Selective Inhibition of Movement

James P. Coxon, Cathy M. Stinear, and Winston D. Byblow

Human Motor Control Laboratory, Department of Sport and Exercise Science, University of Auckland, Auckland, New Zealand

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Coxon JP, Stinear CM, Byblow WD. Selective inhibition of movement. J Neurophysiol 97: 2480–2489, 2007. First published January 24, 2007; doi:10.1152/jn.01284.2006. In studies of volitional inhibition, successful task performance usually requires the prevention of all movement. In reality, movements are selectively prevented in the presence of global motor output. The aim of this study was to investigate the ability to prevent one movement while concurrently executing another, referred to as selective inhibition. In two experiments, participants released switches with either their index and middle fingers (unimanual) or their left and right index fingers (bimanual) to stop two moving indicators at a fixed target (Go trials). Stop trials occurred when either one or both indicators automatically stopped before reaching the target, signaling that prevention of the prepared movement was required. Stop All and selective Stop trials were randomly interspersed among more frequently occurring Go trials. We found that selective inhibition is harder to perform than nonselective inhibition, for both unimanual and bimanual task contexts. During selective inhibition trials, lift time of the responding digit was delayed in both experiments by ≈100 ms, demonstrating the generality of the result. A nonselective neural inhibitory pathway may temporarily “brake” the required response, followed by selective excitation of the to-be-moved digit’s cortical representation. After selective inhibition trials, there were persistent asynchronies between finger lift times of subsequent Go trials. The persistent effects reflect the behavioral consequences of nonspecific neural inhibition combined with selective neural disinhibition.

INTRODUCTION

In daily life we encounter situations where it is desirable to suddenly prevent ourselves from executing a prepared action. Inhibitory control, the suppression of behavior in response to either internal or external influences, is a cognitive function represented in the prefrontal cortex (Fuster 1997). When motor areas of the brain are already engaged in the preparation of movement, the prefrontal cortex often needs to exert a “top-down” influence for effective inhibitory control.

Stop signal and Go–NoGo paradigms are commonly used in laboratory experiments to explore inhibitory control. Participants typically respond to a Go cue with hand movement and attempt to prevent the response when a Stop cue is infrequently presented. In this paradigm, correct Stop trial performance occurs when participants do not respond at all. In reality, movements are selectively prevented in the presence of global motor output. However, only a few experiments have attempted to examine the selectivity of inhibitory control (Bedard et al. 2002; De Jong et al. 1995; van den Wildenberg and van der Molen 2004). In these studies, participants performed a choice reaction time task. A Stop signal was associated with one of the stimulus–response alternatives. Inhibition was required only when the Stop signal was valid (conditional stopping). Although these studies investigated selective discrimination of the Stop signal, correct Stop trial performance required that no movement be produced. In this situation, the simplest strategy is to prevent all movement from occurring. Thus these studies did not test selective inhibition of motor output.

The aim of this study was to investigate, at the behavioral level, selective inhibition of motor output. Selective inhibition is defined as the ability to prevent one movement while concurrently executing another. To test this, we developed a novel task where participants were required to stop two moving indicators at a fixed point (Fig. 1A). Each indicator was under the independent control of switches operated by the index and middle fingers of one hand (unimanual experiment) or the index finger of each hand (bimanual experiment). For most trials, participants released the switches together, to stop both indicators as close to the target as possible (Go trials). On some trials, one or both indicators automatically stopped moving, before reaching the target. This signaled that movement of either one or both digits was to be prevented (Stop trials). The unimanual and bimanual experiments were conducted to investigate selective inhibition of within and between hemisphere movement preparation, respectively. We hypothesized that participants would be less able to prevent part of a prepared movement (selective inhibition) than all movement (nonselective inhibition), regardless of whether movements were relegated to single- or dual-hemispheric control. In addition, for the unimanual experiment, we hypothesized that it should be easier to selectively prevent movement of the middle finger and respond with the index finger than vice versa because individuated neural control is greater for the index finger relative to that of other fingers (Hager-Ross and Schieber 2000; Keen and Fuglevand 2004a; Schieber et al. 2005).

Volitional inhibition of primary motor cortex (M1) is exerted by a nonselective neural pathway, affecting not only the agonist muscle representation but also nearby muscle representations within the same hemisphere (Coxon et al. 2006) and the homologous representation of the opposite hemisphere (Leocani et al. 2000). We therefore hypothesized that the lift time of the responding digit would be delayed when selective inhibition was required. Given the left hemisphere dominance for movement preparation (Schulte et al. 1998; Serrien et al. 2006; Verstynen et al. 2005), we also hypothesized that in the bimanual experiment, there would be greater responding delays when right-side movement was selectively inhibited than vice versa. Finally, we investigated whether selective inhibi-
tion produces a residual uncoupling of the digits during performance of subsequent Go trials. There are recent reports that stopping all movement delays response times of the following Go trial (Barton et al. 2006; Mirabella et al. 2006). We demonstrate for the first time that this effect is observed in the context of selective inhibition.

