig. 2B).

The flexor muscles, on the other hand, showed little difference during T3 among the three conditions. The same ANOVA for IEMGs of the FCU showed neither significant conditional differences nor significant interaction.

DISCUSSION

All subjects accurately recognized passively flexed wrist angles, suggesting that the illusory wrist angles reported in this study might be highly reliable. However, we should take individual differences into account in the ability to manipulate kinesthetic motor imagery, which was reflected in the large variance in the CMI test scores. Although subjects scoring lower in the CMI test could perceive only lower angles of the illusory flexion during motor imagery of wrist flexion, the subject who got the lowest score still could imagine simple flexion or extension movements.

Activities in the extensor muscles were enhanced more than those in the flexor by the vibration stimuli on the extensor tendon. The kinesthetic motor imagery of the wrist flexion led to a major increase in the angles of the illusory flexion without a significant increase in EMG activities for the flexor muscles. On the other hand, the motor imagery of extension always led to a reduction in the illusory angles with an increase in extensor activities.

Neural substrates for tonic vibration reflex and antagonistic vibratory response

The differences between the ECU and FCU in the pattern of muscle responses to the vibration stimuli might be due to differences in neuronal mechanisms under the tonic vibration reflex (TVR) for the extensor and antagonist vibratory response (AVR) for the flexor.

EMG activities resembling TVR were observed in all subjects. The neuronal circuits producing TVR may be more automatic and intrinsic, so that ECU was always more activated than FCU at any time and under any condition. TVR has been considered to be a kind of spinal reflex, while tendon vibration can elicit a 'stretch reflex' by high-frequency activation of the myotatic pathway (Matthews, 1966; Nordin and Hagbarth, 1996; Calvin-Figuiere et al., 1999). Many studies have shown that the GIa afferent is the most sensitive to vibration stimuli at 80 Hz, with firing patterns harmonic for the vibration cycles, while the group Ib and II afferents show sub-harmonic firing patterns (Burke et al., 1976a,b; Roll and Vedel, 1982; Roll et al., 1989). In fact, neurons in the primary motor cortex in the monkey were found to fire in the same manner when its wrist was flexed and when the extensor tendon was vibrated (Colebatch et al., 1990). These studies clearly suggest the importance of the GIa afferents in eliciting the kinesthetic illusion.

In this study, kinesthetic motor imagery of extension induced a large increase in activities in the vibrated muscle. This modulation of EMG activities may reflect the excitability level of the spinal cord. Motor imagery might amount to a miniature and simulation process for movement execution in the brain (Naito and Matsumura, 1994; Beisteiner et al., 1995) and has been known to facilitate the excitability of motoneurons (Bonnet et al., 1997; Rossini et al., 1999). The motor imagery of the extension may facilitate the motoneuron excitability of the extensor muscles. Because of these physiological mechanisms, the motor imagery of the extension might produce a reduction in the illusory angles of the wrist flexion at the perceptual level.

The GIa afferents from the ECU spindles are known to inhibit the excitability of motoneurons innervating the FCU (reciprocal Ia inhibition). This physiological effect at the spinal level alone cannot explain our result. Top-down information flow from the CNS, including visual information and mental conditions, can influence spinal reflex loops (Feldman and Latash, 1982). Jankowska et al. (1981) also suggested that the inhibitory or excitatory nature of the effects of GIa afferents seem to be determined by supraspinal mechanisms. Calvin-Figuiere et al. (1999) added that the AVR may result from a perceptional-to-motor transformation of proprioceptive information, rather than from spinal reflex mechanisms. All these previous studies indicate that AVR have a more complex physiological basis involving supraspinal mechanisms.

Central process involving motor imagery and kinesthetic illusion

Motor imagery of the wrist flexion increased illusory flexion angles at the perceptual level, without significant enhancement of EMG activities of either the extensor or the flexor muscles. Yue and Cole (1992) showed that mental training of finger movements enhanced the maximum voluntary contraction of fingers, meaning that one can simulate dynamic aspects of movements during motor imagery. The kinesthetic motor imagery observed in our study significantly influenced the dynamic illusory angles without a significant increase in EMG, which was in good agreement with Yue and Cole's results. Our results also demonstrated the interaction of neural processes occurring within the CNS, suggesting the existence of common neural substrates accessible by motor imagery (top-down motor system) and kinesthetic illusion (bottom-up motor system).

Neuroimaging data have shown that similar motor-related brain areas such as the cingulate cortex, supplementary motor areas, dorsal premotor cortex, ventral premotor cortex, and sensorimotor cortex are involved in motor imagery (Roland et al., 1980; Stephan et al., 1995; Roth et al., 1996; Porro et al., 1996), and illusory arm movements (Naito et al., 1999). Moreover, electrical stimulation on certain sites of the supplementary motor areas evoked a preliminary sensation of an 'urge' to perform a movement or anticipation that a movement was about to occur (Fried et al., 1991; Lim et al., 1994). These facts lead us to speculate that kinesthetic motor imagery and kinesthetic illusion may share common neural substrates in motor-related areas and that interaction between them might occur in the CNS.

We conclude that (1) the interaction between kinesthetic motor imagery and kinesthetic illusion may occur in the CNS as a result of the existence of common neural substrates shared by imagery and illusion, and (2) different physiological mechanisms contribute to the enhancement of muscle activities in vibrated muscles and their antagonists.

Acknowledgements—This study was supported by grants in aids from the Japanese Ministry of Education, Science, Sports and Culture, and by a grant from the Nakayama Foundation for Science, Technology and Culture. We thank Mr. T. Kochiyama for technical assistance and valuable comments.

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(*Accepted* 27 *August* 2001)