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The effect of motor overflow on bimanual asymmetric force coordination

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Abstract

Motor overflow, typically described in the context of unimanual movements, refers to the natural tendency for a ‘resting’ limb to move during movement of the opposite limb and is thought to be influenced by inter-hemispheric interactions and intra-cortical networks within the ‘resting’ hemisphere. It is currently unknown, however, how motor overflow contributes to asymmetric force coordination task accuracy, referred to as bimanual interference, as there is need to generate unequal forces and corticospinal output for each limb. Here, we assessed motor overflow via motor evoked potentials (MEPs) and the regulation of motor overflow via interhemispheric inhibition (IHI) and short-intracortical inhibition (SICI) using transcranial magnetic stimulation in the presence of unimanual and bimanual isometric force production. All outcomes were measured in the left first dorsal interosseous (test hand) muscle, which maintained 30% maximal voluntary contraction (MVC) while the right hand (conditioning hand) was maintained at rest, 10%, 30% or 70% of its MVC. We have found that as higher forces are generated with the conditioning hand, MEP amplitudes at the active test hand decreased and interhemispheric inhibition increased, suggesting reduced motor overflow in the presence of bimanual asymmetric forces. Further, we found that subjects with less motor overflow (i.e. reduced MEP amplitudes in the test hemisphere) demonstrated poorer accuracy in maintaining 30% MVC across all conditions. These findings suggest that motor overflow may serve as an adaptive substrate to support bimanual asymmetric force coordination.

Keywords

Bimanual Interference; Motor Overflow; Transcranial Magnetic Stimulation; Interhemispheric Inhibition; Intracortical Inhibition

Introduction

Many everyday tasks require coordination of asymmetric upper-limb forces. For example, when lifting groceries with two hands there is often unequal force production generated between limbs. The ability to coordinate asymmetric forces between limbs has been shown to be difficult because there is a natural tendency for two limbs to become functionally coupled (Swinnen and Walter 1991; Gerloff et al. 1998). One reason both limbs become coupled is because of 'motor overflow.' Motor overflow, typically described in the context of unimanual movements, refers to the natural tendency for a 'resting' limb to move during movement of the opposite limb and is thought to be influenced by inter-hemispheric interactions and intra-cortical networks within the 'resting' hemisphere (Meyer et al. 1995; Stedman et al. 1998; Tinazzi and Zanette 1998; Muellbacher et al. 2000; Hortobágyi et al. 2003; Perez and Cohen 2008). For instance, Perez and Cohen (2008) explain that corticospinal output to the 'resting' limb increases in association with a decrease in intra-cortical inhibition within the resting hemisphere and inter-hemispheric inhibition imposed from the opposite hemisphere. Because motor overflow creates a natural tendency for both limbs to simultaneously generate equal amounts of force, bimanual symmetric movements are performed with a relative degree of ease (Beaule et al. 2012).

Generating bimanual asymmetric forces, however, poses a behavioral and a neurophysiologic challenge because there is need to generate unequal forces and corticospinal output from each limb. While motor overflow is critical to facilitate interactions between both limbs, it needs to be regulated so both hemispheres can uncouple to some degree and independently generate required levels of output. Many studies have shown the behavioral difficulties that are imposed by bimanual asymmetric forces (Steglich et al. 1999; Rinkenauer et al. 2001; Diedrichsen et al. 2003; Hu and Newell 2011; Hu and Newell 2012; Kenway et al. 2014a; Kenway et al. 2014b). For example, maintaining unequal forces at both hands exaggerates error and variability compared to maintaining a target force with only one hand. This exaggeration of error and variability in movement of one hand due to the added constraint of maintaining forces with the other is called bimanual interference (Hu and Newell 2012). Specifically, the hand that is required to generate lower target forces experiences more error than the hand that is designated to generate higher target forces. Interference increases as the degree of asymmetry between designated levels of target forces increases (Hu and Newell 2011). One hypothesis is that interference increases because the hemisphere that is producing the lower force has to regulate motor overflow originating from the hemisphere that is generating the higher forces (Hu and Newell 2012). While this hypothesis appears to be intuitive based on findings of Perez and Cohen (2008), it has not been directly tested.

