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RESEARCH ARTICLE

Neural mechanism of selective finger movement independent of synergistic movement

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Abstract

Muscle synergy is important for simplifying functional movement, which constitutes spatiotemporal patterns of activity across muscles. To execute selective finger movements that are independent of synergistic movement patterns, we hypothesized that inhibitory neural activity is necessary to suppress enslaved finger movement caused by synergist muscles. To test this hypothesis, we focused on a pair of synergist muscles used in the hand opening movement, namely the index finger abductor and little finger abductor (abductor digiti minimi; ADM), and examined whether inhibitory neural activity in ADM occurs during selective index finger abduction/adduction movements and/or its imagery using transcranial magnetic stimulation and F-wave analysis. During the index finger adduction movement, background EMG activity, F-wave persistence, and motor evoked potential (MEP) amplitude in ADM were elevated. However, during the index finger abduction movement, ADM MEP amplitude remained unchanged despite increased background EMG activity and F-wave persistence. These results suggest that increased spinal excitability in ADM is counterbalanced by cortical-mediated inhibition only during selective index finger abduction movement. This assumption was further supported by the results of motor imagery experiments. Although F-wave persistence in ADM increased only during motor imagery of index finger abduction, ADM MEP amplitude during motor imagery of index finger abduction was significantly lower than that during adduction. Overall, our findings indicate that cortical-mediated inhibition contributes to the execution of selective finger movements that are independent of synergistic hand movement patterns.

Keywords Transcranial magnetic stimulation · Hand synergy · F-wave · Selective finger movement · Inhibitory neural activity

Introduction

Selective finger movement plays an important role in producing coordinated and dexterous finger movements. Previous studies have demonstrated that inhibitory neural activity, such as surround inhibition (Sohn and Hallett 2004; Beck et al. 2008) and short-interval intracortical inhibition (SICI) (Stinear and Byblow 2003, 2004), contribute to the control of selective finger movement. However, humans cannot perform their intended movements completely independently, and movements of other body parts not directly related to that movement may occur. This unintended finger movement is called "enslaving." A number of previous studies have investigated the anatomical, biomechanical, and neurophysiological mechanisms of this phenomenon (Schieber 1991; Zatsiorsky et al. 1998; Slobounov et al. 2002; Reilly and Schieber 2003). In particular, the strength of enslaving depends on which finger is instructed to move as well as its movement direction (Hager-Ross and Schieber 2000; Reilly and Hammond 2000; Park and Xu 2017). For example, considering the combination of index and little finger movement, index finger abduction is often accompanied by little finger abduction during hand opening movement in

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daily life. Conversely, index finger adduction movement does not involve little finger abduction. Thus, when selective index finger abduction movement is required, neuronal activity to suppress little finger abduction would be necessary. However, to the best of our knowledge, no studies have addressed the association between the movement direction of the instructed finger and inhibition of the corticospinal excitability of the enslaved finger muscle. We hypothesized that the corticospinal excitability of the little finger abductor muscle (abductor digiti minimi; ADM) is suppressed only during index finger abduction and not during adduction movement. To test this hypothesis, in the present study, we investigated whether the inhibition of corticospinal excitability of the enslaved finger muscle (ADM) during index finger movement occurs depending on the movement direction (abduction and adduction) using transcranial magnetic stimulation (TMS). In addition, the contribution of spinal excitability to corticospinal excitability was examined by F-wave experiment under the same condition. However, one methodological consideration should be mentioned. MEP amplitude obtained using TMS increases in proportion to the size of background EMG activity (Hasegaw et al. 2001). Therefore, when EMG activity occurs, MEP amplitude alone may not be sufficient to assess inhibition of the enslaved finger muscles. Therefore, we evaluated the relationships between the size of background EMG activity and MEP amplitude in enslaved finger muscle during each movement direction. In addition, it is not possible to simply compare the sizes of MEP for tasks with different sizes of background EMG activity. In this study, because the size of background EMG activity of ADM was predicted to differ depending on the direction of index finger movement, we normalized MEP amplitude with background EMG activity size (Yahagi et al. 2005; Kazennikov et al. 2008) and verified the difference with the movement direction.

