Exp Brain Res (2001) 140:387–396
DOI 10.1007/s002210100842

RESEARCH ARTICLE

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Further insight into the task-dependent excitability of motor evoked potentials in first dorsal interosseous muscle in humans

Received: 8 January 2001 / Accepted: 19 June 2001 / Published online: 31 August 2001

Abstract We have reexamined the contradictory evidence in which task-dependent excitation of motor evoked potentials (MEPs) in the first dorsal interosseous (FDI) muscle was stronger with increasingly more complex finger tasks than with individual finger movement tasks. In the first step of the experiment, based on previous findings, we investigated remarkable functional differences between intrinsic and extrinsic hand muscles during complex finger tasks (precision and power grip). During the performance of the tasks, the optimal stimulus intensity of the transcranial magnetic stimulation (TMS) was applied to the contralateral motor cortex. MEPs of the FDI, extensor carpi radialis (ECR), and flexor carpi radialis (FCR) muscles were recorded simultaneously with increased background EMG activity step by step in both tasks. The intensity threshold of TMS was lower in the precision grip. Furthermore, the MEP amplitudes of FDI muscle dependent on the background EMG activity were different between these two tasks, i.e., MEP amplitudes and regression coefficients in a precision grip were larger than those in a power grip. Although our results for MEP amplitude and threshold in the FDI muscle were similar to previous reported evidence, the different contributions of a synergistic muscle (in particular, the ECR muscle) during performance in these tasks was new evidence. Since there were no differences in cutaneous afferent effects on both tasks, corticomotoneuronal (CM) cells connected to FDI motoneurons seemed generally to be more active during precision than power gripping, and there were different contributions from synergistic muscles during the performance of these tasks. In the second part of the experiment, the results obtained from the complex tasks were compared with those from a simple task (isolated index finger flexion). MEP amplitudes, dependent on the background EMG activity during isolated index finger flexion, varied among subjects, i.e., the relationship between the MEP amplitude and the background EMG of the FDI muscle showed individual, strategy-dependent modulation. There were several kinds of individual motor strategies for performing the isolated finger movement. The present results may explain the previous contradictory evidence related to the contribution of the CM system during coordinated finger movement.

Keywords Motor-evoked potentials · First dorsal interosseous muscle · Synergistic muscle · Cutaneous afferent · Task-dependent · Human

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Introduction

The importance of coordinated finger movement is evident in many daily task involving precision grip and in fine motor skills. Many of our finger movements are remarkably fast as is apparent from observing typists or musicians. One central question in motor control is how the nervous system generates the complex spatiotemporal commands needed to vary the speed, amplitude and direction of finger movement. To answer this question, several researchers have chosen to examine the generation of different finger movements (see Sanes and Donoghue 1997). In particular, the motor evoked potentials (MEPs) of the first dorsal interosseous (FDI) muscle induced by transcranial magnetic stimulation (TMS) have been investigated during the performance of different manual tasks carried out by the index finger. Based on previous reports, the MEP amplitude of the FDI muscle is larger when the index finger is used in a relatively isolated

manner than it is when FDI is cooperating with many other muscles to produce a power grip (Datta et al. 1989). One explanation for this difference is that cortico-motoneuronal (CM) cells are more active and therefore more excitable during a relatively isolated movement of one digit than during a power grip. However, Flament et al. (1993) have found that MEPs were larger during the performance of manual tasks requiring the activation of several muscles than in a simple abduction task when only the prime mover was active. Furthermore, Flament et al. (1993) indicate that methodological differences between the different studies might account for this discrepancy, i.e., the trial-to-trial variability, mean numbers of responses, delivery of stimulus, muscle contraction level, and stabilization of the head and coil position. However, they could not explain the task-related neural mechanisms which produce MEP responses of such different amplitude. More recently, Huesler et al. (1998) have demonstrated that TMS has a stronger effect during a precision grip than a power grip, i.e., a stronger contribution of the CM system in a precision grip occurs than in a power grip.

Experiments in monkeys have demonstrated task-related changes in CM cell activity and have suggested a flexible relationship between the activity in an identified CM cell and the EMG activity in its target muscles (Cheney et al. 1991). The CM system can be activated by TMS (Edgley et al. 1990; see also Rothwell et al. 1991), and it would be interesting to investigate whether CM cells are related to muscle activity in a simple manner, during the performance of different manual tasks (Hess et al. 1987; Kischka et al. 1993; Ravnborg et al. 1991). The present study was undertaken to reexamine the discrepant results of task-dependent excitation of MEPs in the FDI muscle. In addition, we investigated how MEP responses of the FDI muscle and its synergists behave in a task-related fashion. Differences in participation by extrinsic synergistic muscles probably account, at least in part, for some of the discrepancies. The extrinsic muscles provide the major grip force and all of the extrinsic muscles are involved in a power grip and are used in proportion to the desired force to be used against the external force. In contrast, during precision gripping (handling), the FDI muscle is important in imposing the necessary forces on the object (Long et al. 1970; Napier 1956). In the first series of experiments, to examine task-related MEP responses in detail, we paid particular attention to the investigation of the MEP amplitude, dependent on the background EMG activity. Although relationships of MEP amplitudes dependent on the background EMG activity are not solely related to different patterns of motor unit recruitment between the proximal and the distal muscles (Turton and Lemon 1999), two basic mechanisms (rate coding and recruitment order) for performing tasks may play an important role in the same distal muscle (De Luca et al. 1996; Kukulka and Clamann 1981), and their interactions in different tasks could be reflected in the MEP amplitude dependent on the background EMG activity. In addition, we tested a hypothesis to investigate which of the two grip types and the isolated finger movement might induce changes of the gain in the central neural encoding. This hypothesis predicts that changes of the gain between these different responses should be reflected in the slopes of the regression lines that consisted of the MEP amplitude and background EMG activity, when equal ranges of background EMG activity are present (see Ashe 1997).

