Cortical Topography of Human First Dorsal Interosseus During Individuated and Nonindividuated Grip Tasks

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Abstract: Neural activity in the motor cortex and its descending projections is modulated in a task-related manner. Several TMS studies have shown that when normal human subjects execute different manual tasks requiring similar contraction levels in first dorsal interosseus (FDI) there is a task-related modulation of the amplitude of FDI motor evoked potentials (MEPs). Not all studies of task-related changes show the same pattern of results, however. One reason for this might be methodological. Studies have assessed task-related changes by stimulating a single site, which can provide information about task-related changes in the excitability of the cortex at that site, but which is not sensitive to excitability changes throughout the muscle's cortical representation. We investigated how the execution of an individuated versus a nonindividuated isometric grasping task affected the excitability of FDI's entire cortical representation. We examined FDI MEP amplitudes while subjects grasped an object between their thumb and index finger, or when they grasped the same object between their thumb and all four fingers, keeping the background level of EMG in FDI constant for the two tasks. We found no overall task-related change in the excitability of FDI or its cortical topography, possibly due to behavioral differences of individual subjects. The stability of FDI's cortical representation during two different manual tasks expands the possibilities for studying cortical reorganization in the context of active muscle contraction, which will enable us to better understand whether changes in the motor system observed when muscles are at rest are also present during voluntary muscle recruitment. *Hum Brain Mapp* 29:594–602, 2008. © 2007 Wiley-Liss, Inc.

Key words: transcranial magnetic stimulation; motor cortex; individuated; precision grip; power grip; task-related

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INTRODUCTION

There is now increasing evidence that neural activity in the motor cortex is modulated not only according to which muscles are contracted, but by the task being executed during the muscle contractions. In monkeys, single-cell recordings from primary motor cortex show that some corticomotoneuronal cells are more active during a precision grip than a power grip, despite similar levels of activation of these cells' target muscles during both tasks [Muir and Lemon, 1983]. In humans, functional imaging studies show that the primary sensorimotor cortex is more active during

movement of a single digit—like index finger flexion, than when the index finger is flexed as part of a whole hand movement [Kitamura et al., 1993; Remy et al., 1994]. Transcranial magnetic stimulation (TMS) studies in humans also support the idea that the output of the motor cortex is task-related. When TMS is applied over the motor cortex, the response to this stimulation is recorded at the muscular level as a motor-evoked potential (MEP). Several TMS studies have shown that when normal human subjects execute different manual tasks there is a modulation of the amplitude of MEPs evoked in the first dorsal interosseous (FDI). For example, stimulation over the motor cortex during an individuated finger movement (a precision grip) evoked a larger MEP in FDI than when the muscle had the same level of background EMG but was engaged in a nonindividuated movement (a power grip) [Hasegawa et al., 2001; Huesler et al., 1998; Tinazzi et al., 2003]. Datta et al. [1989] also observed larger MEPs during an individuated finger movement (index finger abduction) than during a nonindividuated power grip.

These findings are consistent with other evidence suggesting that the motor cortex makes an important distinction between isolated (individuated) versus coordinated (nonindividuated) muscle contractions. In both humans and nonhuman primates damage to the corticospinal tract selectively impairs the ability to produce relatively isolated muscle contractions (e.g. precision grip) without affecting the ability to simultaneously contract multiple muscles (e.g. power grip) [Colebatch and Gandevia, 1989; Lang and Schieber, 2003; Lawrence and Kuypers, 1968; Raghavan et al., 2006]. Thus, task-related modulation of motor cortex activity might be related to a greater cortical engagement during individuated versus nonindividuated muscle contractions. The problem with this idea, however, is that not all TMS studies of task-related changes show larger MEPs during individuated tasks. When comparing a number of complex movements with a simple index finger abduction task, Flament et al. [1993] reported that FDI MEPs were *smaller* during index finger abduction (a highly individuated movement) than during both the less individuated precision grip, and the nonindividuated power grip. Furthermore, they also saw no differences in MEP amplitudes during the individuated precision grip and the nonindividuated power grip. This latter finding is in contrast with numerous other studies that found greater excitability during individuated precision than nonindividuated power grips [Hasegawa et al., 2001; Huesler et al., 1998; Schieppati et al., 1996; Tinazzi et al., 2003]. Individuated muscle contractions are not always associated with *larger* MEPs in intrinsic hand muscles, however, as Hess et al. [1999] also reported no differences in FDI MEP amplitudes when subjects performed nonindividuated muscle contractions (coordinated activity of many muscles during exploration of the physical features of an object) or when they performed an individuated thumb to index precision grip.