Furthermore, we adopted a motor imagery task as another way to eliminate the effect of background EMG size on MEP amplitude. Motor imagery is defined as the mental simulation of a motor act, which is internally reproduced within the brain without any overt movement (Jeannerod 1995; Decety and Grezes 1999). Functional imaging studies have revealed that brain regions activated during actual motor execution are also recruited during motor imagery (Case et al. 2015). Many TMS studies have shown that corticospinal excitability of the agonist muscle increases, even though there is no muscle activity during motor imagery (Yahagi et al. 1996; Fadiga et al. 1999; Kaneko et al. 2003). Therefore, motor imagery has been used as a method to independently examine human motor system without being affected by actual motor output and accompanying sensory input. Some studies have recently reported that MEP amplitude during motor imagery combined with action observation (MI + AO) is greater than that during action observation alone (Wright et al. 2014; Mouthon et al. 2015; Cengiz et al. 2018; Kaneko et al. 2018). In addition, Sakamoto et al. (2009) have reported that MEP amplitude during MI + AO was larger than that during motor imagery alone. However, no studies have examined the neural mechanisms of "enslaving phenomenon" during MI + AO (including motor imagery or action observation alone). Based on these backgrounds, we hypothesized that cortical inhibition of the enslaved finger muscle (ADM) during MI + AO could be selectively evaluated using TMS without the effect of background EMG and accompanying afferent input. Therefore, we examined whether inhibition of the corticospinal excitability of the enslaved finger muscle occurs during MI + AO of the index finger depending on the imagined movement direction using TMS. Furthermore, spinal contribution to corticospinal excitability under similar conditions was examined using F-wave analysis.

Materials and methods

Subjects

A total of 29 subjects [age (mean ± SD), 20.4 ± 0.9 (range 19–22) years] participated in this study. All subjects were right-handed according to the Edinburgh handedness inventory (Oldfield 1971). All subjects provided written informed consent prior to participation. The ethics committee of the Ibaraki Prefectural University of Health Sciences approved the experimental protocol, and all procedures conformed to the standards in the World Medical Association Declaration of Helsinki.

Motor execution and MI + AO tasks

The motor execution and MI + AO tasks examined in this study were identical to those previously reported (Aoyama et al. 2019). The subjects were instructed to be seated in a chair with their right hand on a side table. They performed the motor execution task while observing the moving images used in MI + AO task to unify the visual conditions between motor execution and MI + AO tasks. A 10-s movie comprising three phases, namely a static image of the hand (rest, 8 s), right index finger abduction movement (1 s), and adduction movement (1 s), was repeatedly displayed on a computer screen placed in front of the subjects. The subjects executed right index finger abduction–adduction movement as selectively as possible while observing the movie during the motor execution task and practiced the task until they could move their index finger synchronously with the movie while confirming no EMG activity during the rest phase.

During the MI + AO task, the subjects were instructed to observe the movie projected on the screen, while

simultaneously imagining the kinesthetic sensation generated by the actual index finger movement. They practiced the task without any muscle activity, using EMG feedback from the finger muscles. Similar to the motor execution task, the subjects were instructed to imagine the index finger movement as selectively as possible in the MI + AO task. The Kinesthetic and Visual Imagery Questionnaire (KVIQ) was administered to assess the motor imagery ability of the subjects (Malouin et al. 2007). In this questionnaire, the subjects answered the vividness of visual and kinesthetic imagery for five types of movements using the 5-point Likert scale. The range of possible score is 10–50, with higher scores indicating greater imagery ability.

Electromyography

The skin of subjects was prepared by rubbing with alcohol and abrading with abrasive skin prepping gel. Surface Ag–AgCl electrodes were placed over the ADM and FDI muscles in a belly tendon montage. ADM, the little finger abductor, and FDI, the index finger abductor, represent a pair of synergist muscles during the hand opening movement. EMG signals were amplified (Neuropack MEB2300; Nihon Kohden, Japan) and band-pass filtered at 5 Hz–5 kHz. All signals were sampled at 10 kHz and stored for offline analysis in a laboratory computer.

Experiment 1: TMS experiment

Fourteen healthy subjects [age (mean ± SD), 20.5 ± 0.8 years, 4 men and 10 women] participated in this experiment. A Magstim 200^2 stimulator (Magstim Co., Whitland, UK) connected to a figure-of-eight coil (diameter of each loop = 70 mm) was used to elicit motor-evoked potential (MEP) from the right ADM muscle. The handle of coil was positioned pointing backward and laterally at a 45° angle from the midline to induce anteromedial current direction in the left brain and to activate the pyramidal cells trans-synaptically (Kaneko et al. 1996; Di Lazzaro et al. 2001). TMS was applied over the optimal scalp site to elicit the most consistent MEP amplitude from the ADM muscle, with the stimulus intensity slightly above the threshold. The resting motor threshold (RMT) was defined as the lowest intensity that produced an MEP amplitude of > 50 μV in at least five of the ten trials. In the test trials, a stimulus intensity of 140% RMT was used (Sohn and Hallett 2004; Beck et al. 2008; Thirugnanasambandam et al. 2015). TMS was applied at rest (6 s after the beginning of the rest phase), the middle phase of the index finger abduction (0.5 s after the beginning of the abduction movement), or adduction (0.5 s after the beginning of each movement) phases in a randomized order using the LabVIEW program (National Instruments, USA) to avoid prediction of the stimulus timing. The inter-trial interval of TMS was at least 6.5 s. During each phase of the motor execution and MI + AO tasks, at least 14 MEPs were recorded. Trials in which the subject contracted the ADM and FDI muscles involuntary during the MI + AO task or the rest phase of the motor execution task were rejected and another trial was recorded. The effect of the "condition" (i.e., rest, index finger abduction, and adduction) on ADM peak-to-peak MEP amplitude and average rectified value (ARV) of the background EMG activity (0–50 ms prior to stimulation) for both motor execution and MI + AO tasks were tested using one-way repeated-measures analysis of variance (ANOVA). Multiple comparison tests were performed using the Bonferroni correction, with the level of significance set at $p < 0.05$. In addition, Cohen's d effect sizes were calculated for pairwise comparison.

