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Research Article

Ipsilateral contraction increases map area and decreases motor threshold for contralateral hand muscle

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ABSTRACT

Ipsilateral motor pathways projecting from primary motor cortex (M1) to the distal upper limb exist in humans, and activation of these ipsilateral pathways also facilitate corticomotor excitability of the contralateral homologous muscle. Handedness and biological sex potentially influence the motor cortical representations, however their influence on ipsilateral representations remain largely unexplored. Here, we investigated the effects of ipsilateral contraction on hand motor representation size and excitability, and examined whether these effects were dependent on handedness and/or biological sex. In 80 individuals (40 right-handed, 40-left handed, equal males and females), we performed transcranial magnetic stimulation (TMS) to obtain motor threshold and motor map area of the contralateral first dorsal interosseus (FDI) muscle of each hemisphere, at (1) rest and during (2) ipsilateral FDI muscle contraction at approximately 10% of maximum voluntary contraction. Results showed that ipsilateral contraction increased motor map area and decreased motor threshold within M1. These changes were independent of handedness and biological sex, and similar between hemispheres. Our findings demonstrate that an ipsilateral hand contraction increases the size and excitability of motor representations within ipsilateral M1, and these increases are irrespective of one's handedness and biological sex.

Introduction

The neurobiological pathways governing motor control of the upper limb has been a focus of investigation across decades of research. Initial discoveries of crossed corticospinal projections, largely arising from the primary motor cortex (M1), established that motor control operates contralaterally, such that one hemisphere controls the opposite upper limb (Armand, 1982). In 1933 however, Bucy and Fulton first demonstrated movement of the ipsilateral upper limb from cortical stimulation on monkeys (Bucy and Fulton, 1933). Subsequent electrophysiological and neuroanatomical investigations in non-human primates expanded on this finding by demonstrating activation of ipsilateral M1 neurons during unimanual hand movement (Matsunami and Hamada, 1981; Donchin et al., 2002), and showing that approximately 10 % of dorsolateral corticospinal projections, responsible for hand motor control, descend ipsilaterally in the spinal cord (Rosenzweig et al., 2009; Lacroix et al., 2004). These findings ignited interest in studying ipsilateral motor projections in humans, and potential factors influencing the structural and functional organization of this motor pathway.

In humans, the existence of ipsilateral motor pathways to the distal upper limb is documented by the presence of ipsilateral motor evoked potentials from the hand when transcranial magnetic stimulation (TMS) is delivered to M1 (Bernard et al., 2011; Wassermann et al., 1994; Ziemann et al., 1999), and activation of ipsilateral M1 during unimanual hand movements assessed via functional magnetic resonance imaging (fMRI) (Buetefisch et al., 2014; Kim et al., 1993). Additionally, activation of ipsilateral M1 during unimanual hand contraction also facilitates excitability of the resting muscle on the opposite side, as evidenced by

Abbreviations: contra-MEPs, Contralateral motor evoked potentials; EMG, Electromyography; FDI, First dorsal interosseus muscle; fMRI, Functional magnetic resonance imaging; IHI, Interhemispheric inhibition; MVC, Maximum Voluntary Contraction; MEPs, Motor evoked potentials; M1, Primary motor cortex; RMSE, Root mean square error; TMS, Transcranial magnetic stimulation.

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increases in the amplitude of contralateral motor evoked potentials (contra-MEPs) (Muellbacher et al., 2000; Stedman et al., 1998; Perez and Cohen, 2008; Liang et al., 2008). Though not yet demonstrated, ipsilateral contraction may also influence the size of motor representations in M1, given that representations for ipsilateral upper limb muscles overlap with the same areas controlling the homologous muscle on the contralateral side (Donchin et al., 2002; Cisek et al., 2003; Diedrichsen et al., 2013; Heming et al., 2019; Brus-Ramer et al., 2009). TMS motor mapping is one technique that can map the size of motor representations, by pairing a specified stimulation site to the amplitude of MEPs. In this manuscript, 'ipsilateral contraction' refers to a unimanual contraction of the hand located on the same side as the M1 being probed by TMS.

Factors that influence the recruitment of ipsilateral motor pathways are still debated. Handedness is a trait recognized for contributing to asymmetries in the organization of cortical motor regions between hemispheres (Triggs et al., 1999; Wassermann et al., 1992; Nicolini et al., 2019; Amunts et al., 2000; Volkmann et al., 1998). Likewise, handedness may influence ipsilateral M1 activation patterns, although the evidence is mixed. Studies observing an effect have shown that in right-handers, stronger ipsilateral M1 activation occurs in their motor dominant hemisphere (left) (Hayashi et al., 2008; Kawashima et al., 1993; Verstynen et al., 2005; Reid and Serrien, 2014; Ghacibeh et al., 2007; Ziemann and Hallett, 2001). For left-handers, greater ipsilateral M1 activation is seen in either their motor dominant hemisphere (right) (Kawashima et al., 1997; van den Berg et al., 2011) or non-dominant hemisphere (left) (Kim et al., 1993; van den Berg et al., 2011). Other reports however, show no interhemispheric differences in ipsilateral M1 activation in right- (Stinear et al., 2001) and left-handers (Verstynen et al., 2005; Reid and Serrien, 2014; Singh et al., 1998). Biological sex is another influencing factor in the functional organization of the brain. In general, females display reduced structural and functional asymmetries in motor regions (Amunts et al., 2000) and other areas of the brain (Shaywitz et al., 1995). However, sex-based differences in ipsilateral motor control are not well explored. One study conducted by Lissek and colleagues observed greater activation of ipsilateral premotor cortex in females than males during unimanual movements of either hand (Lissek et al., 2007).