A task-related coding of motor cortex output would constrain the number of possible muscle combinations, and therefore reduces the degrees of freedom that the brain

must control when moving the upper limb. When tasks are categorized as individuated versus nonindividuated, however, TMS studies do not produce a coherent picture of task-related modulation of motor cortex activity. One interpretation of this is that motor cortex activity is not related to whether a muscle contraction is individuated or nonindividuated. Indeed, Schieppati et al. [1996] have suggested that task-related modulation might be more closely related to the precision or complexity of the task rather than whether or not the task requires individuated or nonindividuated muscle contractions. Results of a recent study by Bonnard et al. [2007] support this view by showing that increasing precision demands results in larger MEPs in intrinsic hand muscles during an isometric dynamic force tracking task performed with a thumb-index grip. Despite this, the precision demands of a task are not sufficient to explain all the discrepant results of studies examining task-dependent excitability of MEPs in human FDI. Some of these discrepancies might also arise from the methods used in these studies.

Because of the time required to stimulate many different cortical sites it is common practice in TMS studies to examine task-related effects by stimulating a single site while subjects perform different experimental tasks. Indeed, in all of the studies discussed so far, FDI responses to TMS stimulation were recorded following stimulation only at the site over the cortex from which MEPs were evoked at the lowest stimulation intensity with the muscle at rest (the resting hotspot). Although stimulating at one cortical site can provide information about task-related changes in the excitability of the cortex *at that site*, this technique is not sensitive to excitability changes throughout the muscle's cortical representation. As such, care must be taken when interpreting the results of studies in which stimulation of the hotspot during two different tasks leads to changes in MEP amplitude. For example, when Datta et al. [1989] stimulated the FDI hotspot they recorded higher amplitude MEPs in FDI during index finger abduction than during a power grip. Their interpretation of this result was that there is a "higher level of cortical activity during a voluntary index finger abduction than during a grip" (p. 13), but this conclusion is true only for the one site they stimulated—these results cannot be used to discuss *overall* changes in motor cortex excitability during these two tasks. Instead, different tasks might not uniformly affect the excitability of a muscle throughout its cortical representation, which could explain why stimulating at a single cortical site results in the conclusion by some studies that the cortex is more active during individuated versus nonindividuated tasks [Hasegawa et al., 2001; Huesler et al., 1998; Tinazzi et al., 2003], while other studies report the opposite [Flament et al., 1993] or find no differences [Hess et al., 1999].

Here we investigated the hypothesis that the outputs of the motor cortex engaged during voluntary contraction of FDI are different when this muscle contracts in a relatively isolated manner (individuated task) from when it contracts in coordination with multiple other muscles (nonindivid-

uated task). To investigate how the execution of different tasks affected the excitability of FDI's entire cortical representation, we asked subjects to voluntarily contract FDI under two different task conditions while we measured the amplitude of FDI MEPs throughout the extent of FDI's cortical representation. We examined FDI MEP amplitudes while subjects grasped an object between their thumb and index finger, or when they grasped the same object between their thumb and all four fingers, keeping the background level of EMG in FDI constant for the two tasks. We then examined task-related differences in cortical excitability throughout FDI's cortical representation.

METHODS

We examined task-dependent changes in cortical excitability throughout the cortical representation of FDI by performing a cortical mapping procedure using single-pulse TMS during the execution of two different motor tasks; grasping an object between the thumb and index finger (2-finger task) and grasping the same object between the thumb and all four fingers (5-finger task). In both tasks, the shoulder, arm, and hand posture, and level of EMG activity in FDI remained the same. The tasks differed only with respect to the involvement of surrounding fingers and muscles; in the 2-finger task subjects grasped the object by flexing the index finger in opposition to the thumb while keeping the other fingertips in contact with the object but as relaxed as possible, whereas in the 5-finger task subjects grasped the object by flexing all four fingers in opposition to the tip of the thumb. The object was a plastic cylinder, 12 cm high with a 5 cm diameter.

Subjects

Five male and five female volunteers aged 21–29 years (median age 24) participated in the study. All were right-handed by self-report and none had any history of trauma, degenerative, or neurological disease affecting the upper limbs. The Committee for Human Rights at the Centre Léon Berard, Lyon, France, approved the experimental procedure, which conformed to the Declaration of Helsinki, and all participants provided informed consent.