To clarify the association between changes in background EMG and MEP amplitudes, percentage of the ADM MEP and background EMG from rest to movement (abduction or adduction) was calculated for each subject as follows:

$$\Delta\text{background EMG (\%)} = \text{background EMG (abduction or adduction)} / \text{background EMG (rest)} \times 100$$

$$\Delta\text{MEP (\%)} = \text{MEP (abduction or adduction)} / \text{MEP (rest)} \times 100.$$

Spearman's rank correlation coefficients, which are less sensitive to outliers in the data (de Winter et al. 2016) between Δbackground EMG and ΔMEP for each movement direction, were calculated to evaluate the effects of movement direction on the association between changes in EMG activity and corticospinal excitability. In addition, to compare the modulation of MEP by background EMG activity change (ΔMEP/Δbackground EMG × 100) between two movement directions, Student's t test was performed.

Experiment 2: F-wave experiment

Fifteen healthy adults [age (mean ± SD), 21.4 ± 1.5 years, 4 men and 11 women] participated in this experiment. F-waves and M-waves were recorded from the ADM muscles. Supramaximal electrical stimulation was applied to the ulnar nerve at the wrist using a rectangular electrical pulse of 0.2 ms. Similar to the TMS experiment, three stimulus timings (rest, abduction, and adduction) were used in a randomized order. At least 30 F-waves and M-waves were recorded during each phase. Amplifier gains of 200 or 500 μV/division for F-wave and 5 or 10 mV/division for M-wave were used. All trials in which the subject contracted the ADM and FDI muscles involuntarily during the MI + AO task or the rest phase of the motor execution task were rejected and another trial was recorded. F-wave persistence was defined as the number of measurable F-wave responses divided by all trials of

supramaximal stimulation (Suzuki et al. 2014; Aoyama et al. 2019). In addition, F/M amplitude ratio was calculated. The effects of "conditions" on F-wave persistence, F/M amplitude, and ARV of the background EMG activity (0–50 ms prior to stimulation) for both tasks were tested using one-way repeated-measures ANOVA. Multiple comparisons were performed using the Bonferroni correction, with the level of significance set at $p<0.05$. The Cohen's d effect sizes were calculated for pairwise comparison.

Results

Experiment 1: TMS experiment

Superimposed ADM MEP raw data and background EMG activity for a representative subject are shown in Fig. 1. ADM MEP amplitudes (a) and background EMG signals (b) (mean ± SD), respectively, for each phase during the motor execution task are shown in Fig. 2. There were main effects of "condition" on the ADM MEP amplitude [F (2, 26) = 9.55, $p=0.001$] as well as on background EMG signals [F (2, 26) = 17.69, $p<0.0005$] during the motor execution task. Bonferroni's multiple comparison tests showed that the ADM MEP amplitudes in the adduction phase (2.26 ± 1.20 mV) were significantly greater than those in the rest phase (1.28 ± 0.84 mV, $d=0.95$). There was no significant difference in ADM MEP amplitudes between the abduction (1.87 ± 1.28 mV) and rest phases ($d=0.55$). However, background EMG signals were significantly increased in the abduction (7.10 ± 3.22 μV, $d=1.60$) and adduction (5.58 ± 2.75 μV, $d=1.12$) phases compared with those in the rest phase (3.22 ± 1.23 μV). In addition, there was a significant difference in background EMG signals between the abduction and adduction phases ($p=0.028$, $d=0.51$).

There was a significant correlation between Δbackground EMG (adduction) and ΔMEP (adduction) ($p=0.021$, $\rho=0.609$, Fig. 3b). However, there was no correlation between Δbackground EMG (abduction) and ΔMEP (abduction) ($p=0.659$, $\rho=0.130$, Fig. 3a). Student's t test showed that ΔMEP/Δbackground EMG from rest to adduction (120.8 ± 52.0%) was significantly larger than that from rest to abduction (77.8 ± 38.1%, $p=0.002$, $d=0.94$, Fig. 3c).

