TITLE: Motor training reduces surround inhibition in the motor cortex

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ABSTRACT

Objective: Surround inhibition (SI) is thought to facilitate focal contraction of a hand muscle by keeping nearby muscles silent. Unexpectedly, SI is reduced in skilled pianists. We tested whether repeated practice of focal contraction in non-pianists could reduce SI.

Methods: Motor-evoked potentials were elicited by transcranial magnetic stimulation in the relaxed abductor digiti minimi randomly at the onset and 5s after offset of a 2s focal contraction (10% maximum) of the first dorsal interosseous (FDI). Over 5 blocks of 40 trials participants obtained points for increasing contraction speed and stability in FDI. In a final block, the interval between contractions was varied randomly to increase attention to the task.

Results: Over the first 5 blocks, SI declined as performance (points scored) improved. In the final "attention" block SI increased towards baseline without affecting performance.

Conclusions: Although SI may be useful during the early stages of learning, skilled focal finger movement does not require SI to prevent activity in non-involved muscles. This could be due to better targeting of the excitatory command to move. Results from the final block suggest that increased attention can re-engage SI when task parameters change.

Significance: SI is not necessary for successful focal contraction, but may contribute during learning and during attention to task.

KEYWORDS: Surround inhibition, motor-evoked potentials, TMS, attention

HIGHLIGHTS

- Surround inhibition (SI) is not necessary for the successful generation of skilled isolated finger movement.
- SI may be utilised during the early stages of motor learning to limit co-contraction of uninvolved hand muscles.
- Attention may play a role in modulating SI; increased attention appears to engage a stronger SI.

ABBREVIATIONS

ADM, abductor digiti minimi; FDI, first dorsal interosseus; MVC, maximum voluntary contraction; ITI, inter-trial interval; FHD, focal hand dystonia; EMG, electromyography; MEP, motor-evoked potential; RMS, root mean square; SI, surround inhibition; TMS, transcranial magnetic stimulation

1 INTRODUCTION

Surround (or lateral) inhibition (SI) is a physiological phenomenon first described in the visual system more than 60 years ago, where neuronal activation was found to be associated with active inhibition in surrounding neurons (Hartline, 1949). The original function proposed in the visual system was to improve contrast perception at the edge of images. This concept was extended to include the idea that SI could increase the efficiency of encoding of information by “normalization” of a constant bias in the signal to maintain the neuronal signal distribution within the dynamic range of the receptive neurons, similar to a DC offset in electrical recordings (Srinivasan et al., 1982).

The suggestion that a similar mechanism might be present in the motor system is a more recent development. In 2004, Sohn and Hallett reported that motor evoked potentials (MEP) triggered by transcranial magnetic stimulation (TMS) over the motor cortex at the onset of a self-paced flexion movement of the index finger were reduced in amplitude in “surround” muscles of the hand (e.g. the abductor digiti minimi (ADM) and the abductor policis brevis (APB)). It was suggested that this phenomenon represented surround inhibition in the motor system, which served to facilitate individuated finger movements and to prevent unwanted overflow of muscle activity to surrounding muscles.

Support for this hypothesis comes from the finding of reduced SI in patients with focal hand dystonia, a disorder characterized by overflow of muscle activity into non-task relevant muscles (Beck et al., 2008). Furthermore, SI is more prominent in the

dominant hemisphere of right-handed subjects than in the non-dominant hemisphere (Shin et al., 2009). SI is also enhanced and appears earlier with increasing task difficulty (a choice reaction time task vs. a simple reaction time task) (Beck and Hallett, 2010). SI is modulated by force exertion; varying the force in the active muscle shows that SI peaks at 10% of maximal force and is lost when more than 40% of maximum force is exerted (Beck et al., 2009), which has been interpreted as a demonstration of its role in enabling fine control of finger movements.

Despite the suggestion in the literature that SI facilitates individuated finger movement, there is no direct evidence to date on the presence or absence of a relationship between motor performance on a task of individuated finger movement and the level of SI. In this regard, it is interesting that electromyographic (EMG) activity in surround muscles does *not* correlate with the degree of SI in healthy people (Kassavetis et al, 2014). The previously reported reduction of SI in patients with focal hand dystonia is also very variable and does not appear to correlate with severity of symptoms. Lastly a peculiar reduction in SI has been reported in healthy professional musicians who are highly skilled in performing individuated finger movements (Shin et al., 2012). While this latter result has been used to argue for why professional musicians are at risk of developing focal hand dystonia, it could also suggest that SI might relate to aspects of task novelty/difficulty, assuming that for professional musicians the task employed to assess SI is a simpler and more familiar one than for non-musicians.