Specifically, it remains unclear whether motor overflow from the hemisphere producing higher forces is suppressed so that relatively lower forces and corticospinal output can be generated at the other limb. It is also unknown whether the ability to suppress motor overflow introduces error and variability in maintaining different forces and thus contributes to bimanual interference. While a few studies have explained that inter-hemispheric inhibition imposed from the opposite hemisphere is related to bimanual interference

(Diedrichsen et al. 2003; Fling and Seidler 2012), it is unclear how all substrates involved in motor overflow- corticospinal output, intra-cortical inhibition and inter-hemispheric inhibition- interact to help generate lower forces at one limb compared to the other limb in a bimanual asymmetric condition.

Therefore, we investigated how motor overflow is regulated in the presence of step-wise increases in asymmetric bimanual forces in young, healthy participants. We also investigated whether regulation of motor overflow explains interference in bimanual asymmetric tasks. Specifically, we built upon the design and findings of Perez and Cohen (2008). Subjects were required to maintain the left hand (test hand) at 30% maximal voluntary contraction (MVC) while the right hand (conditioning hand) was maintained at rest, 10%, 30% or 70% of its MVC. As an extension of Perez and Cohen's work, we studied changes in corticospinal output, intracortical inhibition and inter-hemispheric inhibition devoted to the test hand using transcranial magnetic stimulation (TMS). We hypothesized that motor overflow would decrease when force generated by the conditioning hand exceeds the force generated by the test hand i.e. corticospinal output would decrease and intra-cortical and inter-hemispheric inhibition would increase within the test hemisphere, so the test hand could maintain its relative, low-force output. We further hypothesized that the ability to suppress motor overflow from the conditioning hemisphere would be associated with bimanual interference in performance of the test hand.

Methods

Subjects

Fourteen right-handed healthy volunteers (5 men and 9 women) with an average age of 27 +/- 6 SD years participated in the study. We identified the dominant hand based on the Edinburgh Handedness Inventory assessment (Oldfield 1971). Subjects were excluded if they had experienced any musculoskeletal or neurologic condition, or if they possessed any contraindication to TMS (Rossi et al. 2009). All participants provided written informed consent to participate in the experimental protocol, which was approved by the Cleveland Clinic Institutional Review Board.

Motor Task

Subjects were seated in an armchair with the shoulders relaxed, both arms resting 90 degrees at the elbow and with both hands positioned in prone posture (palms down). During the test, subjects were instructed to abduct their index fingers against force transducers (Omega LCKD 5-lb, Stamford, CT), which measured forces exerted by the subject. Surface electrodes (Ag/AgCl, 10 mm diameter) were positioned bilaterally on the skin overlying the first dorsal interosseous muscles (FDI) placed in belly-belly montage with a reference electrode placed on the lateral epicondyle. The amplified ($\times 500$) EMG signals were filtered (bandpass, 10 Hz – 2 kHz, and mains filter at 50 – 60 Hz), sampled at 4 kHz and stored on a personal computer for off-line analysis (LabChart, version 7.3, AD Instruments Inc. Colorado Springs, CO). Force signals were amplified (range = 10 V), low-pass filtered at 2 kHz and with a mains filter at 50 – 60 Hz, and sampled at a rate of 4 kHz.

Each subject performed four different task conditions presented in a randomized order: one unimanual and 3 bimanual. For each, subjects were instructed to abduct against the force transducers with the right and left hands. They were provided with visual feedback of the force produced by each hand to ensure they maintained target forces for each condition. The visual feedback for each condition was normalized to the target force line, where the visual feedback was set to $\sim \pm .3$ V from the target force. The left hand served as the test hand. For the unimanual condition, the left (test) hand always generated 30% MVC finger abduction while the right (conditioning) hand was at rest (unimanual condition; 30/R). The bimanual conditions required the left (test) hand to always generate 30% MVC and the right (conditioning) hand to generate either 30% (bimanual symmetric, 30/30), 10% (bimanual asymmetric, 30/10) or 70% MVC (bimanual asymmetric, 30/70) (figure 1) [This experimental design differs from that of Perez and Cohen (2008), as their test hand was always at rest, while the conditioning hand performed 10%, 30% and 70% isometric MVC]. For each condition, our participants were asked to follow the target force for each hand as accurately as possible. In order to measure accuracy, all subjects performed each condition for 30 seconds in a randomized order at the beginning of the experiment. All participants were familiarized with each condition prior to testing.