There was a main effect of "condition" on ADM MEP amplitude during the MI + AO task [F (2, 26) = 4.43, $p=0.022$, Fig. 4]. Post hoc test showed that ADM MEP amplitude during the abduction (0.91 ± 0.44 mV) phase was significantly smaller than that during the adduction (1.14 ± 0.59 mV) phase ($d=0.45$). There was no main effect of "condition" on both FDI and ADM background EMG activities during the MI + AO task [FDI; F (2, 24) = 0.24, $p=0.76$, rest; 3.11 ± 1.47 μV, abduction; 3.15 ± 1.57 μV, adduction; 3.16 ± 1.43 μV, ADM; F (2, 24) = 2.85, $p=0.076$, rest; 2.44 ± 1.29 μV, abduction; 2.47 ± 1.28 μV, adduction;

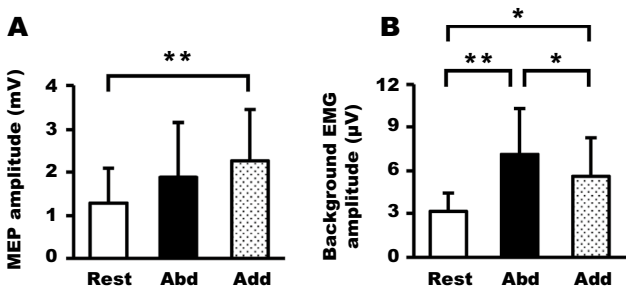

Fig. 2 Summary of the results of motor execution task in Experiment 1. Mean ± SD of the ADM MEP amplitude (**a**) and background EMG amplitude (**b**) during three phases of the motor execution task [rest, abduction (abd), and adduction (add)] (*$p<0.05$, **$p<0.01$)

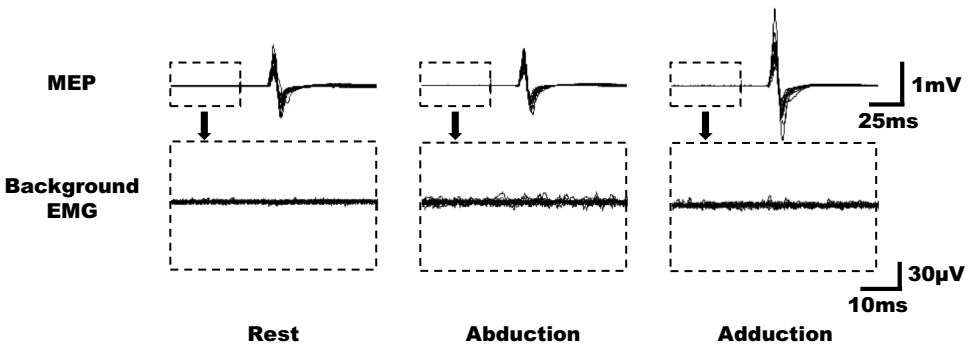

Fig. 1 Raw data of a representative subject during the motor execution task in Experiment 1. Superimposed raw MEP amplitude (upper) and background EMG (lower) for a representative subject recorded from ADM muscle during the motor execution task. In the resting condition (left), no EMG activity was observed. During abduction condition (center), although obvious EMG activity was observed, there was no increase in MEP amplitude compared with rest. Compared with abduction condition, the increase in EMG activity during adduction condition (right) was low, but there was a clear increase in MEP amplitude

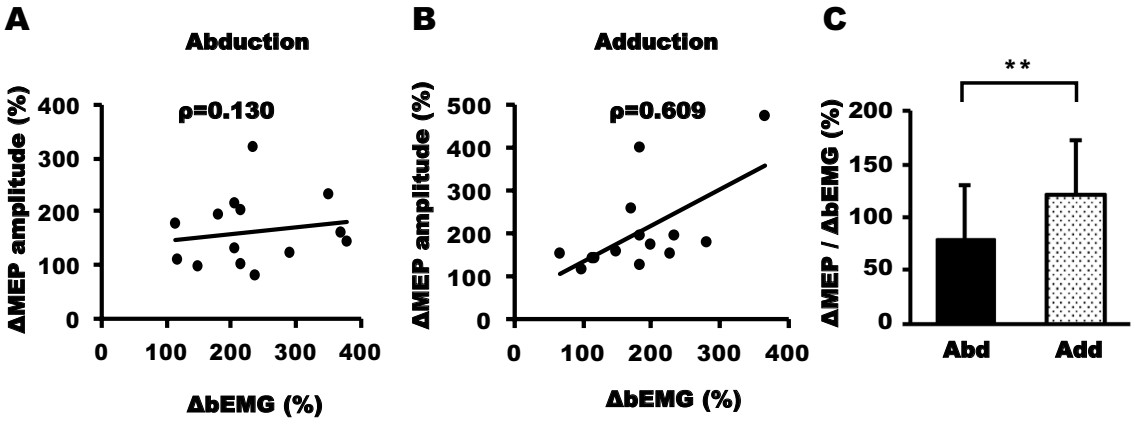

Fig. 3 Association between Δbackground EMG and ΔMEP amplitude from rest to movement in the ADM muscle. **a** Correlation between Δbackground EMG (abduction/rest × 100) and ΔMEP amplitude (abduction/rest × 100). **b** Correlation between Δbackground EMG (adduction/rest × 100) and ΔMEP amplitude (adduction/rest × 100). **c** Comparison of the ADMΔMEP/Δbackground EMG between abduction and adduction

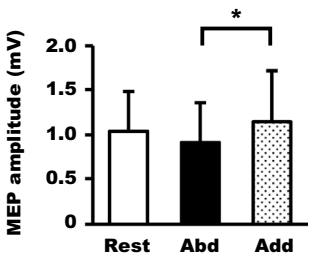

Fig. 4 Summary of the results of MI + AO task in Experiment 1. Mean ± SD of the ADM MEP amplitude during three phases of the MI + AO task [rest, abduction (abd), and adduction (add)] (*$p < 0.05$, **$p < 0.01$)

2.62 ± 1.57 μV]. The mean (± SD) KVIQ scores was 40.7 (± 6.2).