EMG Recording and Behavioral Task

Surface EMG was recorded from four muscles in the right arm and hand; first dorsal interosseus (FDI), ulnar portion of flexor digitorum superficialis (FDS_u), little finger portion of flexor digitorum profundus (FDP₅), and Opponens Pollicis (OP). Electrodes, 10 mm in diameter (VerMed, Bellows Falls, VT), were placed in a bipolar configuration over each muscle such that signal from the target muscle was optimized. EMG activity was amplified by a factor of 5,000–20,000 and band pass filtered to produce a signal that fell within a ± 5 V range (Neurolog Instruments; Digitimer Ltd).

Spike2 software and a Power 1401 interface (Cambridge Electronic Design, Cambridge, UK) were used to collect surface EMG data at 1,000 Hz.

Subjects were seated in a reclining chair with their right arm resting on a support grasping the object. Once subjects were comfortable, the positions of the elbow, forearm, and wrist were fixed using a vacuum cast. With this arrangement they were unable to change the position of the right upper limb between 2-finger and 5-finger tasks. Prior to the start of the experiment, the subject was asked to perform three maximal voluntary contractions (MVCs) of the thumb and index finger in opposition. We then calculated the average integrated EMG in FDI and retained the largest of the three values as the MVC. Throughout the experiment, the subject was required to perform either a 2-finger or a 5-finger task while maintaining a tonic FDI contraction of between 5 and 10% of MVC. A screen in front of the subject displayed the integrated EMG signal as well as horizontal cursors indicating 5 and 10% of MVC, providing them with constant on-line feedback about the FDI contraction level.

TMS Mapping Procedure

TMS was applied using a Magstim 200 (Magstim, Dyfed, UK) stimulator connected to a 70-mm figure-of-eight coil. The stimulation intensity for delivery of TMS was different for each subject and was based upon the threshold for activation of the right FDI when the muscle was at rest. For each subject, before mapping the representation of FDI, we identified the optimal location for TMS-activation of FDI by placing the coil near the estimated hand area of the motor cortex, stimulating using a suprathreshold intensity, and then moving the coil in 10-mm steps in order to identify the stimulation site that evoked the largest MEPs in FDI (resting hotspot). Once this site was identified the FDI resting motor threshold was determined as the minimal intensity of stimulation that produced MEPs larger than 50 μ V in 50% of the stimulations delivered to this site.

To facilitate the mapping, subjects wore a tight cap with a grid consisting of a set of points placed 10 mm apart. We were able to obtain a precise estimate of the stimulation site by localizing the TMS coil relative to the brain surface. This was achieved by first acquiring an anatomical magnetic resonance image (MRI) of the brain of each subject. We then used this image to achieve real-time guidance of the positioning of the stimulating coil relative to the brain surface [Noirhomme et al., 2004]. To do this we coregistered the subject's MRI with the actual position of his head by placing a Polhemus receiver on the forehead and then measuring the 3D location of 200 points on the scalp with an electromagnetic position sensor (Polhemus Isotrack II[®]).

During the construction of the task-related TMS maps, stimulation intensity was set as the subject's FDI resting motor threshold (since motor threshold decreases when a muscle is actively contracted, this resulted in suprathreshold stimulation), and across subjects this varied between 40 and 77% of maximal stimulator output, with an average

of 61%. Once the TMS coil had been localized to a point on the brain a trial began. At the beginning of each trial the subject was told which task to perform (2-finger or 5-finger), and a screen in front of the subject showed the real-time amplitude of the integrated FDI EMG activity. During map construction each grid locus was stimulated with one stimulation train (six pulses, with random intervals of between 3 and 5 s between each pulse) during the 2-finger task and another stimulation train during the 5-finger task. Subjects were instructed that throughout the two stimulation trains they were to monitor the FDI EMG level such that they maintained a contraction of between 5 and 10% of MVC (this range was indicated by two horizontal cursors on the display viewed by the subjects). As soon as the FDI EMG level was within the required range, a train of six stimuli was delivered to a single position over the left primary motor cortex. Without moving the position of the coil the subject then performed the second task and the second stimulation train was delivered with a delay of at least 1 min between the two trains. The coil was then moved to another position on the scalp, and the same procedure was repeated, with the order of execution of the two tasks randomized across all stimulation sites.