The primary aim of this study was to investigate whether over-training healthy non-musicians on an isolated finger movement task would result in a reduction of SI,

similar to that seen in musicians. Subjects were over-trained on a precise force exertion task and SI was assessed during all stages of motor learning. Using a direct indicator of motor performance, we were further able to characterise the relationship between SI and motor performance. It has been previously demonstrated that as a motor task becomes overlearned and the movement performed becomes automatic, attention to action can be redirected with little interference with the task at hand (Passingham, 1996). This interplay between motor performance and attention, in addition to evidence that attention enhances intracortical inhibition (Liepert et al., 1998; Conte et al., 2007), makes attention an interesting variable to consider in the modulation of SI in the motor system.

In light of this, a secondary aim of this study was to explore a possible modulatory role of attention in motor SI. We hypothesised that an over-training of the task would lead to lower levels of attention and reduced SI. In turn, manipulating attention back to the task would enhance SI.

2 MATERIALS AND METHODS

2.1 Subjects

The data from 22 right-handed healthy volunteers (mean age: 27.7, SD: 4.4, 12 women) were analysed. None of the participants had any history of neurological disease, and none of them were professional musicians. All the participants gave their informed consent before taking part in the experiment, which was approved by

the local ethics committee and conducted in accordance with the Declaration of Helsinki.

2.2 Experimental design

There were 6 blocks of experimentation. Each block consisted of 40 trials. Each trial lasted 10s and included the motor task and a single TMS pulse either at movement onset (test) or 5s after movement onset (rest) (Fig 1B); we pseudo-randomized 20 trials for the test and 20 trials for the rest stimuli over the 40 trials of each block.

It has been demonstrated that successive presentation of signal events taxes sustained attention performance. Meanwhile, a high frequency of signal events (high event rate) combined with an unpredictability of the time of signal presentation (event asynchrony) enhances the demands on sustained attention (Parasurman, 1986; Sarter et al., 2001). As such, in the first 5 training blocks the inter-trial interval (ITI) was set to 3s, and in a final 'attention' block, the ITI was varied randomly between 1 and 5s (Fig 1B). A final block of varied ITI following five blocks of successive, predictable signal presentation was designed to increase demands on sustained attention and redirect subjects' attention back to the task. Subjects were not aware of the nature of the manipulation, they were simply informed that 'something is going to change, but the nature of the task will remain the same', and instructed to continue performing the task as they were in the previous blocks.

2.3 Motor task

During the experiment, subjects sat in a comfortable chair with their right hand resting on a desk. With their hand lying flat and relaxed on the desk, the tip of their

index finger was placed on a force transducer (Fig 1A). They were asked to briefly press down on the force transducer after a ‘go’ signal by flexing their index finger in the metacarpo-phalangeal joint. This movement has been shown to activate the FDI and suppress activity in the ADM through SI (Sohn and Hallett 2004). FDI is a synergist rather than primary muscle for this movement, but it has been demonstrated that synergists show the same type of modulation as prime movers (Sohn and Hallett, 2004).

At the beginning of the experiment, subjects were asked to press down on the force transducer with maximum force in order to measure the individual maximum EMG activity which could be produced in the FDI during that movement. They were then instructed to perform the same movement with 10% of their maximum voluntary contraction (MVC), and to do so as quickly and accurately as possible. They were also asked to keep their ADM completely relaxed while performing the motor task. Practice sessions were not provided, as the aim of the study was to monitor changes in SI during all stages of motor learning. However, trials where background ADM EMG activity exceeded 0.1mV were excluded.