Experiment 2: F-wave experiment

Table 1 presents mean ± SD of F-wave persistence and F/M amplitude during the motor execution and MI + AO tasks. There were main effects of "condition" on ADM F-wave persistence [F (2, 24) = 9.92, $p = 0.001$], F/M amplitude ($F = 18.9, p < 0.0005$), and background EMG signals [F (2, 24) = 10.98, $p < 0.0005$] during the motor execution task. The ADM F-wave persistence in the abduction (95.0 ± 5.8%, $d = 1.06$) and adduction (92.2 ± 11.4%, $d = 0.73$) phases was significantly larger than that at rest (81.7 ± 16.7%) during the motor execution task. F/M amplitude during the motor execution task was significantly greater in the abduction (1.51 ± 0.48%, $d = 1.28$) and adduction (1.20 ± 0.52%, $d = 0.56$) phases than at rest (0.94 ± 0.39%). In addition, F/M amplitude in the abduction phase was significantly larger than that in the adduction phase ($d = 0.61$). ADM background EMG activity in the abduction (7.01 ± 0.24 μV, $d = 2.4$) and adduction (6.62 ± 4.89 μV, $d = 1.1$) phases was significantly greater than that at rest (2.77 ± 0.71 μV) phase.

There was a main effect of "condition" on ADM F-wave persistence during the MI + AO task [F (2, 24) = 3.594, $p = 0.041$]. Bonferroni multiple comparison tests showed that ADM F-wave persistence in the abduction phase (87.9 ± 16.8%) was significantly higher than that in the

Table 1 Summary of the results of F-wave experiment

	Rest	Abduction	Adduction
ME			
Persistence (%)	81.7 ± 16.7 b*, c**	95.0 ± 5.8 a*	92.2 ± 11.4 a**
F/M amplitude (%)	0.94 ± 0.39 b**, c*	1.51 ± 0.48 a**, c*	1.20 ± 0.52 a*, b*
MI + AO			
Persistence (%)	83.6 ± 18.5 b*	87.9 ± 16.8 a*	86.7 ± 16.3
F/M amplitude (%)	0.87 ± 0.34	0.96 ± 0.34	0.90 ± 0.34

Mean ± SD of F-wave persistence and F/M amplitude recorded from the ADM muscle during the motor execution and MI + AO tasks of abduction, adduction, and rest phases. The significant differences are indicated by different letters and symbols (a: Rest, b: Abduction, c: Adduction, **$p < 0.01$, *$p < 0.05$)

rest phase (83.6 ± 18.5%, $d = 0.24$). There was no significant main effect of "condition" on ADM F/M amplitude [F (2, 24) = 1.12, $p = 0.34$, rest; 0.87 ± 0.34%, abduction; 0.96 ± 0.44%, adduction; 0.90 ± 0.34] and on both FDI and ADM background EMG activities [FDI; F (2, 28) = 1.47, $p = 0.25$, rest; 2.47 ± 0.79 μV, abduction; 2.56 ± 0.60 μV, and adduction; 2.36 ± 0.64 μV, ADM; F (2, 24) = 1.22, $p = 0.31$, rest; 2.45 ± 0.62 μV, abduction; 2.50 ± 0.67 μV, adduction; 2.34 ± 0.56 μV] during the MI + AO task. The average (± SD) KVIQ score was 44.1 (± 4.3).

Discussion

We examined whether inhibitory neural activity is required when performing index finger abduction movement independently of the synergistic hand movement pattern (hand opening movement) using TMS and F-waves. ADM MEP amplitude remained unchanged during index finger abduction movement, but was significantly greater during index finger adduction. Nevertheless, the background EMG activity of ADM was significantly higher during index finger abduction than at rest or during adduction. Spinal reflex excitability of ADM, as examined by F-waves, was significantly higher during index finger abduction than at rest and during adduction. Furthermore, although ADM F-wave persistence increased only during MI + AO of index finger abduction, ADM MEP amplitude during the MI + AO of index finger abduction was significantly lower than that during adduction. These results suggest that inhibitory neural activity may be required to perform selective finger movement independently of the synergistic hand-movement pattern.