The number and extent of cortical sites stimulated differed for each subject as we continued to stimulate at various grid loci until stimulation of sites at the boundary of the stimulated area no longer evoked MEPs in FDI during either of the tasks.

Analysis of Background EMG Activity

For each TMS pulse (six pulses per stimulation train), we calculated the background EMG level in the 500 ms prior to the pulse. We then calculated the average background EMG level in each muscle, for each stimulation site, and for each of the two tasks. We examined whether FDI contraction levels differed between tasks by using a paired *t*-test to compare the average background EMG in FDI at each stimulation point during the two tasks. This test was done separately for each subject, and for seven of the 10 subjects there were no significant differences between the EMG levels in FDI during the two tasks. For the remaining three subjects there was significantly more EMG during the 2-finger than the 5-finger task, but this difference represented less than 1% MVC.

We reasoned that the additional contraction of the middle, ring, and little fingers in the 5-finger task should have resulted in EMG levels in FDS_u and/or FDP₅ that were higher during the 5-finger than the 2-finger task. Thus, to examine whether subjects followed the instructions and performed two different grasping tasks (since we could not assess this visually as hand posture remained constant between the two tasks), we examined the background EMG activity in FDP₅ and FDS_u at each stimulation point during the two tasks. For all 10 subjects there was more EMG during the 5-finger than the 2-finger task in at least one of these

two muscles, indicating that subjects followed the task instructions (see Fig. 1 for an example).

Analysis of MEPs

A custom-made program (Matlab[®] software—Mathworks) was used to measure peak-to-peak MEP amplitudes from the FDI EMG recordings. For each task, we calculated the mean amplitude of FDI MEPs at each stimulated point and then projected these values onto the brain in order to create separate cortical representation maps of FDI for the 2-finger and 5-finger tasks. To compare with other studies in which MEPs were only evoked from the hotspot, we first examined the average MEP amplitude at the resting hotspot during the 2-finger and 5-finger tasks (Fig. 2A). We then examined the 2-finger and 5-finger maps and compared the average MEP amplitude recorded at the site from which the largest average MEPs were recorded during the 2-finger (MAX₂) and 5-finger (MAX₅) tasks.

To quantify between-task differences in MEP amplitude throughout the FDI cortical representation, for each subject we first calculated the average MEP amplitude for each task across *all stimulation sites* and performed a one-sample paired *t*-test with data from all 10 subjects. We then examined the data from each subject separately by performing a one-sample paired *t*-test on the average MEP amplitude at each stimulation site during each task. We also measured the centers of gravity (COG) of the 2-finger and 5-finger FDI maps [Noirhomme et al., 2004] and the spatial extent of each map. To measure spatial extent, we took the largest MEP amplitude recorded at either the MAX₂ or MAX₅ site and expressed the average MEP amplitude recorded during each task and at each site as a percentage of this value. Map extent was calculated as the number of sites at which the average MEP amplitude was at least two thirds of the maximal TMS-elicited MEP amplitude [Classen et al., 1998].

RESULTS

MEP Amplitudes at the FDI Resting and Active (MAX₂/MAX₅) Hotspots

Figure 2A shows the average MEP amplitude evoked by stimulation at the FDI resting hotspot (measured prior to the mapping procedure while the muscle was at rest) during the 2-finger and 5-finger tasks. For seven of the 10 subjects the average MEP amplitude at the hotspot was greater (on average by 25%) during the 5-finger than the 2-finger task. For the other three subjects we observed the reverse; the average MEP amplitude was greater during the 2-finger than the 5-finger task (on average by 17%). Across all subjects the average MEP amplitude at the hotspot during the 5-finger task was 3.49 (SD = 2.93) and during the 2-finger task was 2.84 (SD = 2.16), this difference did not reach significance ($t_9 = 2.02$, $P = 0.07$).

Since we recorded MEPs throughout the extent of FDI's cortical representation, we were able to examine whether

Figure 1.