TMS measurements

Single pulse TMS (Magstim 200², Wales, U.K.) was delivered using a figure-of-eight coil (diameter 70mm) to the subjects' left and right primary motor cortices (M1) during each condition described above (30/R, 30/10, 30/30 and 30/70), where the right hemisphere served as the test hemisphere. Subjects' own MRI scan was used to stereotactically guide TMS [BRAINSIGHT software (Rogue Research, Montreal, Canada)] to M1.

TMS-evoked responses, called motor evoked potentials (MEPs), were recorded in the contralateral FDI muscle using surface EMG electrodes. To evoke MEPs, the TMS coil was placed tangential to the scalp with the handle oriented backward and laterally at a 45° angle to the midsagittal axis. We identified the motor 'hot spot' which is the scalp site eliciting reliable criterion MEPs ($\geq 50\mu\text{V}$ in at least 3/5 trials) with the lowest % maximum stimulator output (%MSO) for each hemisphere, commonly referred to as resting motor threshold (rMT). We also defined active motor threshold (aMT) at the 'hotspot' location which was the % MSO that elicited reliable criterion MEPs ($\geq 200\mu\text{V}$ in at least 3/5 trials) when the left hand FDI was contracted at 30% MVC.

Corticospinal Output

Corticospinal output was measured for the test (right) hemisphere across all conditions. At the beginning of the experiment, we identified a suprathreshold %MSO that could elicit 1.5–2.5 mV MEP in the left (test) hand (contracted at 30% MVC) in 5 out of 10 trials. The same stimulator intensity was used to obtain 1.5–2.5 mV MEP in the test hand during 30/R and when subjects performed 30/10, 30/30 and 30/70. The suprathreshold stimulator intensity ranged between 21% and 55% MSO (mean $36\% \pm 9\%$) across subjects. A total of twenty MEPs were recorded for each condition. Several periods of rest were given to minimize muscle fatigue.

IHI

We measured IHI exerted upon the test (right) hemisphere during all conditions (using Magstim 200² and Magstim Bistim). A conditioning pulse was applied to the left hemisphere 12 ms prior to a test pulse delivered to the right hemisphere. This conditioning stimulus (CS) was supra-threshold and was set at an intensity (expressed as % rMT) that could suppress corticospinal output in the test hand by ~50 % (Perez and Cohen 2008). The same CS intensity was used across all conditions. The CS ranged between 35% and 72% MSO (mean $50.36 \pm 12.70\%$ across subjects), corresponding to ~124% of the rMT. The test stimulus (TS) for each condition, as mentioned earlier, was set to an intensity that could evoke a 1.5–2.5 mV MEP in the test hand while it was maintained at 30% MVC. During each condition, a total of 20 MEPs were collected; 10 MEPs were collected during single pulse trials delivered to the right hemisphere and 10 were collected during paired-pulse trials delivered to the left (conditioning) and right (test) hemispheres. The order in which single pulse and paired-pulse trials were given was randomized for each condition. All MEPs elicited in the test hand from single pulse TMS or paired-pulse TMS were calculated as peak-to-peak amplitude.

SICI

We measured SICI within the test (right) hemisphere during all conditions (using Magstim 200² and Magstim Bistim). A subthreshold CS was applied to the right hemisphere 3 ms prior to a TS on the right hemisphere. The CS was set to 70% of the aMT (Ortu et al. 2008) and the TS was set to an intensity that could evoke a 1.5–2.5 mV MEP in the test hand while it was maintained at 30% MVC. During each condition, a total of 20 MEPs were collected; 10 MEPs were collected during single pulse trials and 10 were collected during paired-pulse trials (conditioning and test pulses). The order in which test pulses and paired pulses were given was randomized for each condition.

Data Analysis: Bimanual Interference

Bimanual interference was measured in the performance of the left (test) hand in maintaining the designated 30% MVC force during each condition (30/R, 30/10, 30/30, and 30/70) using an accuracy index (AI) given by:

$$AI = 100 * (P - E) / P,$$

where E is the root mean squared error (RMSE) between the target force and the subject's response, and P is the target force. The maximum score is 100%.