In general, MEP amplitude is strongly affected by changes in background EMG activity. Therefore, when EMG activity increases, MEP amplitude should increase. However, this association was only observed in ADM during index finger adduction but not during index finger abduction. The dissociation between background EMG activity (or spinal reflex excitability) and corticospinal excitability, as examined by TMS in ADM during index finger abduction, suggests that increased spinal reflex excitability is counterbalanced by cortically mediated inhibition (Ethier et al. 2007). This hypothesis is also supported by the results of additional analyses, demonstrating that the ΔMEP/Δbackground EMG ratio was significantly smaller in abduction than in adduction (Fig. 3c). Furthermore, considering that the MEP amplitude is directly proportional to the background EMG amplitude (Hasegaw et al. 2001), our findings of a significant positive correlation between Δbackground EMG and ΔMEP in index finger adduction, while no correlation was observed between Δbackground EMG and ΔMEP in index finger abduction, suggest the involvement of additional inhibitory effects only during index finger abduction.

To exclude the effect of background EMG activity and thereby of sensory afferent input, we further investigated ADM MEP during the MI + AO task of index finger abduction and adduction. The ADM MEP amplitude in the MI + AO task was significantly smaller during index finger abduction than during adduction. This result further supports our assumption that the neural activity associated with the enslaved little finger movement is differently modulated depending on the instructed movement direction of the index finger. Although a significant reduction in the ADM MEP was not observed during the MI + AO task of index finger abduction compared to rest ($p = 0.182$), 11 of the 14 subjects showed reduced ADM MEP. In addition, spinal reflex excitability in ADM was increased during the MI + AO task of index finger abduction compared with that at rest. These results indicate that cortical inhibitory mechanisms might have been recruited to counterbalance the increased spinal excitability of the ADM muscle during the MI + AO task of index finger abduction. Previous TMS studies have shown that the corticomotor excitability of the agonist muscle increases, while antagonist muscle decreases during MI + AO (Wright et al. 2014; Eaves et al. 2016; Aoyama et al. 2019). However, to our knowledge, no study has investigated the neural mechanism associated with enslaving during MI + AO (including motor imagery alone condition). The results of this study suggest that similar inhibitory neural activities may occur in the enslaved finger muscle during motor execution and MI + AO and provide new insights into the neurophysiological similarities between motor execution and MI + AO.

In summary, the present findings support our hypothesis that the neural activity of the enslaved finger muscle is differently modulated depending on the direction of the instructed finger movement. In general, the index finger abductor (FDI) and little finger abductor (ADM) act synergistically during the hand-opening movement. The definition of muscle synergy refers to each muscle working in coordination to simplify the functional movement, which comprises spatiotemporal patterns of activity across muscles (Santello et al. 2013). In particular, the hand-opening movement is the most fundamental synergistic hand movement, since this movement pattern is already present at birth (Connolly and Forssberg 1997). Consistent with this idea, Ehrsson et al. (2002) reported that a broad range of brain areas (e.g., bilateral frontal motor areas, parietal cortex, and lateral cerebellum) show stronger neural activities during non-synergistic hand-movement tasks than during innate synergistic hand opening and closing movement tasks. From a neuroanatomical perspective, a single corticospinal axon has divergent projections to the spinal motoneurons of multiple muscles (Shinoda et al. 1981). There is also evidence that individual muscles have distributed, overlapping representation in the motor cortex, with each cortical point linked by extensive

horizontal connections (Capaday et al. 1998; Schneider et al. 2002; Ethier et al. 2007). These neuroanatomical substrates are considered to be involved in coordinated synergistic hand movement (McMorland et al. 2015). Consequently, even a single finger movement, as adopted in this experiment, does not necessarily imply the neuronal activation of somatotopically segregated brain regions, although it may represent distribution throughout the M1 hand area, including excitatory and inhibitory neurons (Jacobs and Donoghue 1991; Schieber and Hibbard 1993; Schneider et al. 2002; Capaday et al. 2009). Therefore, to execute selective index finger abduction independent of the little finger abduction movement, the cortical-mediated inhibition of the ADM muscle, which is supposed to have strong neuronal connections with FDI as a synergistic muscle, should be required. As a result, seemingly contradictory results that ADM MEP amplitude did not change while spinal excitability and background EMG activity significantly increased might have been obtained. Conversely, because index finger adduction and little finger abduction have a non-synergistic relationship, the necessity of the inhibitory activity of the ADM muscle during index finger adduction movement may be low. Consequently, inhibitory neural activity similar to that during index finger abduction could not be obtained. These results indicate that inhibitory neural activity of enslaved finger muscles occurs only during execution of selective finger movements that are independent of the synergistic movement pattern.