The neural control of hand movements has received increasing attention in recent years, in particular the role of sensory feedback in shaping motor patterns. With regard to the role of these signals in controlling one's grasp, Collins et al. (1999) have recently indicated that the sensory activity that signals contact plays a key role in regulating EMG activity during human grasping. Much of this feedback action is attributable to cutaneous receptors in the digits and probably involves both spinal and supraspinal pathways. In the second experiment, we investigated the contribution of the afferent signals evoked by contact with the grasped object to the modulation of EMG activity during precision and power gripping. Different receptor populations may mediate responses in different muscles (see Prochazka 1989). Thus cutaneous feedback from the digits to control two different grip responses may play different roles, because the nervous system may preferentially use signals from skin receptors in the digits as described here. To investigate this possibility, we examined the effects of ischemic nerve block on MEPs and the background EMG activity of the FDI muscle.

Materials and methods

Two series of magnetic stimulation experiments were performed using different motor tasks, which were controlled in a task-dependent manner, i.e., an isolated and a complex activation of the FDI muscle. An index finger flexion was used as a motor task of isolated activation of the FDI muscle. Precision and power gripping that involved index finger flexion were used as examples of complex activation of the FDI muscle.

Subjects

This study was performed using eight healthy, right-handed adult subjects (six men and two women, 21–44 years) with no known neuromuscular or other physical disabilities. Three of the eight subjects were tested twice on different dates to check the reproducibility of the results. All subjects gave informed consent before participating in the study. Experiments were performed in accordance with the Declaration of Helsinki (1964) and approved by the Local Ethics Committee of Hiroshima University.

General experimental procedures

In the first step of the experiment, the subjects were asked to perform two motor tasks (precision and power gripping; see Fig. 1a) that involved isometric contraction of the FDI muscle. Using a laboratory-made EMG bio-feedback system, all subjects were asked to increase the amount of muscle contraction step by step in response to the experimenter's instruction. The experimental situation required the production of several consecutive force steps, with monitoring of the EMG activity at each required force

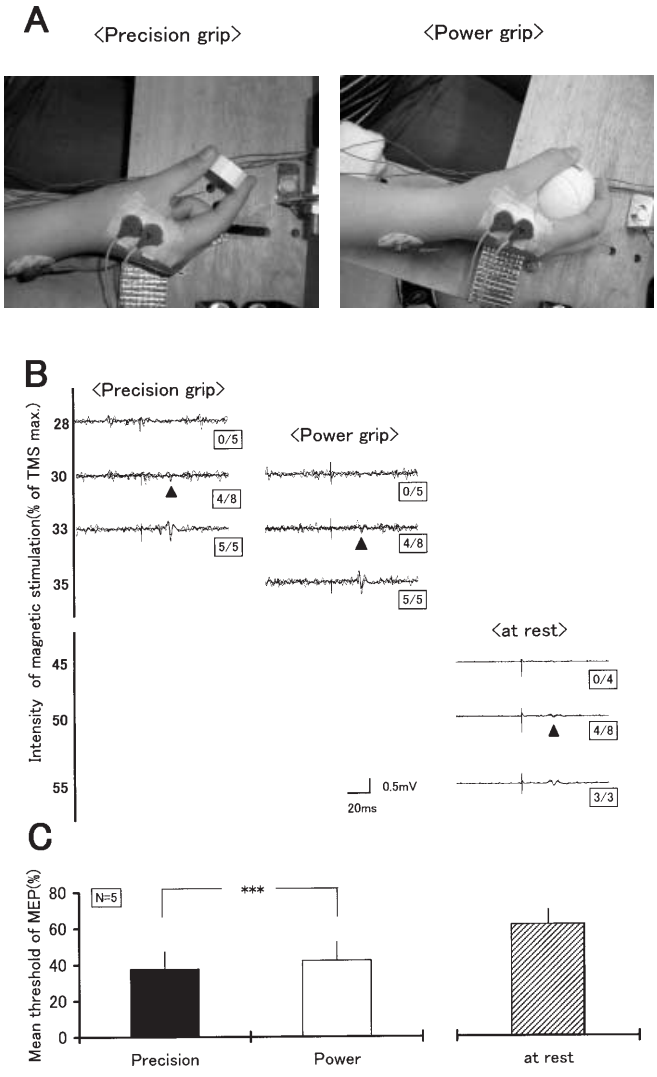

Fig 1 **a** The tasks. Each subject performed the tasks with their dominant hand. Precision grip was performed by using the thumb and the index finger and power grip involved coordinated activation of more digits. **b** Specimen records of motor evoked potentials (*MEPs*) to focal transcranial magnetic stimulation (*TMS*) of the motor cortex at various intensities (*ordinate:* percentage of maximum intensity, 100%) from the right first dorsal interosseous (FDI) muscle of a single subject. During performance of two different motor tasks (10% MVC of precision grip and power grip) and at rest (relaxed FDI muscle), intensity of TMS was increased by 2–3% in a step-by-step mode up until the threshold where the TMS intensity produced responses to 50 μV in at least 50% of successive trials (*filled triangles*). **c** The grand means of threshold in all subjects tested (n=5). The *bars* represent the grand mean of the threshold with standard deviations. Differences of threshold between precision grip and power grip were statistically significant. ***P<0.001