In this study, we investigated the potential influence of handedness and biological sex on the recruitment of ipsilateral motor projections. To accomplish this, we examined the modulatory effects of ipsilateral contraction on the size and excitability of motor representations within ipsilateral M1, and investigated whether these effects depend on handedness and biological sex. We used TMS to examine changes in motor map area and motor threshold of the resting contralateral first dorsal interosseus (FDI) muscle from a sustained contraction of ipsilateral FDI, in both hemispheres separately. This study provides an important opportunity to explore the factors of handedness and biological sex and its potential to influence the efficacy of neurorehabilitation approaches. For example, if differences between sexes or handedness are observed, rehabilitative approaches involving unimanual movement may be designed to capitalize on these differences.

Methods

Participants

We recruited 102 healthy adults between the ages of 18–35 for the study. Exclusion criteria included: i) contraindications to receiving TMS including presence of head injury or head surgery, metal implants, history of neurological disease or psychiatric illness, blood relatives with a history of seizures, headaches or migraines, and sleep deprivation; or ii) individuals taking any prescription medication.

Twenty-two eligible participants did not complete the experimental protocol for the study, for reasons including: i) time constraints regarding scheduling of the experimental session; ii) discomfort with TMS stimulation; iii) a motor threshold that was at an %MSO where performing motor mapping at 120 % of motor threshold was not possible to elicit.

Therefore, eighty healthy adults completed the experiment and are included in the analysis. Forty were right-handed (21.9 ± 3.8 years, range 18 – 34) and forty were left-handed (20.9 ± 2.9 years, range 18–28) with equal numbers of males and females in each group. Degree of handedness was assessed using a modified version of the Edinburgh Handedness Questionnaire (Handedness Questionnaire), which assigns a laterality quotient from −100 (strongly left-handed) to + 100 (strongly right-handed). Individuals with contraindications to TMS were excluded from participation (Keel et al., 2001). All participants provided informed written consent and attended one session spanning ~ 3 h in duration. Approval to conduct this study was granted by the Hamilton Integrated Research Ethics Board (REB #16360, April 2023), and all procedures conformed to the Declaration of Helsinki.

Electromyography (EMG)

Surface EMG electrodes were used to record muscle activity from the FDI muscle, and MEPs evoked via TMS were recorded at the contralateral FDI muscle. The FDI was chosen as the muscle of interest since several previous studies have shown that ipsilateral FDI muscle contraction can modulate contra-MEPs at the opposite resting FDI (Reid and Serrien, 2014; Ghacibeh et al., 2007). Surface electrodes (9 mm, Ag-AgCl) were placed on the muscle belly (active electrode) and the metacarpal joint of the first digit (reference electrode). An additional electrode (ground) was placed on the styloid process of the ulna. All EMG recordings were band pass filtered between 20 Hz and 2.5 kHz and amplified by 1000x (Intronix Technologies Corporation Model 2024F, Bolton, Canada). Signals were digitized at 5 kHz by an analog–digital converter (Power1401; Cambridge Electronics Design, Cambridge, UK) and subsequently analyzed through computer software (Signal v7.01; Cambridge Electronics Design, Cambridge, UK).

Maximum voluntary contraction (MVC)

Participants were instructed to perform a brief five-second isometric voluntary maximum contraction (MVC) of the FDI muscle at each hand separately, and the largest rectified EMG value within the contraction window was recorded as the MVC, tracked using an oscilloscope (Keysight DSOX1204A, California, USA). Throughout the active condition, participants maintained an isometric FDI muscle contraction at 10 % of MVC, by matching a target line on the oscilloscope set to the 10 % MVC value.

TMS & motor mapping

We used TMS to examine the motor threshold and motor map of the FDI muscle, under the following task conditions within both the right and left hemisphere (Fig. 1):

1. Resting condition: Both hands remained at rest.
2. Active condition: The FDI muscle ipsilateral to TMS maintained an isometric contraction at 10 % of maximum voluntary contraction (MVC), while the contralateral hand remained at rest.

For the purposes of the present study, the motor dominant hemisphere was defined as the left hemisphere for right-handers and right hemisphere for left-handers, and the motor non-dominant hemisphere was defined as the right hemisphere for right-handers and the left hemisphere for left-handers.