The task was more demanding than those usually employed in experiments on SI. Visual feedback of their performance was displayed on a screen in front of the subjects as an interface designed specifically for this task (Fig 1B). Feedback was provided after each trial to facilitate faster and more effective motor training (Adams, 1987; Blackwell and Newell, 1996). Finger flexion force was displayed as in Fig 1A. Participants had to press onto the transducer to place a cursor within the region indicated by the dotted lines (10% MVC ± 0.25 N) as it moved from left to right across

the screen. Force was sampled at 150 Hz. Each sample that lay within the target scored 10 points; 7, 5 and 3 points were awarded respectively for samples 0.5, 1, and 1.5 N outside of the target range. Points were summed over the whole 2s of the task, and then divided by 1000, giving a maximum possible score of 3. At the end of each trial, subjects were presented with the numerical score as a measure of their performance. Optimal scores were obtained if participants reacted quickly and placed the cursor immediately into the target zone without overshoot/undershoot, and remained there for the duration of the trial. Subjects were instructed to aim to maximise their scores i.e. gain better control of their force production, throughout the experiment. This provided an indication of the change in motor performance throughout the experiment.

2.4 EMG recording

EMG activity was recorded from the right FDI and ADM using a pair of Ag-AgCl surface electrodes in a belly-tendon montage (Fig 1A). The EMG signal was amplified (1000 X) and band-pass filtered (bandwidth 3-1000 Hz) with a Digitimer NL844 amplifier (Digtimer, UK). The signal was digitised at a frequency of 5 kHz and fed into a laboratory computer for storage and off-line analysis. Data were collected with SIGNAL software V5.11 (Cambridge Electronic Design).

While an improvement in scores on the motor task (as described in section 2.3) indicates better control of the output command to the FDI, it was important to ensure that this was accompanied by EMG silence in the ADM, indicating focality of FDI contraction. Therefore, EMG activity was analysed in the ADM during FDI contraction to assess whether any change in surround inhibition (SI) throughout training had an

effect on EMG activity in the ADM muscle. The 20 trials where TMS was delivered at rest (TMS pulse 5s after movement onset), and an interval of 100 ms after onset of FDI activity were used. The duration of 100 ms after movement onset was chosen as it is a time interval during which SI is known to be active (Sohn and Hallet, 2004). The EMG activity measured was expressed as the root mean square (RMS) amplitude of the raw EMG signal.

The amplitude of MEPs is affected by ongoing EMG activity at the time of stimulation. Therefore, background EMG activity in the ADM was analysed in the 20ms prior to stimulation in the trials where TMS was delivered at the onset of FDI movement. This was to ensure that background EMG activity in the ADM remained as stable as possible throughout the experiment, and did not influence MEP measures. The EMG activity measured was expressed as the RMS amplitude of the raw EMG signal.

2.5 TMS

TMS was delivered by a figure-of-eight shaped coil with an external diameter of 9cm connected to a monophasic Magstim 200 stimulator (Magstim, Carmarthenshire, UK). The intersection of the coil was positioned tangentially on the scalp over the left M1 at the optimal site for eliciting maximal amplitude MEPs in the contralateral ADM i.e. the ‘hot spot’. This position was marked with a felt pen to ensure consistent coil positioning throughout the experiment. The handle of the coil was pointing backwards and laterally at a 45˚ angle to the sagittal plane, this induced a P-A directed current in the brain and stimulated corticospinal neurons (di Lazzaro et al., 2004). The intensity of the stimulation was set to evoke MEPs with a peak-to-peak amplitude of

approximately 1-1.5 mV in the ADM at rest in a minimum of 5 out of 10 consecutive trials.

For the assessment of SI, single TMS pulses were delivered at rest and at the onset of the movement (test). In order to assess MEP amplitude size at movement onset, the peri-triggering function of SIGNAL software was set to trigger TMS immediately when EMG activity in the right FDI exceeded 0.1 mV. MEPs at rest were assessed by a TMS pulse delivered 5s after movement onset, when subjects were resting waiting for the next 'go' signal. This time point is considered to be sufficient for measurements at rest. The duration of the movement was 2s, meaning the TMS pulse was delivered with a delay of 3s after the end of the movement. MEPs from the FDI and ADM muscles have been shown to return to baseline from 500 ms after EMG onset (Sohn and Hallett, 2004).

Peak-to-peak ADM MEP amplitude was measured off-line for each trial, and the average amplitude in 40 trials was calculated for each block. SI was expressed as the ratio between test MEP amplitudes and rest MEP amplitudes, in percentage. [SI = (MEP*test* / MEP*rest*)*100 [%]].