step. During the production of the required force level, MEPs were simultaneously recorded along with background integrated EMG (iEMG) activity. The slopes of the regression lines were then calculated and taken as an index of the MEP amplitude dependent on the background iEMG activity. During performance of the motor tasks, particular care was taken to check that the background iEMG activity increased in a step-by-step fashion. TMS was always delivered during the background iEMG activity during each motor task. It is well known that the postspike response increases with EMG activity and can show saturation at higher levels of EMG activity (Bennett and Lemon 1994). Thus, we used the optimal background iEMG activity from low to middle muscle contraction levels (below 30% of maximum voluntary contraction; MVC). The overall motoneuron pool drive was, therefore, reflected in the background EMG measured during precision and power gripping before TMS (see Kasai and Yahagi 1999). To confirm the level of the motoneuron pool drive in both tasks, the paired comparison of MEP amplitudes and background iEMGs (a 100-ms window just prior to the muscular response elicited by TMS) was calculated.

It is known that the tonic cutaneous input from the palm skin enveloping the contracted FDI muscle is essential in energizing the corticospinal output toward that specific muscle. For example, sensory deprivation induces a marked reduction of the physiological latency jump in the FDI muscle, i.e., the difference between onset latencies of contracted and relaxed MEPs (Rossi et al. 1998; Rossini et al. 1996). This evidence indicates that the FDI muscle is selectively affected not only during active contraction but also during relaxation, and that the tonic sensory flow from the skin receptors and the phalangeal joint receptors plays a significant role in selectively energizing the corticospinal tracts governing this muscle (Rossi et al. 1998). To test whether the different cutaneous influences of precision grip and power gripping were effective, we used the ischemic nerve block method. In three subjects, the MEP amplitude and background EMG activity of both grip responses were recorded before and after inflating a blood pressure cuff to 200 mmHg, just above the elbow for 20 min, and monitoring the M-wave.

In the second step of the experiment, the subjects were asked to perform an isolated index finger flexion similar to a precision grip (see Fig. 5a). During performance of the isolated index finger flexion, particular care was taken to check that the background EMG activity increased step by step and TMS was always delivered in similar ways for both precision and power grip responses.

Brain stimulation and recording MEP

TMS was applied using a Magstim 200 stimulator (Novametrix) connected to a circular, 9-cm-mean-diameter flat circular coil (maximum output intensity, 1.5 T, stimulus duration of less than 1 ms). The position of the coil was systematically adjusted on the scalp over the left motor cortex with the current flowing in the coil (anticlockwise direction) at the beginning of each experiment to find the optimum location for activation of the right FDI muscle. In general, the optimum position was the vertex. Starting from a suprathreshold level, stimulus intensity was reduced in steps of 2–3% of the maximum stimulator output (100%), and the motor threshold at rest was defined as the highest intensity that yielded MEPs. That is, the motor threshold was defined as the intensity of stimulation needed to produce EMG responses (peak-to-peak amplitude) more than 50 μV in at least four out of eight successive trials (50%) in a completely relaxed FDI muscle under visual EMG feedback control (1.0×MT). On the other hand, an active motor threshold ($A \times$ MT) was determined in the tonically activated FDI muscle (10% MVC) and was defined as the highest stimulus intensity with MEP amplitude more than 50 μV in at least four out of eight trials, which is the same as the motor threshold at rest or the mean of eight consecutive unrectified trials. Thus, the test intensity of the stimulation was adjusted to be subthreshold at rest ($0.8 \times$ MT) for the recording MEP. Since it has been suggested that it is essential to use small MEPs in order to demonstrate excitability changes at a cortical level (Rothwell 1997), particular care was taken that the control MEP was the same size in all experimental series (Hasegawa et al. 2001).

EMGs were recorded with surface electrodes from the FDI, the flexor carpi radialis (FCR), and the extensor carpi radialis (ECR) muscles, with filters set at 5 Hz to 5 kHz. The sampling rate of the EMG recordings was 5 kHz. The peak-to-peak amplitude of the nonrectified MEP was measured in the present experiment.