Example EMG traces obtained during stimulation trains delivered to the same site during the 2-finger (left) and 5-finger (right) tasks. Each row represents the raw EMG data recorded from four different muscles on the right hand while one subject gripped the object with 2 or 5 fingers. Activity from each muscle is represented on the same scale, but scales differ between muscles. Single pulse TMS was delivered six times throughout a single trial, and the time of each stimulation is indicated by the large spikes in the EMG activity, which represent the artifact produced by the TMS stimulation. The six MEPs recorded from FDI during each task have been superimposed and are shown at the top of the figure.

the hotspot identified with the muscle at rest was identical to the site at which the largest MEPs were evoked when the muscle was voluntarily activated. For four of the 10 subjects, the site of the resting hotspot was identical to that from which the MAX was recorded during both the 2- and 5-finger tasks (MAX₂ and MAX₅). For two subjects the rest-

ing hotspot and either the MAX₂ or MAX₅ sites were identical, for another two the resting hotspot and the MAX₂ and MAX₅ sites were all different, and for the remaining two the MAX₂ and MAX₅ sites were identical but were not at the same site as the resting hotspot. It is important to note that, despite not being identical, these sites were always within a 1 cm radius of each other.

Given that the site of maximal excitability was not always the same for the two tasks, we investigated whether the average MEP amplitude evoked by stimulation at the MAX₂ and MAX₅ sites differed between tasks (Fig. 2B). For six of the 10 subjects the average MEP amplitude was greater at MAX₅ than MAX₂ (on average by 19%). For the other four subjects the average MEP amplitude was greater during MAX₂ than MAX₅ (on average by 18%). Overall, this analysis revealed a pattern of results similar to that observed at the resting hotspot; on average MEPs were larger for the 5-finger task (3.84, SD = 3.31) than the 2-finger task (3.40, SD = 2.61), but MEP amplitude did not differ significantly between tasks ($t_9 = 1.38$, $P = 0.20$).

MEP Amplitudes Throughout the FDI Cortical Representation

To quantify between-task differences in MEP amplitude throughout the FDI cortical representation, we first calculated the average MEP amplitude across all stimulation sites. Averaged across all subjects, FDI MEPs were slightly larger during the 5-finger (1.12, SD = 1.11) than the 2-finger task (1.01, SD = 0.89). Similar to the results obtained at the hotspot and MAX₂/MAX₅ sites, this between-task difference was not significant ($t_9 = 1.13$, $P = 0.25$). Figure 3 shows scatter plots of the average MEP amplitude during the 2-finger and 5-finger tasks for three subjects, where each point represents a different stimulation site. When we analyzed these data separately for each subject we found mixed

Figure 2.

Average FDI MEP amplitudes during 2-finger and 5-finger tasks recorded at the resting hotspot (A) and the MAX sites (B). **A.** Average MEP amplitudes from the site at which stimulation at the lowest intensity produced the largest response with the

muscle at rest ("resting" hotspot). **B.** Average MEP amplitudes from the sites at which stimulation during voluntary contraction of between 5 and 10% MVC, during the 2-finger and 5-finger tasks, produced the largest response (MAX₂ and MAX₅ sites).

results; paired *t*-tests revealed no between-task differences for half of the subjects, three subjects had average MEP amplitudes greater during the 5-finger task than the 2-finger task (e.g. Subject 4), and two subjects had greater MEP amplitudes during the 2-finger task (e.g. Subject 9). For all three subjects in Figure 3 (and for the other seven subjects whose data are not shown) there was a significant linear relationship between MEP amplitude during the two tasks, suggesting that both tasks equally affected the excitability of each stimulation site (range of Pearson *r* values: 0.87–0.96).

COG and Spatial Extent of FDI Maps During 2-Finger and 5-Finger Tasks

Our analyses of MEP amplitudes suggest that the two tasks did not differentially affect the excitability of FDI's cortical representation. Despite this, inspection of Figure 4, which shows FDI maps for the 2- and 5-finger tasks for three different subjects, reveals that the two tasks did not produce identical maps. While there were no obvious differences in the region over the motor cortex where the muscle was represented or in the extent of the muscle's representation during each task, the sites at which stimulation produced the largest responses, indicated by the hot colors, were not always identical for the two task conditions.

To quantify differences between the two maps, we examined whether the COG changed between tasks. For each subject we took the coordinates of the COGs of the 2-finger and 5-finger maps and then calculated the three dimensional (3D) distance between these two sites. A one-sample *t*-test showed that there was a significant shift in the COG site for each task ($t_9 = 6.52$, $P = 0.0001$), but this was extremely small, on average 1.1 mm (SD = 0.54), and is well within the normal limits of variation observed during repeated mapping of the same muscle [Corneal et al., 2005; Noirhomme et al., 2004; Wolf et al., 2004].