TMS was performed using a figure-of-eight coil (50 mm diameter) attached to the Magstim 200^2 stimulator (Magstim, Whitland, UK). Stereotactic neuronavigation (Brainsight, Rogue Research, Montreal, Canada) was used to guide the position of the coil over a template brain

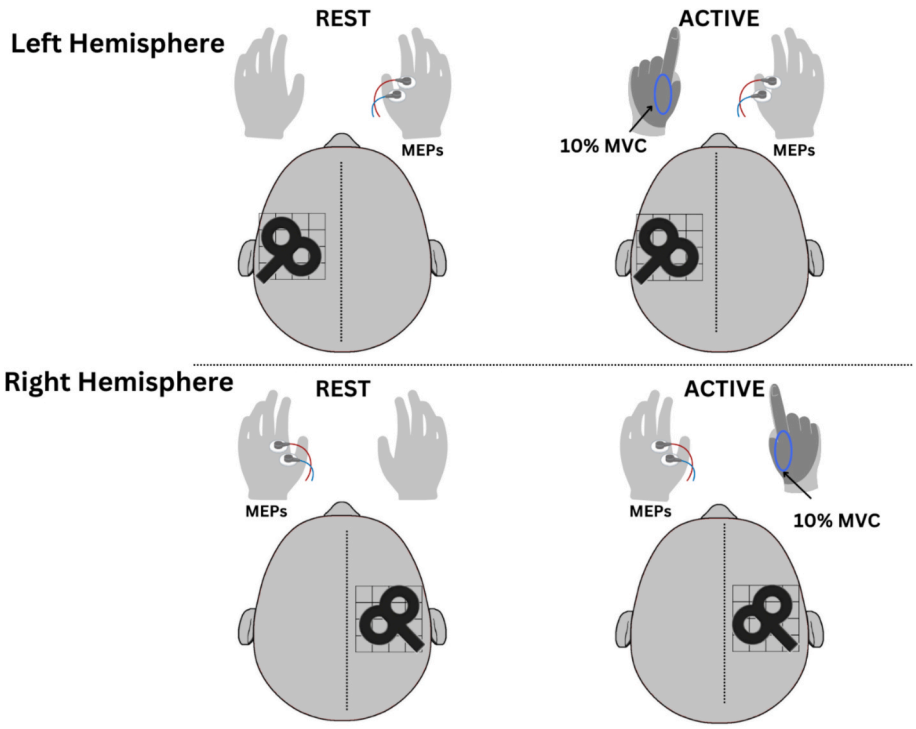

Fig. 1. Overview of the experimental design. Motor threshold and motor map outcomes were obtained within the left and right hemisphere, at (1) rest and (2) an active state, which involved an isometric contraction of the ipsilateral first dorsal interosseous (FDI) muscle to 10% maximum voluntary contraction (MVC). MEPs were recorded from the FDI contralateral to the hemisphere receiving TMS. Top, left hemisphere is the dominant hemisphere for right-handers and non-dominant hemisphere for left-handers. Bottom, right hemisphere is the dominant hemisphere for left-handers and non-dominant hemisphere for right-handers.

MRI fitted to each participant (coil positioned at a 45° in the posterior-to-anterior direction). The hand motor region was probed to determine the motor hotspot of the contralateral FDI muscle within each hemisphere, defined as the cortical site eliciting the largest and most consistent contra-MEP when stimulated.

Motor thresholds, defined as the minimum TMS stimulus intensity that evokes a contra-MEP (peak-to-peak amplitude > 0.05 mV) 50 % of the time, were determined using the maximum likelihood parameter estimation by sequential testing method, employed through the use of the TMS Motor Threshold Assessment Tool (MTAT 2.0) freeware. Twenty pulses were delivered at the FDI motor hotspot to identify motor threshold. Motor thresholds were acquired under both task conditions (rest, active) and from the right and left hemisphere.

To perform TMS mapping over the motor cortex, we employed the 'fast motor mapping' technique (van de Ruit et al., 2015), which provides equivalent results to traditional mapping techniques in a more time-efficient manner (van de Ruit et al., 2015; Cavaleri et al., 2018). Briefly, a 6x6 cm grid was first centered over the motor hotspot and positioned parallel to the longitudinal fissure. Within this grid, 80 TMS pulses were delivered in a pseudo-randomized manner at 120 % of resting motor threshold, with an interstimulus interval of 2.5 s between each pulse. The neuronavigation program was referred to throughout the mapping procedure to ensure an even distribution of stimuli across the grid (stimulus distribution density of 2–3 stimuli per cm^2), and to ensure that two consecutive pulses were not delivered within close proximity to each other (van de Ruit et al., 2015). A total of 4 motor maps were created for each participant (two conditions x two hemispheres), in a randomized order between participants.