2.6 Statistical analyses

The SIGMAPLOT (version 12.0) software was used for the statistical analysis. Normality of data distribution was assessed with the Shapiro-Wilk test.

Time-dependent changes (effect of BLOCK) in SI, performance scores and reaction time (RT) were evaluated through repeated measures analysis of variance

(rmANOVA). Where significant effects were observed, multiple comparisons were conducted with the Holm-Sidak test to further analyse the results.

The relationship between SI and performance scores in the first 5 training blocks was explored by conducting a two-tailed regression analysis on the time-dependent changes in SI and performance scores using Pearson's correlation coefficient.

The data presented in the figures correspond to the data used for statistical analyses. Statistical significance was set to $P < 0.05$. All results are expressed as mean values ±SEM.

3 RESULTS

A total of 22 subjects completed the study. A further 2 participants (1 man and 1 woman) were excluded from the study because they showed insufficient surround inhibition (SI), i.e., larger test MEPs than rest MEPs in the ADM. While subjects were instructed to maintain EMG silence in the ADM (<0.1mV), there were nonetheless trials where this was not the case. Of the total trials analysed, 3% were excluded because background EMG activity exceeded 0.1mV.

3.1 Motor performance

The performance score was related to the time on target which depended on both the reaction time as well as the steadiness of the contraction. Higher scores reflect faster and more precise force exertion. All participants could perform the task and improved with practice (Fig 2A) over the first 5 repeating blocks. There was a tendency for performance to drop in the final attention block, but this was not significant.

This was confirmed by a significant effect of BLOCK in a one-way rmANOVA ($F(5,21) = 14.025$, $P < 0.001$). Post hoc pairwise comparisons demonstrated that scores in all blocks were larger than in the first block ($P<0.05$), but there was no significant change in score between subsequent pairs of blocks. The BLOCK effect remained strongly significant ($F(5,21) = 8.188$, $P < 0.001$) after the removal of the first 10 trials in the first training block, ensuring that performance improvement was not a result of task familiarization. Reaction times did not change over the blocks. There was a small increase in reaction time in the final attention block but this was not significant (one-way rmANOVA: no significant effect of BLOCK ($F(5,21) = 0.842$, $P = 0.523$) (Fig 2B).

Performance was also assessed as subjects' ability to maintain ADM silence during FDI contraction. A one-way rmANOVA was conducted to analyse any change in ADM EMG activity during FDI contraction throughout the experiment (Fig 3B). This revealed no significant change ($F(5,21) = 1.56$, $P = 0.178$). Motor training had no significant effect on ADM EMG activity during FDI contraction.

3.2 Surround inhibition

SI was quantified in terms of the amplitude of the MEP evoked in ADM at the onset of FDI contraction relative to the MEP evoked in ADM in the rest period between trials. Analysis of the data with a one-way rmANOVA revealed a significant effect of BLOCK ($F(5,21) = 6.451$, $P < 0.001$). Post hoc pairwise comparisons showed that SI was significantly lower than baseline in practice blocks 4 and 5 ($t = 3.450$ $P = 0.010$; t

= 4.163 $P < 0.001$ respectively). There was also a significant enhancement in SI between practice block 5 and the final attention block ($t = 4.144$ $P < 0.001$) (Fig 3A).

We confirmed that the amplitude of the resting MEPs in ADM and FDI were constant over all blocks and were unaffected by practice on the task (Fig 4). This was confirmed in a one-way rmANOVA that revealed no significant effect of BLOCK ($F(5,21) = 1.462$, $P = 0.209$ and $F(5,21) = 0.381$, $P = 0.861$ for ADM and FDI respectively). MEPs are also affected by ongoing EMG activity at the time of stimulation. Although the task instructions were to maintain EMG silence in ADM (< 0.1mV) there were nevertheless small changes in activity from trial to trial. We measured the level of EMG activity in the 20ms prior to the TMS pulse in SI trials (Fig 3C). A one-way rmANOVA confirmed that there was no change in ongoing activity over the trial blocks (no significant effect of BLOCK: $F(5,21) = 2.22$, $P = 0.057$).