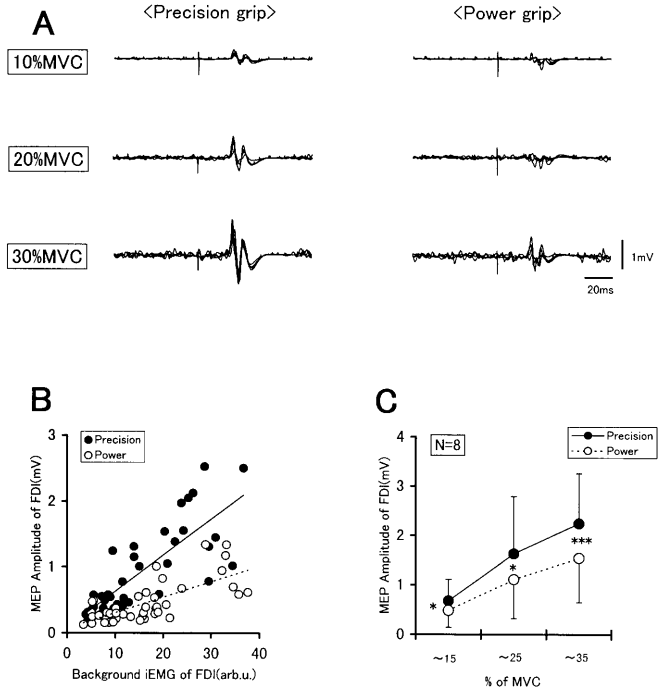

Fig 2 **a** Specimen records of MEP and background integrated EMG (*iEMG*) activity during right FDI muscle contractions during precision grip and power grip obtained from a single subject (four trials superimposed). MEPs were recorded during maintenance of various levels of background EMG activity. MEP amplitudes were larger in precision grip than those in power grip in spite of the same background EMG activity in both grip movements. **b** Correlation between MEP amplitudes (*ordinate*, millivolts) and background EMG activities (*abscissa*, arbitrary units) in precision grip (*filled circles*) and in power grip (*open circles*) obtained from a single subject. The regression line for precision grip was $y=0.0546x+0.0841$ (y is MEP amplitude, x is background EMG) and $y=0.0236x+0.0703$ at power grip. Difference between regression coefficients in both movements were statistically significant ($P<0.01$). **c** The grand means of MEP amplitude for all subjects tested ($n=8$) at three levels of background EMG activity in precision grip (*filled circles*) and in power grip (*open circles*) with standard deviations. MEP amplitudes in precision grip were always larger than those in power grip in spite of the same background EMG activity. $*P<0.05$; $***P<0.001$

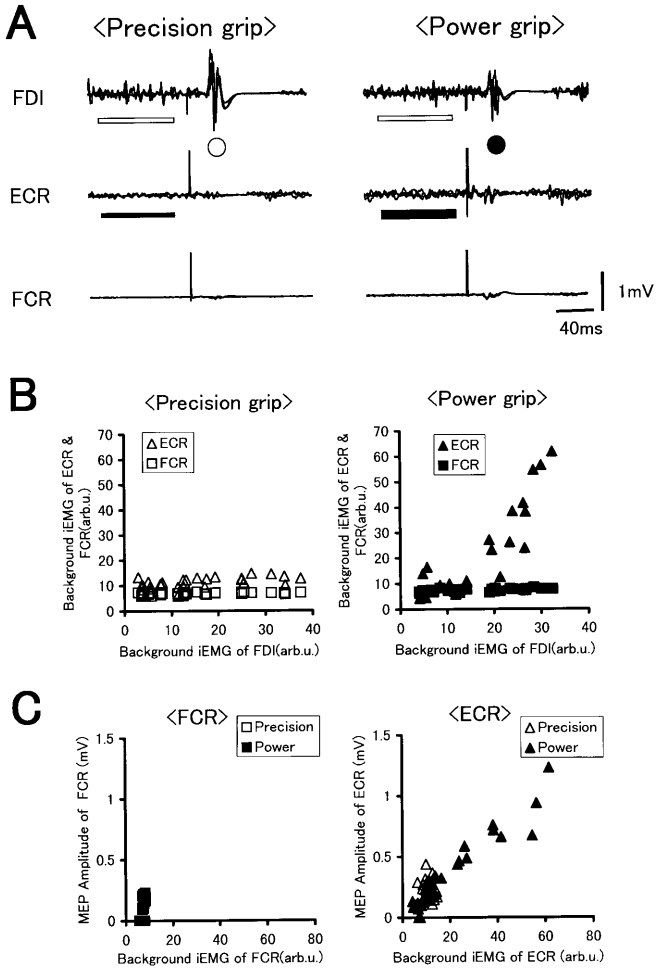

Fig 3 **a** Specimen records of MEPs and background EMG activities of intrinsic (FDI) and extrinsic (extensor carpi radialis, *ECR*, and flexor carpi radialis, *FCR*) muscles in precision grip and power grip obtained from a single subject (superimposed four trials). MEP amplitudes of FDI muscle were larger in precision grip than those in power grip in spite of same background EMG activities (*open bars*). Furthermore, in power grip larger coordinated activation of ECR muscle was observed (*thick filled bar*) than that in precision grip (*thin filled bar*). **b** Correlations between background EMG activity of FDI muscle and activity of ECR or FCR muscles in precision grip (*left*) and in power grip (*right*), respectively. A significant correlation between background EMG activity of FDI and ECR muscle was observed in power grip. The regression line was $y=1.6184x-5.2580$ (where y is background integrated EMG of ECR muscle and x is background integrated EMG of FDI muscle). **c** Correlations between MEP amplitudes and background EMG activity of FCR (*left*) and of ECR (*right*) muscles, respectively. A significant correlation of MEP, the same as was the case for background EMG activities shown in **b**. The regression line was $y=-0.0104x+0.3520$ (where y is MEP amplitude of ECR muscle and x is background integrated EMG of ECR muscle). This evidence reveals the difference of contribution of ECR muscle between precision grip and power grip

Magnetic stimuli were delivered at the previously established optimal site. A 100-ms prestimulus period as described here was used to find the mean level of the background iEMG activity. The data were stored on a personal computer for further analysis.