The spatial extent of each map was calculated as the number of sites at which the average MEP amplitude was at least two thirds of the maximal TMS-elicited MEP amplitude. Across all subjects, an average of 6.6 stimulation sites (SD = 3.4) had MEP amplitudes of at least two thirds of the largest MEP amplitude during the 2-finger task. This did not differ from the number of comparable sites during the 5-finger task, 6.2 (SD = 3.9) (Wilcoxon signed rank test; $P = 0.64$), suggesting that the spatial extent of the FDI representation did not differ between tasks.

DISCUSSION

Previous TMS studies examining task-related changes in the cortical excitability of hand muscles delivered stimuli at one cortical site only, and then examined how different tasks affected MEP amplitudes at that site. Some of these studies used large circular coils, theoretically stimulating a relatively large proportion of the motor map. Simultaneously stimulat-

Figure 3.

FDI MEP amplitudes at each stimulation site during 5-finger and 2-finger tasks. Each panel shows the average MEP amplitude at a given stimulation site during the 2-finger task as a function of the average MEP amplitude at that same site during the 5-finger task. Values have been normalized as a proportion of the largest average MEP amplitude recorded in FDI. Each panel represents data from a different subject. The correlation coefficients for these three subjects were 0.92, 0.92, and 0.93.

ing the whole cortical representation of a muscle might, however, provide a different picture from that obtained by mapping the whole representation by stimulation at multiple sites using a more focal figure-of-eight coil. The present study is the first to examine task-related changes in MEP amplitude throughout the cortical representation of an intrinsic hand

muscle. Using this technique, we found that pressing an object between either the thumb and index finger or the thumb and all four fingers did not systematically change the excitability of FDI or its cortical topography.

Task-Related Excitability Changes in a Muscle's Cortical Representation

When we stimulated at FDI's resting hotspot the excitability of the cells projecting to FDI was similar for both isometric individuated (2-finger) and nonindividuated (5-finger) gripping tasks. While at least one other study also reported no change in the excitability of the circuits projecting to FDI when subjects perform a precision grip versus a power grip [Flament et al., 1993], the majority of studies find that the circuits activated by stimulation at the resting hotspot are *more excitable* when subjects perform an individuated precision grip than when they performed a nonindividuated power grip [Hasegawa et al., 2001; Huesler et al., 1998; Tinazzi et al., 2003]. Studies that compared an individuated index finger abduction task with a nonindividuated power grip have also shown a task-related modulation of FDI excitability [Datta et al., 1989; Flament et al., 1993], but this modulation was not always in the same direction. After stimulating at FDI's resting hotspot, Datta et al. recorded higher amplitude MEPs during index finger abduction than during a power grip, but Flament et al. found the opposite.

Various reasons have been invoked to explain these discrepant findings, including methodological differences between studies, the use of a sustained versus a repeatedly initiated isometric contraction, and the motor strategies used by individuals [e.g. Tinazzi et al., 2003], but it remains unclear exactly how MEP amplitudes in intrinsic hand muscles are affected by different tasks. In the present study, we found no task-related differences in FDI excitability while subjects grasped an object with an individuated precision grip or a nonindividuated power grip. This suggests either that task-related modulation of motor cortex activity is not related to task individuation, or that the degree of task individuation interacts with other factors like precision or complexity. By asking subjects to monitor the level of activity in FDI, we forced subjects to perform two highly precise tasks that differed only with respect to the degree of individuation (2-fingers vs. 5-fingers). In contrast, studies that found differences between the individuated precision grip and the nonindividuated power grip generally used tasks with different precision requirements; the power grip usually required less precise placement of the fingertips and less attention to the distribution of force across the fingertips. But precision cannot explain all task-related differences observed in FDI excitability, as Datta et al. [1989] observed greater excitability during the highly individuated index finger abduction than the nonindividuated power grip while there were no clear differences in the precision required to perform their two tasks.

Since we found no task-related differences in the current study, we cannot answer the question of which task features

Figure 4.