All participants exhibited SI: the MEP evoked in ADM was smaller when triggered at the onset of FDI contraction than it was in relaxed muscles. However, as particpants practised the task, the amount of SI declined (Fig 3A). Thus, MEPs evoked in ADM at the onset of FDI activity gradually increased in size as performance improved. Note that this occurred even though there was no change in preceding background EMG activity nor in the amplitude of the MEP evoked in ADM at rest. In the final attention block, SI increased towards levels seen in the first block of trials.

3.3 Surround inhibition and performance

Pearson's Product-Moment Correlation revealed a significant, weak correlation between SI and performance scores (r = 0.25, *P* = 0.016), indicating that better motor performance is accompanied by less effective SI (Fig 5).

4 DISCUSSION

In the present experiments, healthy individuals made 240 isolated flexion movements of the index finger. Movement accuracy improved over that period while in contrast surround inhibition (SI) in the nearby relaxed ADM muscle was reduced. Analysis of background EMG activity in the ADM preceding stimulation, and of the amplitude of MEPs evoked in the ADM at rest, revealed that neither changed during training. This suggests that the reduction in SI was due to practice-related changes in its central control. The present experimental set-up did not include a measure of spinal excitability; it is possible that training resulted in an increase in the concurrent levels of spinal excitability at the onset of FDI contraction (Adkins et al., 2006) that could have influenced some of the measured changes in SI. Thus, it might be worthwhile to probe this in the future.

SI refers to the reduction in amplitude of MEPs evoked in the ADM muscle at the onset of a focal contraction of a distant hand muscle such as FDI. The amplitude of the MEP depends on the excitability of neural elements in the cortex as well as interneurons and motorneurones in the spinal cord. Since F-waves and ongoing EMG activity in ADM are constant or even increase during SI (Sohn and Hallet, 2004; Kassavetis et al.,

2014), spinal excitability is thought to remain unchanged. The conclusion is that SI is caused by reduced excitability at a cortical level of the corticospinal projection to ADM.

As noted in the introduction, several authors have speculated that SI is a cortical mechanism that helps to focus excitatory output of the motor cortex, enabling isolated finger movements and preventing overflow of unwanted activity to other muscles. However, it was recently reported that SI is less effective in professional pianists compared with non-musicians (Shin et al., 2012). At first sight the result is unexpected since expert pianists might have been thought to have superior control of individuated finger movements. If SI is needed to focus excitatory output at the cortex, it should be recruited more readily in pianists. In explanation it was proposed that pianists routinely practice a wide variety of complex finger movements, some of which may involve co-activation of FDI and ADM. If SI was always present, then it would interfere with such tasks. The hypothesis was that over time pianists reduce the effectiveness of SI, allowing complex combinations of finger movement to be produced. A corollary of this reasoning is that when pianists make isolated finger movements they can direct their motor commands selectively to the agonist muscles without requiring “focus” from surround inhibition. It is possible that reduced SI allows the expert pianist to shift more rapidly between isolated movements of a single finger to complex synergies of many fingers.

In the present experiments we tested this by asking non-musicians to practice a skilled index finger task in which participants improve performance by increasing the accuracy and reducing the variability of their motor output. Our hypothesis was that this would train individuals to focus their commands more accurately and reduce the need for SI

to prevent unwanted contraction of nearby muscles. The present motor task is ecologically limited in its ability to replicate the synergistic contractions required to play the piano. However, pianists utilise both skilled synergistic finger movements, as well as superior finger individuation. This study chose to focus on the latter to allow for a skill simple enough for non-musicians to 'master' in a relatively short amount of time. Moreover, synergistic contractions during synchronized finger exercise of agonist and surround muscles have been previously shown to reduce SI, while individuated contractions of the surround muscle alone had no effect on SI (Kang et al., 2012). The present findings extend those of Kang and colleagues (2012) by demonstrating that sufficient training of isolated contractions of the agonist muscle also appear to reduce SI. Therefore, motor training-related reduction of SI may be associated with both the nature of the task (synchronized vs individuated contractions), as well as the muscle practiced (agonist vs surround).