Motor map analysis

To create the motor maps, offline analysis was done to pair each pulse with its corresponding grid point using a MATLAB script from Van de Ruit et al (2015) (van de Ruit et al., 2015). Trials with background EMG activity > 50 μV 50–5 ms before the TMS pulse were excluded. Trials with contra-MEP values exceeding the mean + 3.5 standard deviations of all contra-MEP values within a map were also excluded (van de Ruit et al., 2015), to prevent distortion of the resultant map. To limit the number of excluded trials, participants were given continual feedback on their level of muscle activity from online recordings on the signal acquisition software (Signal v7.01; Cambridge Electronics Design, Cambridge, UK), and we required that an acceptable map exclude no more than 10 trials. To create a continuous surface map, the 2D grid was divided into 2500 partitions (50x50), and triangular linear interpolation was used to estimate contra-MEP amplitudes using the closest recorded contra-MEP data (van de Ruit et al., 2015).

The outcome variable collected from each motor map was map area. Map area was calculated according to the following equation: $area(cm^2) = \frac{N_{MEP\geq 10\%}}{N_{total}} \times area_{map}$, where $N_{MEP\geq 10\%}$ is the number of partition sites within a given map where the peak-to-peak contra-MEP amplitude was $\geq$ 10 % of the maximum contra-MEP amplitude, N_{total} is the total number of partition sites (2500) within a map, and $area_{map}$ is the total area of the 6x6 cm grid (36 cm^2) (van de Ruit et al., 2015). Accordingly, grid points with contra-MEP amplitudes below 10 % of the maximal contra-MEP within a given map were not considered as sites for the total area of the motor map.

Statistical analysis

Normality for each outcome variable was visually assessed using frequency distributions and Q-Q plots. Systematic deviations from the ideal line were regarded as departures from normality (e.g., positive or negative skew; light or heavy tails). Map area was the only variable that violated the assumption of normality, and was therefore $\log_{10}$ transformed prior to analysis which yielded distributions consistent with approximate normality. We analyzed each outcome variable using a mixed ANOVA, with between-subject factors of handedness (Right, Left) and sex (Male, Female), and within-subject factors condition (Rest,

Active) and hemisphere (Dominant, Non-Dominant). Post-hoc comparisons were conducted using Fisher's Least Significant Difference test. Significance for all tests were set at $\alpha = 0.05$. Background EMG activity of the target contralateral FDI muscle during motor mapping was calculated by computing the root mean square error (RMSE) of the EMG signal within the 30 ms window preceding the TMS pulse for each trial.

Results

Descriptive statistics for all outcome measures are summarized in Table 1.

Motor threshold

Fig. 2A plots motor threshold (%MSO) as a function of handedness, sex, hemisphere, and condition. ANOVA revealed a significant main effect of condition [$F_{(1,76)} = 93.05$, $p < 0.001$, $\eta_p^2 = 0.55$] where motor threshold was lower in the active condition (M = 35.34 %MSO, SD = 5.83 %MSO) compared to rest (37.68 %MSO, SD = 6.08 %MSO) (Fig. 3B). No other significant effects were observed.

Map area

Fig. 3A plots mean map area (mm^2) as a function of handedness, sex, hemisphere, and condition. ANOVA revealed a significant main effect of condition [$F_{(1,76)} = 6.73$, $p = 0.01$, $\eta_p^2 = 0.08$], where a larger map area was found in the active condition (M = 920.85 mm^2, SD = 368.82) compared to the rest condition (M = 871.74 mm^2, SD = 414.30 mm^2) (Fig. 3B). Background EMG activity (expressed as RMSE) at contralateral FDI increased by 0.0002 mV from the rest to active condition. An equivalence test using two one-sided tests was conducted with equivalence bounds set as −0.00139 and 0.00139 based on the average standard deviation of background EMG data across both conditions (Lakens, 2017). This test revealed that the difference in RMSE between conditions fell within the equivalence range ($t(159) = -13.27$, $p < 0.001$ [upper bound], $t_{(159)} = 17.66$, $p < 0.001$ [lower bound]) (Table 2), indicating that changes in map area were unlikely due to voluntary activation of contralateral FDI. For all motor maps included in the final analysis, the number of excluded trials did not exceed 6 for each participant within each condition. Therefore, all motor maps consisted of a minimum of 74 trials. On average, three trials were discarded in each condition.

In addition, there was also found a significant interaction between handedness and hemisphere [$F_{(1,76)} = 5.05$, $p = 0.028$, $\eta_p^2 = 0.06$]. To investigate this further, we performed ANOVA on each condition (rest, active) separately using a between subject factors of handedness and sex, and within subject factor hemisphere. This analysis revealed a significant handedness X hemisphere interaction in the rest condition [$F_{(1,76)} = 5.79$, $p = 0.019$, $\eta_p^2 = 0.06$], that was not found in the active condition [$F_{(1,76)} = 1.95$, $p = 0.16$, $\eta_p^2 = 0.01$]. Post-hoc tests for this interaction revealed that for right-handed individuals, map area was smaller in their dominant hemisphere (M = 759.67 mm^2, SD = 312.43) compared to their non-dominant hemisphere (M = 940.48 mm^2, SD = 464.60) ($p = 0.033$). Further, map area was smaller in right-handers' dominant hemisphere when compared to left-handers' dominant hemisphere (M = 962.24 mm^2, SD = 477.03) ($p = 0.041$) (Fig. 3C). No other significant effects were found.