METHODS

Participants

Seventeen subjects with no neurological impairments participated in two experiments (aged 21–40 yr; seven male). Twelve subjects participated in the first experiment (Unimanual) and 11 in the second experiment (Bimanual). Sixteen subjects were right handed (mean laterality quotient 0.89, SD 0.09) and one was left handed (laterality quotient 0.75) as determined by the Edinburgh Handedness Inventory (Oldfield 1971). Written informed consent was obtained before participation and the University of Auckland Human Participants Ethics Committee approved the experiment in accordance with the Declaration of Helsinki.

Preparation

For the unimanual experiment, the right hand was tested for all subjects. The right forearm was pronated with the index and middle fingertips on the keys of a computer mouse. For the bimanual experiment, forearms were semiprone with the medial aspect of the left and right index fingertips positioned on the computer mouse keys (Fig. 1A). For the unimanual experiment, bipolar surface electromyography (EMG) recordings were made from the right extensor indices proprius (EIP) and extensor digitorum (ED) with ED electrode position optimized for middle finger extension (Keen and Fuglevand 2003). For the bimanual experiment EMG was recorded from the left and right first dorsal intersosseus (FDI) because this is the only muscle involved in producing index finger abduction. EMG signals were amplified (Grass P511AC; Grass Instrument Division, West Warwick, RI), band-pass filtered (30 Hz to 1 kHz), and sampled at 1 kHz using a 16-bit A/D acquisition system (National Instruments, Austin, TX). EMG signals were displayed using custom LabVIEW software and stored to disk for off-line analysis.

Procedure

For both experiments, subjects sat 1 m in front of a 23-in. computer screen positioned at eye level. The display consisted of two vertically oriented indicators, 15 cm high, 1 cm wide, and separated by a 1-cm gap. Each trial began about 1 s after the subject depressed both mouse keys. The subject was instructed to use only as much force needed to maintain the keys in their depressed state. The left and right indicators moved at an equal rate from the bottom up, reaching the target in 800 ms. Subjects were instructed that their primary task was to stop the indicators at the target by releasing the keys (referred to as Go trials). After each trial, the software provided feedback, indicating the time (in milliseconds) each indicator stopped relative to the target. It was emphasized that the Go task was to be performed as accurately as possible. The subject was informed that the indicators may stop unexpectedly before the target, and for these trials they were not to lift their fingers. These trials are referred to as Stop trials. There were three types of Stop trials: 1) Stop All, where both indicators stopped at the same time before reaching the target; 2) Stop Index/Left, where the left indicator stopped before reaching the target; and 3) Stop Middle/Right, where the right indicator stopped before reaching the target. Index and Middle refer to the digit to be prevented from moving in the
unimanual experiment. Left and Right refer to the side prevented from moving in the bimanual experiment. The experiments were identical except for the effectors used.

Practice trials were completed before commencing data collection. This was followed by a preliminary block consisting of 30 Go trials, where subjects were informed that the indicators would not stop unexpectedly. This block served as additional practice and subjects were instructed that performance on subsequent blocks was to be sustained at this level. The experiments consisted of 12 blocks, each block consisting of 30 trials. Within each block, both Go and Stop trials were presented in a randomized order. There were 360 trials in total, 240 of which were Go trials and 120 were Stop trials. Stop All, Stop Index/Left, and Stop Middle/Right trials were presented in equal proportion. For each Stop condition, the indicators stopped randomly 300, 240, 180, and 120 ms before the target, with 10 trials presented at each stop time throughout the experiment (Fig. 1B). Trials were self-paced with a minimum intertrial interval of 1.5 s. EMG collection was triggered by the onset of indicator movement and recorded for 1.2 s.

Dependent measures

Lift time (LT) and lift variability were determined for each subject. LT refers to when the indicator was stopped relative to the target (LT = time of response − 800 ms) and lift variability refers to 1 SD of the distribution of lift times.

EMG burst onsets for both muscles in each experiment were calculated by detecting when the root-mean-square EMG (rmsEMG) first increased by >3 SDs above baseline rmsEMG. These onsets were manually verified by an experimenter who was blinded to trial type. Electromechanical delay (EMD) was determined by subtracting prime mover EMG burst onset from LT.