This study has several limitations. The first limitation is the number of trials recorded. Previous studies have recommended to record more than 20 MEPs to obtain more reliable data (Chang et al. 2016; Goldsworthy et al. 2016). However, considering the effect of mental fatigue caused by repeating the task (Rozand et al. 2015), we recorded 14 trials per condition. Therefore, one of the limitations of this study is that there are fewer number of trials than recommended. Second, although we have shown that supraspinal inhibition likely occurs when executing or imaging the movement independent of the synergistic movement pattern, the detailed neural mechanism is unclear in the present study. Many previous studies have shown that surround inhibition and SICI play a crucial role in selective finger movement (Stinear and Byblow 2003; Sohn and Hallett 2004; Stinear and Byblow 2004; Beck et al. 2008). In addition, it has been clarified that the disturbance of this inhibitory neural control of movement is related to focal hand dystonia, which causes abnormal synergistic movement patterns (Stinear and Byblow 2004; Beck et al. 2008). Therefore, in the future, we have to investigate the relationship between presumed cortical mediated inhibition of the enslaved finger muscle obtained in this study and surround inhibition or SICI.

In conclusion, we provide the first evidence that the neural activity of the enslaved finger muscle is differently modulated depending on the direction of the instructed finger movement. In addition, our findings suggest that inhibitory neural activity contributes to selective finger movement independent of hand synergistic movement patterns. These novel findings provide important insight into the neural mechanisms underlying coordinated human limb movement. In addition, these findings may be useful in understanding the clinical conditions in which it is difficult to perform selective finger movement independent of synergistic movement patterns, such as in focal hand dystonia.

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Compliance with ethical standards

Conflict of interest The authors declare no financial and non-financial competing interests.

References

Aoyama T, Kaneko F, Ohashi Y, Kohno Y (2019) Dissociation between cortical and spinal excitability of the antagonist muscle during combined motor imagery and action observation. Sci Rep 9:13120

Beck S, Richardson SP, Shamim EA, Dang N, Schubert M, Hallett M (2008) Short intracortical and surround inhibition are selectively reduced during movement initiation in focal hand dystonia. J Neurosci 28:10363–10369

Capaday C, Devanne H, Bertrand L, Lavoie BA (1998) Intracortical connections between motor cortical zones controlling antagonistic muscles in the cat: a combined anatomical and physiological study. Exp Brain Res 120:223–232

Capaday C, Ethier C, Brizzi L, Sik A, van Vreeswijk C, Gingras D (2009) On the nature of the intrinsic connectivity of the cat motor cortex: evidence for a recurrent neural network topology. J Neurophysiol 102:2131–2141

Case LK, Pineda J, Ramachandran VS (2015) Common coding and dynamic interactions between observed, imagined, and experienced motor and somatosensory activity. Neuropsychologia 79:233–245

Cengiz B, Vuralli D, Zinnuroglu M et al (2018) Analysis of mirror neuron system activation during action observation alone and action observation with motor imagery tasks. Exp Brain Res 236:497–503

Chang WH, Fried PJ, Saxena S, Jannati A, Gomes-Osman J, Kim YH, Pascual-Leone A (2016) Optimal number of pulses as outcome measures of neuronavigated transcranial magnetic stimulation. Clin Neurophysiol 127:2892–2897

Connolly KJ, Forssberg H (1997) Neurophysiology and neuropsychology of motor development. Cambridge University Press, Cambridge

de Winter JC, Gosling SD, Potter J (2016) Comparing the Pearson and Spearman correlation coefficients across distributions and sample sizes: a tutorial using simulations and empirical data. Psychol Methods 21:273–290

Decety J, Grezes J (1999) Neural mechanisms subserving the perception of human actions. Trends Cogn Sci 3:172–178

Di Lazzaro V, Oliviero A, Saturno E et al (2001) The effect on corticospinal volleys of reversing the direction of current induced in the motor cortex by transcranial magnetic stimulation. Exp Brain Res 138:268–273

Eaves DL, Riach M, Holmes PS, Wright DJ (2016) Motor imagery during action observation: a brief review of evidence, theory and future research opportunities. Front Neurosci 10:514

Ehrsson HH, Kuhtz-Buschbeck JP, Forssberg H (2002) Brain regions controlling nonsynergistic versus synergistic movement of the digits: a functional magnetic resonance imaging study. J Neurosci 22:5074–5080

Ethier C, Brizzi L, Giguere D, Capaday C (2007) Corticospinal control of antagonistic muscles in the cat. Eur J Neurosci 26:1632–1641

Fadiga L, Buccino G, Craighero L, Fogassi L, Gallese V, Pavesi G (1999) Corticospinal excitability is specifically modulated by motor imagery: a magnetic stimulation study. Neuropsychologia 37:147–158

Goldsworthy MR, Hordacre B, Ridding MC (2016) Minimum number of trials required for within- and between-session reliability of TMS measures of corticospinal excitability. Neuroscience 320:205–209

Hager-Ross C, Schieber MH (2000) Quantifying the independence of human finger movements: comparisons of digits, hands, and movement frequencies. J Neurosci 20:8542–8550

Hasegaw Y, Kasai T, Kinoshita H, Yahagi S (2001) Modulation of a motor evoked response to transcranial magnetic stimulation by the activity level of the first dorsal interosseous muscle in humans when grasping a stationary object with different grip widths. Neurosci Lett 299:1–4