Discussion

In this study, we investigated the effects of an ipsilateral contraction on motor cortical responses within ipsilateral M1 using TMS, and examined if handedness and/or biological sex influenced these effects. We are the first to observe that ipsilateral FDI contraction increased motor representation area and decreased motor threshold within ipsilateral M1. Importantly, neither handedness nor biological sex had any influence during contraction. In addition to the effects of ipsilateral contraction, we observed novel findings at rest, such that in right-handers, map area was larger in their non-dominant hemisphere. These findings and their neural mechanisms are further discussed below.

M1 representation area and motor threshold during ipsilateral contraction

Motor threshold provides an index of axonal membrane and synaptic excitability at the cortical and spinal level, as motor threshold increases in the presence of voltage-gated sodium channel blockers (Paulus et al., 2008). At rest, motor neurons are below firing threshold and require the summation of multiple I-waves to elicit an MEP and therefore exhibit a higher motor threshold (Paulus et al., 2008). Contraction of the target muscle brings the motoneuron pool closer to threshold for eliciting an MEP which reduces the motor threshold (Paulus et al., 2008). In our study, ipsilateral contraction of FDI decreased motor threshold for contralateral FDI by 6.2 %, reflecting an increase in motoneuron excitability. In support of this finding, during ipsilateral contraction, F-wave amplitude is increased in the contralateral resting hand (Kosuge et al., 2025), indicating increases in spinal excitability. In contrast to our findings, two studies report no change in motor threshold during ipsilateral contraction, although the sample sizes were small in those studies (n = 9 and 10) (Muellbacher et al., 2000; Perez and Cohen, 2008).

We also observed a significant increase in map area within ipsilateral M1 during ipsilateral contraction using TMS motor mapping. We found that ipsilateral contraction of FDI increased map area of contralateral FDI by 8.36 %. Turco et al (2019) found a ~ 5.55 % increase in map area using TMS, though their result was not statistically significant (Turco

Table 1
Group-averaged means (M) and standard deviation (SD) of all measures.

Measure	Condition	Right-Handed				Left-Handed			
		Male		Female		Male		Female	
		Dominant	Non-Dominant	Dominant	Non-Dominant	Dominant	Non-Dominant	Dominant	Non-Dominant
Motor Threshold (%MSO)	Rest	M = 37.25 SD = 7.09	M = 38.10 SD = 6.41	M = 36.80 SD = 4.72	M = 36.90 SD = 5.06	M = 38.60 SD = 6.25	M = 38.90 SD = 6.64	M = 36.90 SD = 6.18	M = 38.00 SD = 6.80
	Active	M = 35.40 SD = 6.84	M = 35.05 SD = 5.74	M = 34.75 SD = 3.99	M = 34.80 SD = 5.44	M = 36.20 SD = 6.66	M = 35.70 SD = 6.38	M = 35.30 SD = 6.07	M = 35.55 SD = 6.13
Map Area (mm^2)	Rest	M = 743.64 SD = 314.39	M = 989.63 SD = 561.12	M = 775.70 SD = 317.77	M = 881.33 SD = 350.89	M = 931.22 SD = 446.08	M = 802.97 SD = 487.29	M = 993.26 SD = 515.84	M = 846.15 SD = 217.26
	Active	M = 879.91 SD = 375.08	M = 1042.72 SD = 476.51	M = 819.75 SD = 298.68	M = 974.07 SD = 448.15	M = 918.94 SD = 361.09	M = 866.25 SD = 294.76	M = 955.54 SD = 423.67	M = 909.64 SD = 249.84
Laterality Quotient (−100 to + 100)	–	M = 83.25 SD = 14.98		M = 88.75 SD = 14.86		M = -74.25 SD = 27.45		M = -73.50 SD = 27.20	