For Stop trials, the probability of inadvertently responding was determined for each stop time and condition. Linear interpolation was used to determine the stop time where the probability of responding was 50%. The stop signal reaction time (SSRT) is the difference between this stop time and the average Go trial LT. For selective stop trials, LT and EMG onset of the responding digit were determined. This analysis was performed once for all trials regardless of behavioral outcome and, again, including only successful inhibition trials at the two earliest stop times, when the probability of success was >50%.

EMG traces for Go trials and successful Stop trials were rectified and mean EMG traces calculated. The mean traces were filtered with a dual-pass 20-Hz Butterworth low-pass filter and the first derivative was determined. For each condition, the peak rate of change of EMG at burst onset was determined. This measure reflects, at least in part, the gain of the corticomotor pathway, but is dependent on all elements acting on the motor neuron pool.

A separate analysis was conducted to investigate the effect of successful stop trial performance on the lift time asynchrony (LTA) of subsequent Go trials. LTA was defined as LTA = (index finger lift time) − (middle finger lift time) (in milliseconds) for the unimanual experiment and LTA = (left side lift time) − (right side lift time) (in milliseconds) for the bimanual experiment. All Go trials where no Stop trial had been presented in the previous two trials were extracted. Then, all Go trials where a Stop trial had been presented in the previous two trials were extracted and sorted according to Stop condition. A global delay in movement initiation as a result of stopping was tested by comparing the average LT for Go trials with Go trials that followed Stop All trials. For selective Stop conditions, LTA was calculated at each Stop time.

Statistical analysis

For Go trials, LT and lift variability of each finger were compared using two-tailed paired t-tests. Other dependent measures were subjected to repeated-measures ANOVA with planned contrasts and the use of post hoc comparisons when necessary. A 3 × 4 ANOVA tested for differences in the probability of an inadvertent response, with factors Stop Condition (Stop All, Stop Index/Left, Stop Middle/Right) and Stop Time (300, 240, 180, 120 ms before the target). Planned contrasts were conducted to test for differences between Stop All and selective stop conditions at 300, 240, and 180 ms. Bonferroni-corrected post hoc comparisons tested for differences in the probability of responding between Stop Index and Stop Middle and between Stop Left and Stop Right. SSRT was compared across Stop conditions with a two-tailed paired t-test.

For selective Stop trials, a 2 × 5 ANOVA with factors Responding Finger (Index/Left, Middle/Right) and Condition (Go, Stop 300, Stop 240, Stop 180, Stop 120) tested for differences in LT. Planned contrasts compared selective Stop time to Go. This analysis was performed for all data and then again using only successful trials from the two earliest stop times (2 × 3 ANOVA) where participants inhibited responding ≥50% of the time. EMG burst onsets and EMD of the responding finger were analyzed as above with factors Muscle (EIP, ED/Left FDI, Right FDI) and Condition. For each muscle, EMG peak rate of change was analyzed with one-way ANOVA, factor Condition (Go, Stop 300, Stop 240).

LTs after Stop All trials were compared with Go trial LTs with paired t-tests. LTA was analyzed using one-way ANOVA with factor Condition (Go, Stop All, Stop Index/Left, Stop Middle/Right). Post hoc comparisons compared each Stop condition to Go. LTA after selective Stop trials was further investigated as a function of Stop time. For Stop Index/Left and Stop Middle/Right trials, two-tailed paired t-tests compared each stop time with Go.

The criterion for statistical significance was α = 0.05. For non-spherical data, the conservative Greenhouse–Geisser P value is reported. Bonferroni-corrected P values are reported where post hoc comparisons of significant effects were made. All results are shown as group means ± SE.

Results

Go task performance

Participants performed the Go task correctly, stopping the indicators close to the target. Performance was similar to that reported previously (Coxon et al. 2006). EMG traces and Go trial LT are shown, respectively, in Figs. 2 and 3. There was no difference between Index and Middle LT in the unimanual experiment. LT was significantly greater on the Left (15.6 ± 2.2 ms) than on the Right (8.7 ± 2.5 ms) in the bimanual experiment (P < 0.05). Lift variability was 34.8 ± 2.0 ms for Index and 35.4 ± 1.8 ms for Middle in the unimanual experiment and 31.1 ± 1.2 ms for Left and 32.3 ± 1.6 ms for Right in the bimanual experiment. There was no difference in lift variability between the two effectors for either experiment (all P > 0.1).