Data Analysis: Neurophysiologic Variables

Following the collection of the accuracy index, TMS was then applied during each condition to measure corticospinal output, IHI and SICI. Peak-to-peak MEP amplitudes were measured offline, and represented corticospinal output to the test hand. Due to the large error of task performance of the test hand, there was large trial-to-trial variability of MEPs. Therefore, to reduce the trial-to-trial variability of MEPs we only averaged trials where the peak-to-peak amplitude fell within 1 standard deviation of the mean for all trials. This

approach resulted in the inclusion of 14 out of 20 trials for corticospinal output and 7 out of 10 trials each for IHI and SICI. Corticospinal output was calculated as the average peak-to-peak amplitude of MEP evoked during each condition. Both IHI and SICI were calculated as the ratio of the averaged 'conditioned (paired-trial) MEP' to the average 'test (single-trial) MEP' generated in the test hand across all conditions (Perez and Cohen 2008).

Statistical analysis

To study bimanual interference, we compared performance accuracy of the left hand (AI) across task conditions (30/10, 30/30 and 30/70) and to evaluate whether motor overflow is suppressed when incrementally greater forces are exerted by the other limb, we compared corticospinal output, IHI and SICI between 30/R, 30/10, 30/30 and 30/70 conditions using repeated measures ANOVA. A Fischer's Least Squares Difference post hoc test was used for all comparisons. Next, we investigated whether motor overflow to the test limb is regulated via interhemispheric and intracortical inhibition. For this, we performed bivariate Pearson's correlation between corticospinal output and IHI and SICI. In order to understand how this relationship varies with incrementally greater asymmetric forces exerted at the conditioning limb, we performed within-subject correlations (Bland and Altman 1995). This approach is commonly used to assess correlation between repeated observations collected within the same individual. This allowed us to investigate whether changes in corticospinal output observed with incrementally greater asymmetric forces were associated with changes in inhibition witnessed within that individual. Likewise, we determined how motor overflow and inhibition related with bimanual interference by studying bivariate and within-subject correlations between individual task performance and neurophysiologic variables (corticospinal output, IHI and SICI). Statistical analysis was performed using Statistical Package for the Social Sciences (v18, SPSS Inc., Chicago, IL). Significance was set at $p = .05$.

Results

Accuracy Index (AI)

Repeated measures ANOVA showed that accuracy of maintaining forces with the active test hand differed between conditions ($F_{2,1, 26.7} = 5.85$, $p = .007$) (figure 2). Subjects demonstrated poorer AI during bimanual asymmetric conditions (30/10: $93.5 \pm 3.5\%$, $p = .005$; 30/30: $95.3 \pm 2.2\%$, $p = .045$; 30/70: $92.9 \pm 4.2\%$, $p = .009$) than during the unimanual 30/R condition ($96.2 \pm 2.4\%$). AI in the bimanual symmetric condition (30/30) tended to be more accurate when compared to 30/10 ($p = .05$) and 30/70 ($p = .054$) (figure 2).

Corticospinal Output

Repeated measures ANOVA showed that corticospinal output tended to differ between conditions ($F_{3, 39} = 2.7$, $p = .056$). MEPs elicited in the test hand tended to be smaller in amplitude during the highly asymmetric condition (30/70) ($1.9 \pm .7$ mV) than during unimanual condition (30/R) ($2.3 \pm .9$ mV) ($p = .057$). Likewise, MEPs generated during the mildly asymmetric (30/70) were significantly greater than MEPs generated during highly asymmetric condition (30/70) ($p = .002$). MEPs generated during symmetric (30/30) or mildly asymmetric bimanual conditions (30/10) did not differ from MEPs generated during

the unimanual condition (30/R) (figure 3a). Therefore, corticospinal output generated in the active test hand was reduced as the conditioning hand simultaneously produced a high-level of force.

SICI and IHI

SICI within the test hemisphere did not differ between unimanual condition and bimanual symmetric or bimanual asymmetric conditions (figure 3c). IHI, though, tended to differ between conditions ($F_{3, 39} = 2.6$, $p = .062$). IHI imposed upon the test hemisphere tended to be higher in the highly asymmetric (30/70) ($50.7\% \pm 16.7\%$) and the symmetric bimanual (30/30) conditions ($55.4\% \pm 22.3\%$) compared to the unimanual contraction of the test hand (30/R) ($66.1\% \pm 27.7\%$) ($p = .053$ and $p = .071$, respectively) (Cond Stim*100/Test Stim) (figure 3b). Therefore, IHI exerted upon the active test hand tended to increase as the conditioning hand simultaneously produced a high-level of force.