Data analysis

Since there is evidence that a constant input to motoneurons will produce a response which scales with the background (Bennett and Lemon 1994; Mathews 1986), measurement of the MEP size as a proportion of the background iEMG level is expected to be correct. Thus, during performance of the motor tasks we measured iEMG activity just prior to delivery of the TMS and during MEP amplitudes, simultaneously. From the amount of background iEMG activity and MEP amplitude, we calculated the regression and correlation coefficients. Furthermore, to test whether the EMG activity of a particular muscle covaried with that of another muscle during performance of the motor tasks, correlations were also computed over trials between iEMG activity and the MEP amplitude of three muscles. The criterion for synergy activation in the amplitude domain was the presence of a significant correlation coefficient among them. Correlations were examined with Spearman's rank correlation. Differences in MEP amplitude were compared using the paired two-tailed Student's *t*-test. Statistical significance was accepted at $P<0.05$.

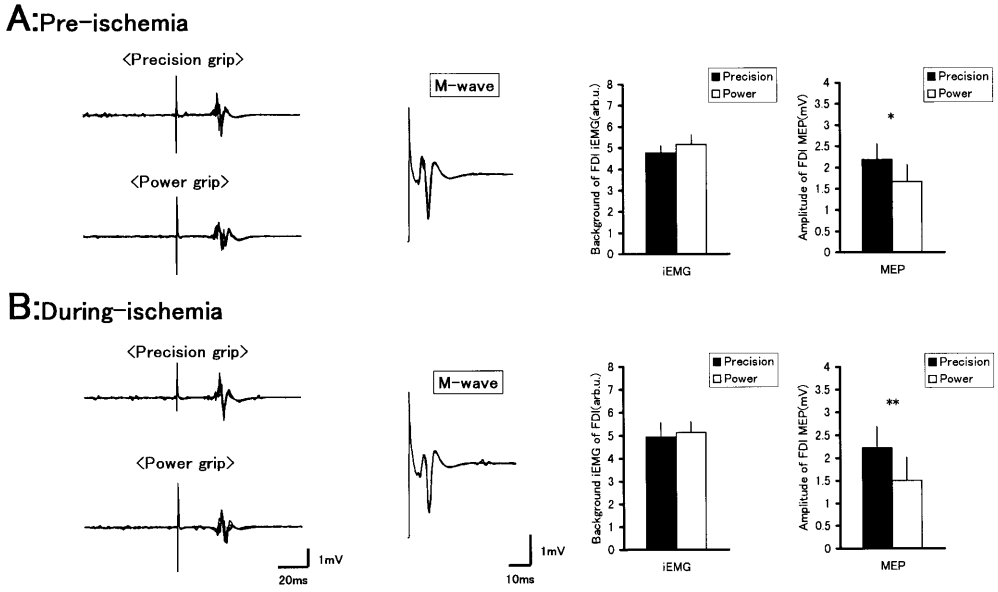

Fig. 4 **a** Specimen records of MEPs and background EMG activity of precision grip and power grip (*left traces*, three trials superimposed), M-wave (three trials superimposed; *trace second from left*), means and standard deviations of rectified background EMG of 100-ms prestimulus period (*histogram, third from left*; calculated for 10–15 trials) and MEP amplitudes (*histogram on right*; calculated 10–15 trials) before ischemic cutaneous nerve block. **b** Same representations as **a** during ischemic cutaneous nerve block (15–20 min after starting ischemic nerve block). M-waves and background EMG activities were not modulated, and differences in MEP amplitude between these two grip responses were maintained before and during ischemic cutaneous nerve block

Results

Differences of active MEP threshold intensity

During the tonic isometric contraction of the FDI muscle with visual feedback of EMG activity, threshold differences of MEP responses between precision and power gripping were measured. The active threshold in precision gripping was lower than that in the power gripping and both thresholds were lower than at rest (Fig. 1b). These threshold differences were reproducible and statistically significant across the subsample of subjects tested (n=5; t=11.50, df=4, P<0.001; Fig. 1c).

Effect of different grips on the relationship between the MEP amplitude and the background EMG activity

To investigate the difference in central motor control between precision and power gripping, we measured MEP amplitudes and background iEMG activities in both grip responses. Figure 2a shows specimen records of MEP amplitudes and background EMG activity at three different contraction levels in precision and power grips obtained from a single subject. MEP amplitudes during a precision grip were always larger than those during a power grip despite the same background EMG activity. Thus, MEP amplitudes were calculated at each of the three contraction levels. MEP amplitudes were significantly larger in precision gripping than in power gripping at all contraction levels (Fig. 2c). Similar results were reproducible across all subjects tested (n=8).

To examine what relationships exist between MEP amplitudes and background EMG activity in both power and precision grips, we calculated the correlation coefficients for both grips (Fig. 2b). We found significant correlation coefficients in both grips, but there was a statistically significant difference between the regression coefficients (P<0.01); i.e., the regression coefficient in precision gripping was larger than that in power gripping, which means a steeper slope obtained in precision gripping. Similar results were obtained in all subjects without exception.