Cortical topography of FDI during 2-finger and 5-finger tasks. Cortical topography of FDI in three different subjects during the 2-finger and 5-finger tasks. Maps are interpolated from the mean peak-to-peak amplitude of FDI MEPs at each stimulation site (six stimulations/site). Red indicates the maximal response intensity [corresponding to 0.90/1.30 mV (Subject 1; 2-finger/5-finger), 5.2 and 5.4 mV (Subject 3; 2-finger/5-finger), and 1.80 and 1.48 mV (Subject 5; 2-finger/5-finger)], and dark blue, no response.

modulate neural activity in the motor cortex. Despite this, the discrepant results of previous studies might be partially explained by our observation that the resting hotspot was not always at the same site as the active hotspot, and that in some subjects the active hotspot for the precision task (MAX_2) was not the same as that for the power task (MAX_5). For example, studies that found task-related differences in MEP amplitude at the resting hotspot might have used tasks that equally affected cortical excitability at every site in the muscle's cortical representation. Thus, stimulating at either the resting or active hotspot would have produced a similar task-related modulation of MEP amplitude. In contrast, studies that did not find task-related differences in MEP amplitude might have used tasks that differentially modulated cortical excitability at specific sites within the muscle's cortical representation (e.g. the active hotspots), but not necessarily at its resting hotspot. Alternatively, the absence of task-related differences in MEP amplitude at the resting hotspot might reflect the fact that the two tasks equally affected excitability throughout the muscle's cortical topography (current results).

In our study, the resting and active hotspots were never separated by more than 1 cm. Thus, although plausible, the hypothesis presented above could explain the discrepant results of previous studies only if different tasks produced extremely focal changes in excitability. The only other study to examine task-related changes throughout the cortical topography of a muscle demonstrated that masseter excitability and topography changed with different tooth-clenching tasks, but that the point of highest excitability and the pattern of activity across the cortical representation of the muscle remained stable [Watson et al., 2000]. Unlike jaw muscles, however, hand and finger movements are associated with more corticomotoneuronal (CM) system activity due to the higher number of corticospinal neurons devoted to hand muscle representations [Colebatch and Gandevia, 1989; Lang and Schieber, 2003; Lawrence and Kuypers, 1968; Phillips and Porter, 1977; Raghavan et al., 2006]. Thus, unlike switching between two teeth-clenching tasks, changing between a precision grip and a power grip could result in a focal, unevenly distributed change in the excitability of cells projecting to hand muscles.

The Contribution of the CM System to Different Manual Tasks

In the absence of complete maps of hand muscles under different task conditions, it is impossible to know exactly why some studies report a greater contribution of the CM system to individuated than nonindividuated tasks while others report the opposite, or no differences. One reason might lie in the behavior of individual subjects. In this study, half of our subjects showed the same pattern of results as that observed in the averaged results—no excitability differences between precision and power grip tasks. For the remaining subjects, however, the CM system was more engaged during either the precision grip (two subjects) or the power grip (three subjects). Thus, it is impossible to make an overall conclusion about the relative contribution of the CM system to our individuated and nonindividuated tasks. The variability between subjects that we observed has also been reported in previous studies. For example, both Bonnard et al. [2007] and Schieppati et al. [1996] found a task-dependent modulation in the excitability of corticospinal projections to either FDI or OP (depending on the subject), but never to both muscles. A more useful approach for the future might be to closely examine the behavior of individual subjects, and to attempt to understand how individual task strategies and prior manual training or experience interact with the degree to which the CM system is engaged in various manual tasks. To fully understand how these factors affect the behavior of the entire population of cells projecting to a muscle, it will be important to stimulate throughout the muscle's cortical representation and not only at its resting hotspot.

Stability of Cortical Muscle Motor Maps

TMS motor mapping is used extensively to evaluate the effect of various interventions (e.g. stroke, skill acquisition, damage to the periphery) on the cortical representation of individual muscles. In all of these contexts, changes in various TMS measurements are taken as indicators of some form of reorganization within the motor system. Thus, accurate interpretation of muscle representation changes relies upon the stability and reliability of TMS measures. While a few studies have investigated the test-retest reliability of TMS measurements [e.g. Carroll et al., 2000; Malcolm et al., 2006; Uy et al., 2002; Wolf et al., 2004], none have examined the stability of hand muscle maps during voluntary muscle contraction. We found that active contraction of FDI within different contexts produced highly stable TMS measurements. While this does not answer the question of the how the CM system contributes to different manual tasks, it does show the stability of cortical maps during active muscle contraction (even when this contraction is in the context of two different gripping tasks). This expands the possibilities for studying cortical reorganization in the context of active muscle contraction, and as such will enable us to better understand whether changes in the motor system observed when muscles are at rest are also present during voluntary muscle recruitment.

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