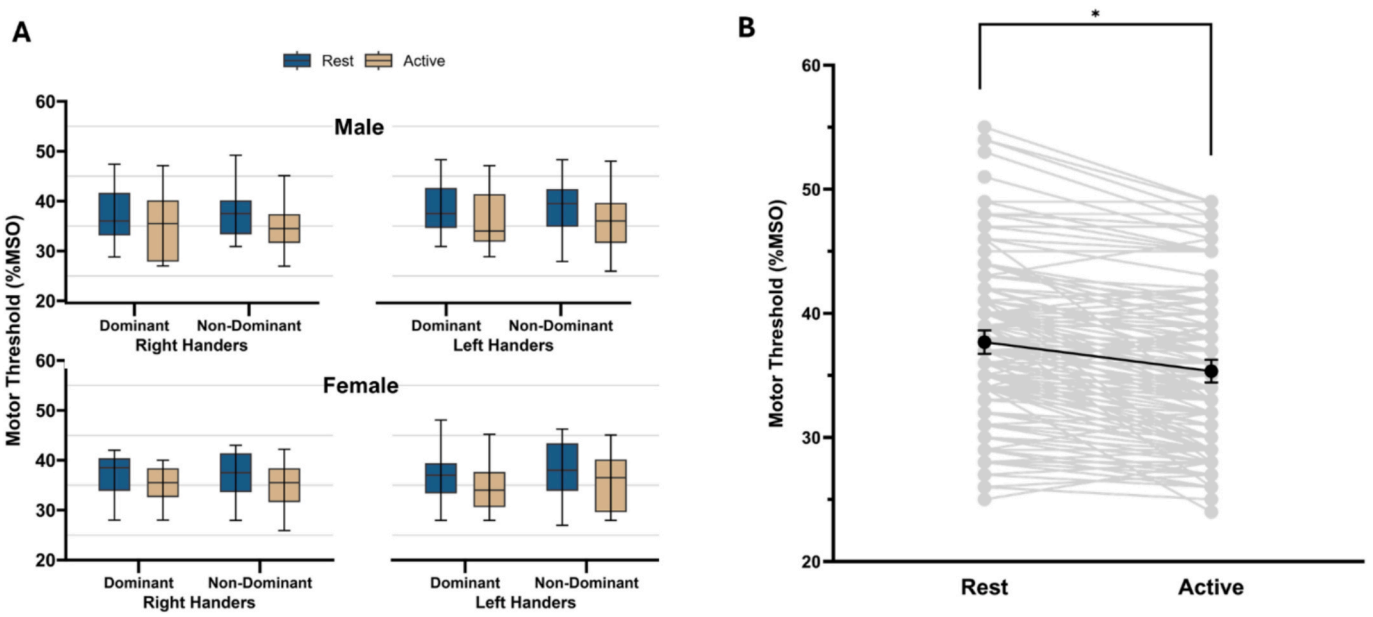

Fig. 2. (A) Box and whisker plots for motor threshold as a function of handedness (right- and left-handers), sex (male and female), hemisphere (dominant and non-dominant), and condition (rest [blue] and active [brown]). Boxplot showcase the median and first and third quartile, and whiskers show the 5th and 95th percentile. (B) Main effect of condition (n = 80): Motor threshold (with 95 % confidence interval) of the target first dorsal interosseus (FDI) muscle demonstrating main effect such that motor threshold is reduced during ipsilateral contraction. The grey dots connected by grey lines represent individual participant data. The black dots connected by black lines represent means across all participants. * indicates significance of $p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2019). Activation of ipsilateral M1 and adjacent sensorimotor areas during unimanual movement has been well documented using fMRI (Buetefisch et al., 2014; Kim et al., 1993; Verstynen et al., 2005; Rao et al., 1993; Kobayashi et al., 2003), magnetoencephalography (Volkmann et al., 1998; Huang et al., 2004), electroencephalography (van Wijk et al., 2012; Muthuraman et al., 2012) and positron emission tomography (Shibasaki et al., 1993). One possible mechanism for the observed increase in map area during ipsilateral contraction may relate to the recruitment of bilateral M1 representations. Animal studies have identified individual M1 neurons that respond to both ipsilateral and contralateral upper limb movement (Matsunami and Hamada, 1981; Donchin et al., 2002; Cisek et al., 2003; Heming et al., 2019; Brus-Ramer et al., 2009). Similar observations have been found in humans using fMRI (Diedrichsen et al., 2013; Cramer et al., 1999), whereby contraction ipsilateral to M1 yields discrete areas of activation that intermittently overlap with areas activated during contralateral movement. During our TMS mapping, we probe a 36 cm^2 area over the M1 region that may encompass the ipsilateral foci observed in fMRI studies, which may lead to the increased map area we observed.

Transcallosal signalling may also play a role in the observed increase in map area. Brus-Ramer et al (2009) demonstrated evoked responses in rat ipsilateral forelimb via electrical stimulation delivered to M1 were diminished after sectioning the corpus collosum. Further, the ipsilateral responses were diminished following deactivation of contralateral M1 via lidocaine injection (Brus-Ramer et al., 2009). Collectively, these data suggest that transcallosal signalling is modulating the corticospinal output to ipsilateral forelimb. In humans, interhemispheric inhibition (IHI), assessed using TMS, can provide insight into transcallosal signaling during ipsilateral contraction. Unimanual hand contraction results in a decrease in IHI onto ipsilateral M1 (Turco et al., 2019; Nelson et al., 2009). Further, the magnitude of IHI is associated with the motor representation area in the ipsilateral hemisphere, such that weaker IHI (less inhibition) corresponds with larger map area (Turco et al., 2019). This relationship exists only during ipsilateral contraction, but not at rest (Turco et al., 2019). These data suggest that our observed increase in map area during ipsilateral contraction may originate from reduced transcallosal inhibitory signaling.

Effects are independent of handedness and biological sex

This is the first investigation to compare changes in map area between right- and left-handers in the context of ipsilateral contraction and we conclude that handedness does not influence the response to ipsilateral contraction as measured herein. Of note, this study was performed using an adequate sample size to statistically consider factors related to handedness and biological sex. Similar to this finding, the presence of ipsilateral evoked MEPs is not different between right- and left-handers (Bernard et al., 2011). Further, using fMRI, the magnitude of ipsilateral activation in right- and left-handers do not differ during ipsilateral contraction (Singh et al., 1998). In contrast, using fMRI, differences are reported such that right-handers display greater ipsilateral activation of M1 during unimanual movement compared to left-handers (Verstynen et al., 2005).