Jacobs KM, Donoghue JP (1991) Reshaping the cortical motor map by unmasking latent intracortical connections. Science 251:944–947

Jeannerod M (1995) Mental imagery in the motor context. Neuropsychologia 33:1419–1432

Kaneko K, Kawai S, Fuchigami Y, Morita H, Ofuji A (1996) The effect of current direction induced by transcranial magnetic stimulation on the corticospinal excitability in human brain. Electroencephalogr Clin Neurophysiol 101:478–482

Kaneko F, Murakami T, Onari K, Kurumadani H, Kawaguchi K (2003) Decreased cortical excitability during motor imagery after disuse of an upper limb in humans. Clin Neurophysiol 114:2397–2403

Kaneko N, Masugi Y, Yokoyama H, Nakazawa K (2018) Difference in phase modulation of corticospinal excitability during the observation of the action of walking, with and without motor imagery. NeuroReport 29:169–173

Kazennikov O, Solopova I, Talis V, Ioffe M (2008) Anticipatory postural adjustment: the role of motor cortex in the natural and learned bimanual unloading. Exp Brain Res 186:215–223

Malouin F, Richards CL, Jackson PL, Lafleur MF, Durand A, Doyon J (2007) The kinesthetic and visual imagery questionnaire (KVIQ) for assessing motor imagery in persons with physical disabilities: a reliability and construct validity study. J Neurol Phys Ther 31:20–29

McMorland AJ, Runnalls KD, Byblow WD (2015) A neuroanatomical framework for upper limb synergies after stroke. Front Hum Neurosci 9:82

Mouthon A, Ruffieux J, Walchli M, Keller M, Taube W (2015) Task-dependent changes of corticospinal excitability during observation and motor imagery of balance tasks. Neuroscience 303:535–543

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97–113

Park J, Xu D (2017) Multi-finger interaction and synergies in finger flexion and extension force production. Front Hum Neurosci 11:318

Reilly KT, Hammond GR (2000) Independence of force production by digits of the human hand. Neurosci Lett 290:53–56

Reilly KT, Schieber MH (2003) Incomplete functional subdivision of the human multitendoned finger muscle flexor digitorum profundus: an electromyographic study. J Neurophysiol 90:2560–2570

Rozand V, Lebon F, Papaxanthis C, Lepers R (2015) Effect of mental fatigue on speed-accuracy trade-off. Neuroscience 297:219–230

Sakamoto M, Muraoka T, Mizuguchi N, Kanosue K (2009) Combining observation and imagery of an action enhances human corticospinal excitability. Neurosci Res 65:23–27

Santello M, Baud-Bovy G, Jörntell H (2013) Neural bases of hand synergies. Front Comput Neurosci 7:23

Schieber MH (1991) Individuated finger movements of rhesus monkeys: a means of quantifying the independence of the digits. J Neurophysiol 65:1381–1391

Schieber MH, Hibbard LS (1993) How somatotopic is the motor cortex hand area? Science 261:489–492

Schneider C, Devanne H, Lavoie BA, Capaday C (2002) Neural mechanisms involved in the functional linking of motor cortical points. Exp Brain Res 146:86–94

Shinoda Y, Yokota J, Futami T (1981) Divergent projection of individual corticospinal axons to motoneurons of multiple muscles in the monkey. Neurosci Lett 23:7–12

Slobounov S, Johnston J, Chiang H, Ray WJ (2002) Motor-related cortical potentials accompanying enslaving effect in single versus combination of fingers force production tasks. Clin Neurophysiol 113:1444–1453

Sohn YH, Hallett M (2004) Surround inhibition in human motor system. Exp Brain Res 158:397–404

Stinear CM, Byblow WD (2003) Role of intracortical inhibition in selective hand muscle activation. J Neurophysiol 89:2014–2020

Stinear CM, Byblow WD (2004) Impaired modulation of intracortical inhibition in focal hand dystonia. Cereb Cortex 14:555–561

Suzuki T, Bunno Y, Onigata C, Tani M, Uragami S, Yoshida S (2014) Excitability of spinal neural function during motor imagery in Parkinson's disease. Funct Neurol 29:263–267

Thirugnanasambandam N, Khera R, Wang H, Kukke SN, Hallett M (2015) Distinct interneuronal networks influence excitability of the surround during movement initiation. J Neurophysiol 114:1102–1108

Wright DJ, Williams J, Holmes PS (2014) Combined action observation and imagery facilitates corticospinal excitability. Front Hum Neurosci 8:951

Yahagi S, Shimura K, Kasai T (1996) An increase in cortical excitability with no change in spinal excitability during motor imagery. Percept Mot Skills 83:288–290

Yahagi S, Takeda Y, Ni Z et al (2005) Modulations of input-output properties of corticospinal tract neurons by repetitive dynamic index finger abductions. Exp Brain Res 161:255–264

Zatsiorsky VM, Li ZM, Latash ML (1998) Coordinated force production in multi-finger tasks: finger interaction and neural network modeling. Biol Cybern 79:139–150