Correlation Analysis

With data from all conditions (30/R, 30/10, 30/30 and 30/70) pooled, we found a significant correlation between IHI and MEP amplitudes elicited in the test hand ($r = .48$; $p < 0.001$) (figure 4a). Overall, greater IHI was associated with smaller MEPs. When we studied this relationship across conditions, we found a significant within-subject correlation ($r = .46$; $p = .002$) (Figure 4b), meaning that a majority of subjects showed decreases in MEP amplitudes across tasks where they showed increases in IHI. For SICI, however, when all conditions were pooled, we found no significant correlation between MEP amplitudes elicited in the test hand and SICI within the test hemisphere ($r = -.005$; $p > .05$) (figure 4c). There was a significant within-subject correlation ($r = .45$; $p = .003$) implying that a majority of subjects showed decreases in MEP amplitudes across tasks where they showed increases in SICI (figure 4d).

We found weak-to-moderate but statistically significant correlation between MEP amplitudes and accuracy index ($r = .35$; $p = .009$); subjects with the smallest MEPs showed the poorest accuracy (figure 5a). Similarly, IHI and accuracy index demonstrated a weak-to-moderate yet significant relationship ($r = .33$; $p = .013$); subjects who experienced high degrees of IHI also showed the poorest accuracy of the test hand (figure 5b). In contrast, we did not find a correlation between SICI and accuracy index ($r = .09$; $p = \text{NS}$).

Discussion

Our study investigated whether motor overflow was regulated in the presence of step-wise increases of volitional bimanual asymmetric forces. The study also explored whether regulation of motor overflow had an association with interference witnessed during the generation of bimanual asymmetric forces. We have found that as subjects generate progressively greater forces with the conditioning hand, corticospinal output to the test hand tended to decrease. At the same time, inter-hemispheric inhibition imposed upon the test hand from the conditioning hemisphere also tended to intensify. These results suggest that motor overflow to the hand maintaining lower forces are suppressed when the opposite hand generates higher forces. Greater suppression (smaller corticospinal output, higher inter-

hemispheric inhibition) is related to greater bimanual interference or poorer accuracy of the hand generating lower forces. Contrary to our hypothesis, these results suggest that suppression of motor overflow exaggerates error and variability in performing bimanual asymmetric tasks. Potentially, motor overflow serves as an adaptive substrate to support bimanual asymmetric movements.

During unimanual force generation there is greater motor overflow from the active conditioning hand to the resting test hand (Meyer et al. 1995; Stedman et al. 1998; Tinazzi and Zanette 1998; Muellbacher et al. 2000; Hortobágyi et al. 2003; Perez and Cohen 2008). In the present study, we sought to investigate how motor overflow was regulated when the test hand was actively maintaining forces as well during bimanual asymmetric force task. First, we have found that when subjects perform bimanual isometric index finger abduction, corticospinal output to the test hand tended to be suppressed as forces exerted at the conditioning hand considerably exceed (70% MVC) forces exerted at the test hand (30% MVC) (albeit, only trended towards significant). These results are opposite to what is witnessed in unimanual conditions (Perez and Cohen 2008). During the unimanual condition, output to the *resting* test hand is increased as forces exerted at the conditioning hand become considerably higher (70% MVC). Therefore, motor overflow is increased during the *unimanual* condition. During asymmetric bimanual condition, however, we find that, output to the *active* test hand (30% MVC) is decreased as forces exerted at the conditioning hand become considerably higher (70% MVC). Our results therefore provide evidence that motor overflow may be suppressed during *bimanual* muscle contractions that are highly asymmetric. Further, our results are supported by previous studies which demonstrate a decrease in corticospinal output during bimanual than a unimanual force production task (Stinear and Byblow 2004; Yedimenko and Perez 2010).

Two sets of networks that regulate motor overflow include intracortical inhibitory and interhemispheric inhibitory networks. Perez and Cohen 2008 have demonstrated during step-wise increases in unimanual isometric forces at the conditioning limb, that SICI and IHI are reduced in the resting test hemisphere. Here, we do show that IHI is increased as forces exerted by the conditioning hand (70% MVC) considerably exceed forces exerted by the active test hand (30% MVC). However, we did not observe any group modulation of intracortical inhibitory networks in the presence of bimanual force production. Still, interestingly, we did witness that increased SICI was associated with decreased corticospinal output on a within-subject level (figure 4d). Stinear and Byblow (2003) have previously demonstrated that modulation of intracortical inhibitory mechanisms play a role in preventing unwanted muscle activation. They hypothesized the suppression of unwanted muscle activation is necessary in order to perform a precision based task that requires high degree of temporal and spatial accuracy. Based on their findings, and ours, it is plausible that intracortical inhibition plays a role in regulating motor overflow and thus prevents unwanted co-muscle activation during bimanual asymmetric force production. Overall, IHI and SICI may have contributed to suppressing motor overflow during the highly asymmetric bimanual conditions.

