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Motor training reduces surround inhibition in the motor cortex

Haya Akkad [a], Flavio Di Stasio [b], Robert Tibold [a], Panagiotis Kassavetis [a,c], John C. Rothwell [a], Mark J. Edwards [a,d,*]

[a] *Sobell Department of Motor Neuroscience & Movement Disorders, University College London Institute of Neurology and The National Hospital for Neurology and Neurosurgery, London WC1N 3BG, UK*
[b] *Neuromed Institute IRCCS, Via Atinense 18, 86077 Pozzilli, IS, Italy*
[c] *Boston University, Neurology Department, Boston, MA, USA*
[d] *Department of Cell Sciences, St George's University of London, Cranmer Terrace, London SW17, UK*

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HIGHLIGHTS

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

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 5 s after offset of a 2 s 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.

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 "normalisation" 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

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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.

[*] Corresponding author at: Department of Cell Sciences, St George's University of London, Cranmer Terrace, London SW17, UK.

E-mail address: medwards@sgul.ac.uk (M.J. Edwards).

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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 pollicis 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 characterised 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 10 s and included the motor task and a single TMS pulse either at movement onset (test) or 5 s after movement onset (rest) (Fig. 1A); 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 (Parasuraman, 1986; Sarter et al., 2001). As such, in the first 5 training blocks the inter-trial interval (ITI) was set to 3 s, and in a final 'attention' block, the ITI was varied randomly between 1 and 5 s (Fig. 1A). 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. 1B). 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 0.1 mV 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. 1A). 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. 1B. 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