The results show that participants improved performance over time, achieving higher scores in each block of trials. Improvement was initially rapid but continued slowly for the rest of the experiment. Simultaneously, SI showed a continuous and gradual reduction. Therefore, as subjects became better at performing the task, their SI declined. It is important to note that training led to a significant reduction, rather than a total absence, of SI. We suggest that SI may have been useful during the early stages of learning to prevent activity in muscles that could interfere with task performance. However, as learning progressed, and control of output became more reproducible, the need for SI declines and its excitability (as tested with TMS) falls. The present study is limited by the lack of assessment of corticospinal excitability during the whole period when SI is known to be active (100ms after movement onset). Therefore, the present

findings are limited to the instantaneous depth of inhibition and do not extend to any potential effect on the duration of inhibition.

It is important to note that although SI decreased over time, there was no increase in "overflow" of activity to the ADM muscle. The level of EMG in ADM during the period when FDI was active was constant throughout the experiment. This confirms that participants were able to focus their motor commands effectively and to keep a constant low level of "overflow" to unwanted muscles. The nature of this overflow is unclear. Data show that phasic contraction of a single muscle or group of synergists is accompanied by a widespread increase in excitability of monosynaptic spinal reflexes in many muscles similar to that seen in the Jendrassik manouvre (Zehr and Stein, 1999). One contributor to this activation may be non-focal activity in descending pathways which is normally suppressed by SI. Our data show that although SI decreased with training, subjects still maintained a constant low level of "overflow" to uninvolved muscles suggesting that with practice, activity can be focused sufficiently well to reduce this non-focal activity without the aid of SI. In effect, training could improve focality of contraction in the agonist muscle, rather than having a direct effect on the surround muscle itself. This could make an active suppression of surround muscles less necessary, driving a reduction in SI. Indeed, isolated finger exercise of the ADM surround muscle which does not stress focality of contraction shows no modulatory effect on SI (Kang et al., 2012). Finally we note that cortical disinhibition is associated motor learning in humans (Floyer-Lea et al., 2006); similarly, repetitive practice of individuated finger movement reduces GABAergic short intra-cortical inhibition (SICI) (Liepert et al., 1998; Rosenkrantz et al., 2007). Therefore, it is possible that that the reduction of SI through training in the present

study is not specific to SI, but is a general phenomenon reflecting motor cortical disinhibition during motor learning.

A role for attention?

There is a second possible explanation for the reduced SI seen in professional pianists as well as after practice in the present experiments. Initial performance of a SI task requires attention. When participants initially attempt individuated flexion of the forefinger, they produce some activity in the ADM muscle. Most people can reduce this by directing their attention to the task. It could therefore be that attention engages SI. Prolonged practice of such movements in pianists and after training in non-pianists allows them to perform the task with little attention, thus reducing SI.

Therefore, as an initial attempt to probe the effect of attention on SI, we introduced a final block after training in which we attempted to re-engage attention back to the task. Unpredictability of events has been shown to increase demands on attention (Parasurman, 1986; Sarter et al., 2001). Therefore we randomly varied the inter-trial interval (ITI) in the final 'attention' block. This meant that, unlike in the training blocks, subjects were unable to predict the time of signal presentation, presumably resulting in greater attention to the task, although this is something that we could not measure directly, and therefore remains a speculative interpretation of our experimental manipulations. The results showed that varying the ITI resulted in an enhancement of SI back to baseline level (Fig 3A). This was consistent across all subjects. Note that there was no significant change in performance (Fig 2A, 3B) that could have influenced the observed enhancement of SI. Therefore, the increase in SI could be due to an increase in attention to the task. This finding is limited by a lack of direct

measure of attention in the current experiment. It is possible that varying the ITI drove an increase in SI to compensate for an increased unpredictability of signal events and maintain a relatively constant level of motor performance. However, it is important to note that none of the subjects perceived the nature of the manipulation. Additionally, longer reaction times (RT) are associated with a less automatic motor performance and higher levels of attention (Jueptner et al., 1997), and an analysis of RT showed that these were slower in the final attention block (Fig 2B), although this did not reach statistical significance.

This final block of the experiment was exploratory and not intended to provide a definitive answer to the role of attention in movement control. Nevertheless it does suggest that attending to a movement may engage additional physiological controls on output, such as SI, that may not be engaged by routine tasks.