Neurophysiologic predictors of task accuracy

Higher suppression of motor overflow related to greater bimanual interference or poorer accuracy. Our findings are in agreement with Fling & Seidler 2012, who have also shown that greater IHI is related to impaired ability to accurately perform complex bimanual movements. Therefore, regulating motor overflow too much via inhibitory networks may be detrimental to bimanual asymmetric task performance. Previous studies have shown that interhemispheric inhibition is required for complex skilled tasks. Contrary to our original hypothesis, our study suggests that motor overflow is important for maintaining corticospinal output to an active test hand during step-wise increases in forces exerted at the opposite conditioning hand.

Limitations and summary

Our aim was to investigate how motor overflow is regulated in the presence of a step-wise increase of volitional bimanual asymmetric force and to determine if the ability to regulate motor overflow introduces error and variability in maintaining different forces. The first limitation is that comparison of corticospinal output and IHI across task conditions only yielded a trend towards significance. This suggests that our study was underpowered due to the small effect size and sample size. Second, even though it was necessary to include two visual targets to investigate our aim, by nature of the task, bimanual force production does introduce an attentional and motor planning confound. It is possible that participants chose to focus on the limb that was required to produce greater amount of force and thus used internal cues to produce the required 30% of MVC for the non-dominant test limb. For example, Kenway et al. 2014b recently showed an increase in fluctuations of a force signal when visual feedback is removed for a single limb during a bilateral task. An additional limitation is that we chose to include only young healthy participants. Previous studies have indicated that the degree of motor overflow differs with age and disease (Addamo et al. 2007), thus the present results may not be generalizable to the population as a whole.

In summary, the present findings suggest that there is, indeed, a balance between regulating motor overflow and accurately performing a bimanual asymmetric force. Still, it is important to recognize that the controlled experimental design may not adequately represent what happens during activities of daily living. Future studies are required to increase the generalizability of our findings to more functional task practice.

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Figure 1.

Experimental design. A) Subjects were instructed by a monitor to generate different levels of force from both their right and their left hands. The right hemisphere served as the test hemisphere (contralateral to the test hand) and the left hemisphere served as the conditioning hemisphere. During each of the four conditions, we measured corticospinal output, IHI, and ICI all within the test hemisphere. B) Visual display of each condition. The left hand served as the test hand and was maintained at 30% MVC for all conditions. The right hand was at

rest, 10%, 30% and 70% MVC in a randomized order. All subjects were instructed to maintain accuracy to the best of their ability for both hands.

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Figure 2. Accuracy Index. A) Subjects were able to maintain 30% of their MVC most accurately during both unimanual (30/R) and bimanual symmetric (30/30) contractions. Error bars indicate standard error.

Figure 3.

Corticospinal output and Inhibition in the test M1. A) For the same amount of isometric force production from the test hand (30% MVC), Corticospinal output was less during the 30/70 condition when compared to the unimanual 30/R and 30/10. B) IHI is expressed as a ratio of the paired-pulse to the single pulse, such that lower values indicated greater inhibition. There was a progressive increase in IHI during the 30/30 & 30/70 condition when compared to unimanual 30/R. C) Similar to IHI, SICI is expressed as a ratio between the paired pulse and conditioning pulse such that smaller values indicated greater intracortical inhibition. SICI was not modulated during any condition. D) Representative MEP tracings for one subject for each of the above outcomes. Error bars indicate standard error.

Figure 4.

The influence of inhibition on corticospinal output. A) Pooled group data shows that less IHI relates to greater corticospinal output. B) Within-subject correlation analysis shows that IHI modulates corticospinal output on an individual basis. C) Pooled group data does not show that SICI modulates corticospinal output. D) Within-subject correlation, however, shows that individual modulation of corticospinal output is modulated with SICI, such that as SICI is reduced individual corticospinal output increases.

Figure 5.

Corticospinal output and inhibition influence on accuracy. A) Relationship between corticospinal output and accuracy shows that subjects with greater corticospinal output were more accurate. B) Relationship between IHI and accuracy shows that subjects with reduced IHI were more accurate.