Figure 3a shows superimposed (three trials) EMG recordings from FDI, ECR, and FCR muscles during precision gripping (left EMG traces) and power gripping (right EMG traces). Although MEP amplitudes in precision gripping were larger than those in power gripping under the same background EMG activity of the FDI muscle and similar to the EMG traces shown in Fig. 2a, there were definite differences in the background EMG activity of the ECR muscle and no difference in the EMG activity in the FCR muscle in both precision and power grips. Thus, we calculated correlation coefficients between the background EMG activity of the FDI and ECR or FCR in each grip response (Fig. 3b). In a precision grip, correlations between the FDI and ECR or FCR were not observed (left graph in Fig. 3b). However, in the power grip, a statistically significant correlation between the FDI and ECR muscles was observed. To further substantiate this finding, we calculated correlation coefficients between the MEP amplitude in the FCR (Fig. 3c, left) or ECR (Fig. 3c, right) muscles and their background EMG activity. For the ECR muscle, a statistically significant correlation was observed in the power grip but not in the precision grip. This

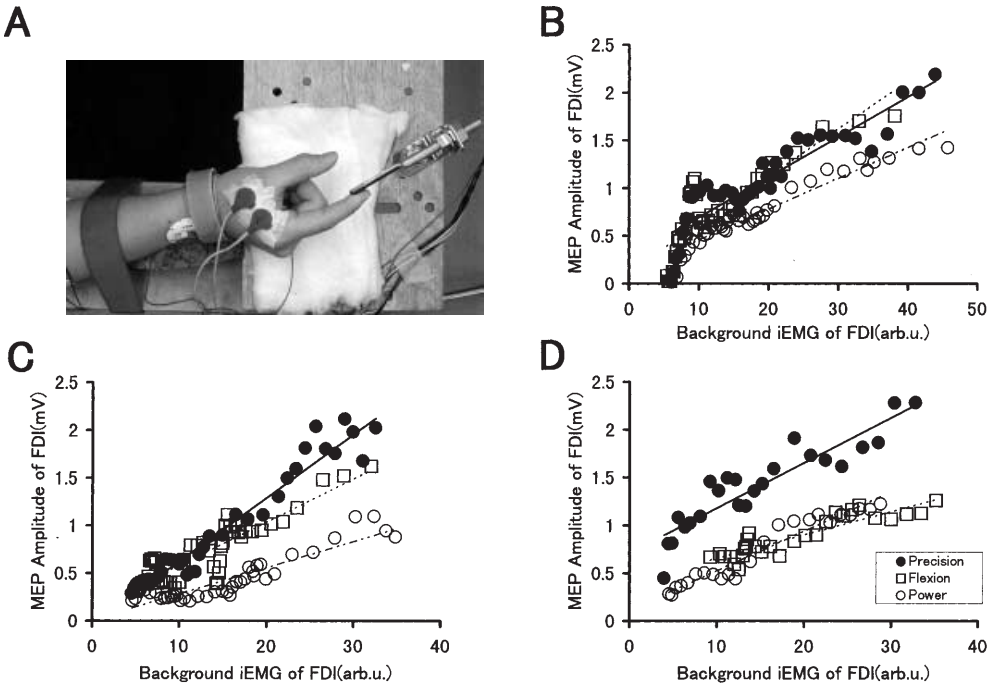

Fig. 5 a The isolated index finger flexion task. Correlations between MEP amplitudes and background EMG activity of FDI muscle in precision grip (*filled circles*), in power grip (*open circles*) and in isolated individual index finger flexion (*open squares*). All representations are same as in Fig. 2b. In isolated individual index finger flexion, there were three different types of MEP amplitude dependent on background EMG activity. In one, the regression line is very similar to that in precision grip: **b** In two out of eight subjects, the regression lines were: precision grip, y=0.0421x+0.2746; power grip: y=0.0323x+0.1348; and individual index finger flexion: y=0.0503x+0.1144. For the second, a regression line comes intermediate between precision grip and power grip: **c** In four out of eight subjects, the regression lines were: precision grip: y=0.0666x–0.0382; power grip: y=0.0275x+0.091; and individual index finger flexion: y=0.0455x+0.1252. In the third case, a regression line is very similar to that in power grip: **d** In two out of eight subjects, the regression lines were: precision grip: y=0.0471x+0.7133; power grip: y=0.0244x+0.4130; and individual index finger flexion: y=0.0213x+0.1117

evidence indicates that the ECR muscle definitely contributes differently to the two different grip tasks.

Since it is well known that tactile sensory information from the skin of the fingertips plays a crucial role in the motor control of prehensile tasks (Johansson and Westling 1987; Westling and Johansson 1987), we investigated the effects of an ischemic cutaneous nerve block on MEPs to examine the different extents of cutaneous afferents from different touches to the objects between precision grip and power grip. The results of ischemic nerve block obtained from a single subject are shown in Fig. 4a (before ischemia) and b (during ischemia). The observation that the MEP amplitudes of the FDI muscle are always larger in precision gripping than in power gripping was repeated during ischemic cutaneous nerve blocking. The M-waves did not change during ischemia, and these results were reproduced across all subjects tested (n=3). These results indicate that cutaneous afferents could not seriously influence MEP generation in either grip tasks. Thus, differences in the MEP amplitude, dependent on the background EMG activity, between precision gripping and power gripping reflect the differences in the central motor command required to perform these complex finger movements.

Figure 5a shows a picture of an index finger flexion in a relatively isolated movement. Figure 5b–d shows results in which the MEP amplitude is dependent on the background EMG activity in three tasks: index finger in a relatively isolated movement (simple movement), and two grip conditions (complex movement) for three different subjects. With regard to the MEP amplitude depending on the background EMG activity, we could find three typical different examples of the index finger flexion in a relatively isolated movement, i.e., the first type has a regression line that is very similar to that in a precision grip (Fig. 5b; two of eight subjects), the second type has a regression line falling between a precision and a power grip (Fig. 5c; four of eight subjects), and the third type has a regression line very similar to that in a power grip (Fig. 5d two of eight subjects). The present results indicate that there are apparently a large number of degrees of freedom in performing isolated index finger responses and therefore the MEP amplitude dependent on background EMG activity is also dependent on individual movement strategies.