4.1 Conclusions

The present findings demonstrate that improved performance of an isolated finger movement is accompanied by reduced SI. Therefore, the direct role of SI in the mechanics of finger individuation remains unclear. Perhaps SI is a mechanism to aid effective finger individuation in an untrained hand, while a hand trained in isolated finger movements utilises alternative mechanisms developed through training, such as enhanced facilitatory networks for the desired movement, which would reduce the need for an active SI. The final part of the experiment provides some evidence that attention to task may be an important factor controlling the excitability of SI but this finding is limited by a lack of direct measure of attention.

CONFLICT OF INTEREST

None of the authors have potential conflicts of interest to be disclosed.

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None.

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FIGURE LEGENDS

Fig 1. (A) Experimental setup. Two pairs of surface electrodes were placed on the FDI and ADM of the right hand. The tip of the index finger was placed on the force transducer and adjacent fingers were kept at rest. **(B)** Time course of the task. Shown are EMG traces of the FDI, and a schematic of the real-time visual feedback that was presented to subjects during the task. At 0s, subjects were signalled to press down on the force transducer placing a cursor into a 10% maximal force target. At 2s, subjects were signalled to stop exerting force and a measure of their performance was given as a numerical score. Placing the cursor into the target as quickly and accurately as possible yielded the highest scores. Self-triggered TMS pulses were delivered randomly 0s after movement onset (condition; top trace), or 5s after movement onset (rest; bottom trace). The inter-trial interval (ITI) was set to 3s in the first 5 training blocks, and varied randomly between 1-5s in the final 'attention' block. **(C)** Example of raw data from one subject. Shown are 10s window EMG traces of the ADM muscle in trials where MEP was recorded at the onset of movement (test/ SI) and at rest. **(D)** Enlarged scale demonstrates an ADM MEP of 1mV at rest and a 30% reduction in ADM MEP size during conditioning. Displayed is a peak-to-peak EMG baseline of 0.02mV 200ms prior to the TMS pulse delivered at rest. Trials where EMG activity exceeded 0.1mV were excluded.

Fig 2. **(A)** Mean performance scores in each experimental block. There was a steep learning curve between the first and second block, performance then plateaued for the remainder of the experiment. Error bars indicate SEM. * indicates $P < 0.001$ compared to baseline. **(B)** Mean reaction time (RT) in each experimental block. As

performance became more automatic, RT gradually decreased, then plateaued. This was followed by a steep increase in RT in the final attention block, which involved a random variation of inter-trial interval (ITI) as a means of manipulating attention back to the task. There was no significant change in RT. Error bars indicate SEM.

Fig 3. (A) Mean calculated surround inhibition (SI) in the ADM muscle in each experimental block. SI is expressed as the ratio of conditioned MEP amplitudes to rest MEP amplitudes, in percentage. An increase in this percentage indicates a reduction of SI. SI was reduced over the course of the first 5 training blocks, and returned to baseline levels in the final block where attention was manipulated back to the motor task. Error bars indicate SEM. ** indicates $P < 0.001$ compared to baseline, * indicates $P = 0.010$ compared to baseline. **(B)** ADM EMG amplitude calculated as the root mean square (RMS) of raw ADM EMG activity during FDI contraction (100ms after movement onset). Background EMG activity in the ADM during FDI contraction showed no significant change throughout training, or in the final attention block ($P = 0.178$). **(C)** Background EMG activity in the ADM 20ms prior to stimulation in trials where TMS pulse was delivered at onset of FDI activity. There was no significant change in this activity throughout the experiment *(*$P = 0.057$).

Fig 4. (A) Motor evoked potential (MEP) in the ADM at rest (5s after onset of movement) in each experimental block. There was no significant change in mean MEP amplitude evoked at rest in each block; $P = 0.209$. **(B)** Motor evoked potential (MEP) in the FDI at rest (5s after onset of movement) in each experimental block. There was no significant change in mean MEP amplitude evoked at rest in each block; $P = 0.861$.

Fig 5. Scatterplot displaying a weak correlation between surround inhibition (SI) and motor performance. SI is expressed as a percentage of the ratio of conditioned to rest MEP amplitudes in the ADM muscle. An increase in this percentage indicates a lower SI. A reduction of SI is associated with an improvement in motor performance. r = 0.25, *P* = 0.016.