Several studies have demonstrated interhemispheric asymmetry in ipsilateral M1 activation during unimanual movement. In right-handers, greater ipsilateral M1 activation is observed in the dominant hemisphere (Kawashima et al., 1993; Verstynen et al., 2005; Reid and Serrien, 2014; Ghacibeh et al., 2007; Ziemann and Hallett, 2001; van den Berg et al., 2011). For left-handers, greater activation is observed in the dominant hemisphere (Kawashima et al., 1997; van den Berg et al., 2011), non-dominant hemisphere (Kim et al., 1993; van den Berg et al., 2011), or no hemispheric differences (Verstynen et al., 2005; Singh et al., 1998). In our study, we did not observe interhemispheric asymmetry in map area changes during ipsilateral contraction. An explanation for this discrepancy may be the type of movement performed. The aforementioned studies observing interhemispheric asymmetries perform dynamic or complex hand movements, which are thought to evoke greater activation of ipsilateral motor cortical areas (Buetefisch et al., 2014; Chen et al., 1997; Morishita et al., 2011). For example, Verstynen et al (2005) observed interhemispheric asymmetry in ipsilateral activation only during complex movements, but not simple hand movement (Verstynen et al., 2005). Obtaining map area during different

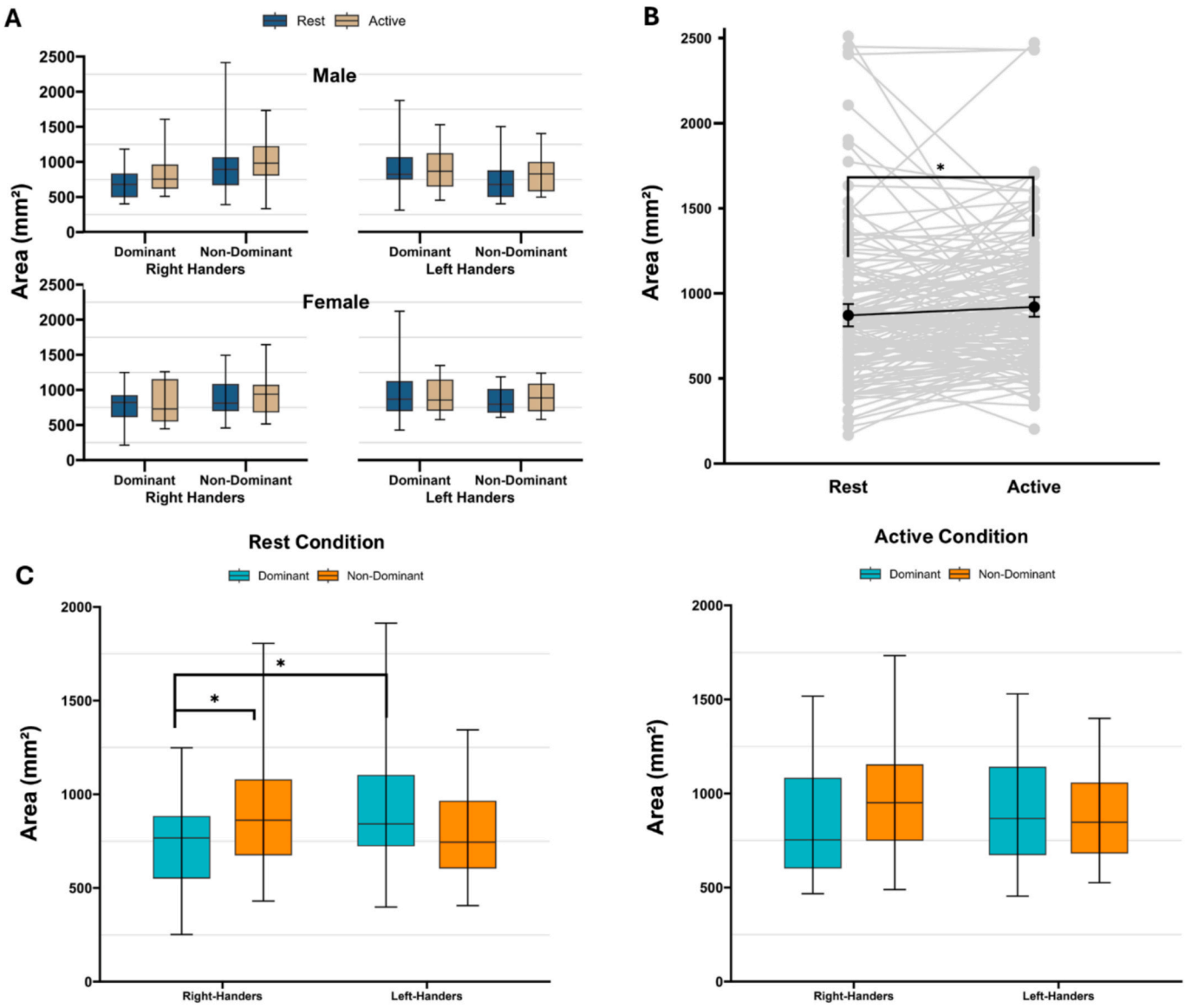

Fig. 3. (A) Box and whisker plots for motor map area as a function of handedness (right- and left-handers), sex (male and female), hemisphere (dominant and non-dominant), and condition (rest [blue] and active [brown]). Boxplot showcase the median and first and third quartile, and whiskers show the 5th and 95th percentile. (B) Main effect of condition (n = 80): Motor map area (with 95 % confidence interval) of the target first dorsal interosseus (FDI) muscle demonstrating main effect such that area was greater during ipsilateral contraction. The grey dots connected by grey lines represent individual participant data. The black dots connected by black lines represent means across all participants. * indicates significance of $p < 0.05$. (C) Box and whisker plots for motor map area as a function of handedness within the rest and active condition, as a function of handedness and hemisphere. * indicates significance of $p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Pre-stimulus EMG (expressed as RMSE) at the target contralateral FDI muscle during TMS motor mapping in the rest condition and active condition, averaged across all participants.

	Rest Condition	Active Condition	Equivalence test
Pre-stimulus RMSE (mV)	M = 0.0044	M = 0.0046	Upper bound: $p < 0.001$
	SD = 0.0013	SD = 0.0015	Lower bound: $p < 0.001$
Normalized to 100 % MVC (%)	M = 0.94 SD = 0.006	M = 0.98 SD = 0.006	–

complexities of ipsilateral movement may have allowed us to observe these interhemispheric differences in map area.

We are the first to explore the influence of biological sex on the effects of ipsilateral contraction using TMS and observed no differences in motor threshold and map area between males and females. To the best of our knowledge, only one study examined the activation of ipsilateral motor regions between males and females, and found that females display greater activation of ipsilateral premotor cortex in both hemispheres during unimanual finger tapping tasks compared to males (Lissek et al., 2007).

Differences in representation size between handedness groups at rest