Discussion

The aim of this study was to reexamine previous discrepant results of task-dependent excitability of MEPs in the FDI muscle. One of them is that both the intrinsic

(FDI) muscle and the extrinsic (ECR) muscle play a key role in producing power grip responses. Another is that performing the isolated index finger movement (simple movement) was definitely different from the cooperating finger movements (complex movement). On the basis of the present findings, the following three view points are discussed: (1) differences of central motor control between precision grip and power gripping, (2) differences between complex tasks and a simple task of voluntary finger movements, and (3) functional implications.

Differences between precision and power gripping

Voluntary contraction of the target muscle lowers the threshold for inducing MEPs by depolarizing both the cortical and spinal motoneurons (Day et al. 1987; Mazzocchio et al. 1994; Ugawa et al. 1995). Therefore, the differences of the active motor thresholds between precision and power gripping could be interpreted as reflecting the magnitude of the voluntary motor drive on the corticomuscular pathway. That is, the magnitude of the voluntary motor drive in a precision grip might be greater than in a power grip. Similarly, Yahagi and Kasai (1998) have recently indicated that the amount of CM cell activity was affected by different motor images utilizing the same muscle. With regard to neural mechanisms related to changes in the motor threshold, production of EPSPs in spinal motor neurons varied depending on the grip. That is, the size of the EPSP was larger in a precision grip than in a power grip. In actual movement recorded in a monkey, a population of neurons that encode the direction of movement can be found in the motor cortex (Taira et al. 1996). These neurons could become active without necessarily changing the level of muscle activity. Therefore, different grip responses are solely due to the production of different EPSPs for the task required. On the other hand, when testing the effects of several antiepileptic drugs on motor cortex excitability, Ziemann et al. (1996) have found that motor thresholds are increased only by agents that block ion channels. It remains unclear whether the threshold differences seen in our results dependent on different tasks were due to membrane mechanisms.

Tactile afference is important for movement accuracy and for the detection of error (Johansson et al. 1994; Lackner and DiZio 1994). In addition, Brochier et al. (1999) have suggested recently that cutaneous feedback to the primary somatosensory cortex was essential for the fine control of grip forces. Similarly, Classen et al. (2000) have suggested that the tactile afferent information changes the gain and gradient of motor cortical inhibition associated with the implementation of certain tasks. However, we did not observe different influences of tactile afference on the two grip responses. Thus, cutaneous information from the grip responses may not have contributed to changes in the gain and gradient of motor cortex excitability. That is, in our experimental situation, tactile afferents could not have been a serious influence on the task-dependent cortical motor output circuits despite the different extent of tactile information between the two different finger postures.

With regard to task-related changes in MEPs of the FDI muscle, Flament et al. (1993) have suggested two important central causes; one refers to substantial changes within the population of CM neurons that project to the FDI motoneuron pool, and the other refers to differences in either the size or strength of the connectivity of the CM cells recruited during performance of the various tasks. With respect to the size of CM cells, the present findings, in which there were clearly different regression coefficients between MEP amplitude and background EMG activity and in which was no difference in cutaneous afferent effects between the two tasks, can provide plausible explanations for the size differences in task-related MEP changes. These results suggest a flexible relationship between excitation of MEP and EMG activity in the target muscles (Fetz 1992). On the other hand, with respect to the strength of connectivity of the CM cells, single CM cells can fire differently according to the target muscle and the force required for different types of movement. For example, Muir and Lemon (1983) have found that CM cells are preferentially active during precision gripping of a force transducer between the thumb and forefinger, but paradoxically the same CM cells are inactive during power gripping, which involved even more intense activity in their target muscles. These results indicate an unexpected variability in the relationship between CM cells and their target muscles under different movement conditions. That is, the control of fingertip actions with a precision grip engages neural circuits different from those engaged during a power grip. The present results showed that the MEP amplitude dependent on background EMG activity was larger during precision gripping than during power gripping. This finding may reflect different neural circuits engaged in these grip responses. That is, the functionally interpretable group of task-related CM cells provides convincing evidence for the coding of different movement patterns and these differences might be reflected in changes in the correlation coefficient between the MEP amplitude and the background EMG activity. These neural explanations of changes in FDI muscle activity confirm the stronger contribution of the CM system in precision gripping than in power gripping, similar to recent evidence demonstrated by Huesler et al. (1998) using muscle synchronization.

In monkeys and man, the exertion of an isometric static grip force is produced by coactivation of at least 15 muscles organized in flexible synergies (Maier and Hepp-Reymond 1995a, 1995b; Rufener and Hepp-Reymond 1988). In the present study, which focused on forearm muscles (FCR and ECR) as flexible synergies, there were definitely different contributions to the EMG activity of the ECR muscle between precision and power grips. This difference in the muscle activity from its central command requires the presence of a rectifier somewhere in the spinal cord or within the cortical

network to explain the control and performance of these two grip responses (Hepp-Reymond et al. 1999). In a steady grip of an object under essentially isometric conditions, the coactivation of the extensor and flexor muscles of the fingers and wrist constitutes the basis of the human repertoire of handling and gripping activities (see Smith 1981). Coactivation of many different muscles stabilizes the thumb and presents a pattern of fractionation (Bennett and Lemon 1996). The different muscles show very different spatiotemporal patterns of contraction, which produce selective movement of the digits. The corticospinal output involved in performing the two tasks might therefore be differentially modulated depending on the CM cell activities when the FDI muscle is acting as the prime mover during a precision grip and when the FDI and ECR muscles are coactivated during a power grip. Thus, it must be kept in mind that the performance of gripping tasks appears to be associated not only with a greater effectiveness of CM cell activity but also with a greater effectiveness of coactivation of several CM cells.

Differences between complex and simple tasks

The motor cortical neurons in man, as has been shown previously in the monkey (Buys et al. 1986), are more active during a relatively independent finger movement than during a power grip (Datta et al. 1989). One factor influencing this relationship is the task dependence of muscle synchronization suggested by Huesler et al. (1998). Their findings are that muscle synchronization is more enhanced during power gripping than during precision gripping, and TMS has a greater effect during precision gripping than during power gripping. Thus, during various tasks, synchronous muscle activation is less frequent with increasingly more complex tasks. That is, CM cells can contribute to the fractionated pattern of muscular activity seen during precision gripping. As a matter of fact, the effectiveness of the corticospinal pathway, as assessed in MEPs induced by TMS, has been found to be greater in the performance of finely adjusted coordinated movements involving many muscles than during single, isolated muscle connections (Lemon et al. 1995). The fact that larger MEPs were produced during the performance of the complex task than during the simple task, suggests that there might be differences in either the size or strength of the connectivity of the CM cells recruited during the performance of the various tasks (Flament et al. 1993). Changes in the size or strength of the connectivity of the CM cells recruited during the performance of the various tasks occurs more frequently and these changes are reflected in MEP amplitude dependence on the background EMG activity.

It is well established that direct CM connections between CM cells and spinal motoneurons innervating hand and forearm muscles are essential for the execution of independent finger movements and can terminate in more than one motoneuronal pool (for a review, see Lemon 1993). Thus, functional effectiveness could be determined by the distribution and weights of the CM connections. For example, Bennett and Lemon (1994) have reported that CM cells with strong positive correlations could play a role in the recruitment of motor neurons at low levels of EMG activity, and they have suggested that each CM cell-muscle combination operates in a particular fashion as the motoneuron pool becomes more active. Thus, the variety of these relationships may allow specific CM cells to exert particularly strong facilitation at given levels of muscular activity. Therefore, our findings could be explained in accordance with these CM cell-muscle combinations, which might be advantageous during different fine control of independent finger movements. Of course, other descending systems of the spinal apparatus sharing some properties with the CM system such as rubromotoneuronal projections should be considered and might provide another source of control (Mewes and Cheney 1991). The present evidence for isolated index finger flexion responses demonstrated indirectly that the distribution of synaptic connections from CM cells within the motoneuron pool could be the basis for the different relationships which can exist between CM cells and their target muscles. This is the case in which the MEP amplitude dependent on the background EMG activity varies in isolated index finger movements. With regard to previous discrepant reports related to MEP amplitude differences between simple and complex finger movements, the present results indicate that, in addition to methodological differences suggested by Flament et al. (1993), MEP amplitudes during the isolated finger movement task are essentially dependent on individual motor strategy.

Functional implications

Various classifications of grasping behavior in human and nonhuman primates have been proposed, including power gripping and precision gripping (Napier 1956). When power gripping all the fingers are active in grasping an object against the palm, usually with large forces. In contrast, when precision gripping, smaller forces are exerted at the tips of the index finger and thumb, requiring another pattern of stability and muscle activation. The most sensible displacement of the fingertip during precision gripping lies approximately tangential to the distal phalanx of the thumb. It seems plausible that this tuning might facilitate the fine position of small objects pinched between index finger and thumb. The present results showed that, in a precision grip, the MEP amplitude dependent on the background EMG activity was larger than that in a power grip. Thus, for stabilizing the fine positioning of the small object, the CM system plays a more important role than in power gripping. Furthermore, the present findings indicate that a definite shift in patterns of muscle use occurs as the hand changes from precision to power gripping. The interpretation of our findings in precision gripping indicate the major role

played by the FDI as an abductor and adductor of the index finger and thumb to pinch the external object. In a power grip, the FDI muscle participates as a rotator of the first phalanx in cooperation with other interosseous muscles as suggested by Long et al. (1970).

In the behavior of intrinsic and extrinsic muscles of the hand, compression in precision gripping is produced by the extrinsic muscles and it is assisted by the metacarpophalangeal-joint flexion force of the FDI muscle (Long 1968; Long et al. 1970). Under the weak precision grip of the present task, however, compression produced by the metacarpophalangeal-joint flexion force might play an important role. In a power grip, the extrinsic muscles provide the major gripping force. All of the extrinsic muscles are involved in the power grip and are used in proportion to the desired force to be used against an external force. In particular, the ECR muscle plays an important role in the present tennis-ball squeezing task.

Acknowledgements The authors would like to thank Dr. G. Anson for his comments and editing English. This work was supported by a Grant-in-Aid for Scientific Research from the Japanese Ministry of Education, Science and Culture (to T.K: C; 10680031).

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