At rest, we observed that right-handers displayed larger motor representation size of the FDI muscle within their non-dominant hemisphere. In contrast, previous studies among right-handers have

demonstrated no differences in representation size across hemispheres (Nicolini et al., 2019; Wilson et al., 1993; Cicinelli et al., 1997), or larger representation in the dominant hemisphere (Triggs et al., 1999; Wassermann et al., 1992; Volkmann et al., 1998; Amunts et al., 1996; Dassonville et al., 1997). Conversely, there were no differences in map area between hemispheres at rest in left-handed individuals. This has been confirmed by other MRI studies (Amunts et al., 1996; Foundas et al., 1998), and may be explained by reduced hemispheric lateralization among left-handers (Johnstone et al., 2021) due to their more equal use of both hands in comparison to right-handers (Nicolini et al., 2019; Borod et al., 1984).

Limitations and considerations for basic and clinical neuroscience

We demonstrate that muscle contraction increases motor representation size within ipsilateral M1. This finding has relevant implications for the methodological design of future basic neuroscience studies, as we highlight the importance of minimizing ipsilateral movement to ensure measured characteristics of motor representations are not influenced by ipsilateral muscle activation, which is often not accounted for in TMS and fMRI research. Additionally, the present study suggests further exploration of the relationship between IHI and map area, as well as the influence of movement complexity and/or degree of force on motor map representation in ipsilateral M1. Results from this study suggest that the enhancement in M1 activity ipsilateral to contraction can be harnessed and targeted by rehabilitation to improve motor function for stroke and spinal cord injury through cross-education (Zazio et al., 2022) and/or bimanual training.

TMS parameters such as coil orientation, current direction, and pulse waveform can influence the activation of cortico-motor circuits (Zazio et al., 2022; Lucarelli et al., 2025; Guidali et al., 2023), and hence future work should consider whether the results obtained in this study are influenced by such factors. In the present study, we used monophasic pulses with the coil positioned at 45° relative to the midsagittal plane for the entire map, and current induced in the posterior-to-anterior direction. Experience with TMS mapping is also an important consideration, as is the post-processing approach (van de Ruit et al., 2015). Finally, we did not consider additional factors that may or may not influence map area, such as physical activity levels, motor skill proficiency related to hand function, hormonal fluctuations (Ramdeo et al., 2024), and time of testing across participants.

CRediT authorship contribution statement

Mustaali Hussain: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Stevie D. Foglia:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Jiyeon Park:** Writing – review & editing, Methodology, Investigation, Data curation. **Karishma R. Ramdeo:** Writing – review & editing, Data curation, Conceptualization. **Faith C. Adams:** Writing – review & editing, Data curation, Conceptualization. **Chloe C. Drapeau:** Writing – review & editing, Data curation. **Ava R. Bobinski:** Writing – review & editing, Data curation. **Michael J. Carter:** Writing – review & editing, Methodology, Formal analysis. **Aimee J. Nelson:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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