Probability of inadvertently responding on Stop trials

The data from two subjects from the unimanual experiment and one subject from the bimanual experiment were discarded because they were unable to perform the selective inhibition task at the earliest stop time. The probability of responding on Stop trials for each experiment is shown in Fig. 4. For both the unimanual and bimanual experiments, there were main effects of Stop Condition [unimanual, F(2,18) = 77.3, P < 0.001; bimanual, F(2,18) = 28.9, P < 0.001], Stop Time [unimanual, F(3,27) = 388.7, P < 0.001; bimanual, F(3,27) = 263.4, P < 0.001], and their interaction [unimanual, F(6,54) = 12.3, P < 0.001; bimanual, F(6,54) = 7.4, P < 0.001]. For unimanual, the probability of responding was...
significantly greater for Stop Index and Stop Middle relative to that of Stop All 300, 240, and 180 ms before the target (all \( P < 0.01 \)). There was a tendency for Index finger responses to occur more often than Middle finger responses at 300 and 180 ms, but this effect was just above the level of significance (both \( P = 0.06 \)). For bimanual, the probability of responding was significantly greater for Stop Right than for Stop All at 300 ms (\( P < 0.05 \)). At 240 and 180 ms, both Stop Left and Stop Right were significantly greater than Stop All (all \( P < 0.01 \)). There was no difference in the probability of responding between Stop Left and Stop Right.

Stop signal reaction time (SSRT)

For unimanual, SSRT was greater for Stop Index (248.1 ± 7.9 ms) and Stop Middle (221.4 ± 4.0 ms) compared with Stop All (169.7 ± 2.6 ms, both \( P < 0.001 \)). SSRT was also greater for Stop Index compared with Stop Middle (\( P < 0.01 \)). For bimanual, SSRT was greater for Stop Left (219.3 ± 7.2 ms) and Stop Right (201.0 ± 10.5 ms) compared with Stop All (173.6 ± 5.0 ms, \( P < 0.001 \) and \( P < 0.05 \), respectively). There was no difference between Stop Left and Stop Right (\( P = 0.1 \)).
There were main effects of Condition in both experiments. For unimanual, $F_{(4,36)} = 61.1, P < 0.001$; bimanual, $F_{(4,36)} = 42.9, P < 0.001$. For bimanual, there was also a main effect of Side [$F_{(1,9)} = 20.1, P < 0.001$] and a Side x Condition interaction [$F_{(4,36)} = 5.4, P < 0.01$]. LT for the Left side was significantly greater than the Right side at 240 ms ($P < 0.05$) and 180 ms ($P < 0.01$) (see Fig. 3C for planned contrast outcomes). Results for selectively inhibited trials also showed a main effect of Condition in both experiments [unimanual, $F_{(2,18)} = 65.5, P < 0.001$; bimanual, $F_{(2,18)} = 59.9, P < 0.001$]. The bimanual experiment also had a main effect of Side [$F_{(1,9)} = 11.6, P < 0.01$] and a Side x Condition interaction [$F_{(4,36)} = 6.0, P < 0.05$]. LT was greater for the Left side than the Right side at 240 ms ($P = 0.01$).

Responding digit performance on selective Stop trials

Group LT results are shown in Fig. 3. Analysis of all trials revealed a main effect of Condition for both experiments [unimanual, $F_{(4,36)} = 28.8, P < 0.001$; bimanual, $F_{(4,36)} = 28.7, P < 0.001$]. There was also a main effect of Muscle for the unimanual experiment [$F_{(1,9)} = 7.2, P < 0.05$]. The results of planned contrasts are provided in Table 1. For selectively inhibited trials there was a main effect of Condition in both experiments [unimanual, $F_{(2,18)} = 54.9, P < 0.001$; bimanual, $F_{(2,18)} = 52.3, P < 0.001$] and no other effects. Responding digit EMG burst onsets during selective inhibition trials occurred significantly later than during Go trials in both experiments (all $P < 0.01$).

For unimanual EMD, there was a main effect of condition [$F_{(4,36)} = 16.2, P < 0.001$] and a condition by muscle interaction [$F_{(4,36)} = 3.7, P < 0.05$]. For bimanual EMD, there were main effects of condition [$F_{(4,36)} = 13.9, P < 0.001$] and of muscle [$F_{(1,9)} = 8.8, P < 0.05$] but no interaction. The results of planned contrasts are shown in Table 1.

Group EMG traces are shown in Fig. 2; peak rate of change of EMG is shown in Fig. 5. There was a main effect of Condition for EMG peak rate of change in the unimanual experiment [$EIP, F_{(2,18)} = 13.6, P < 0.01$; $ED, F_{(2,18)} = 9.6, P < 0.01$] and in the bimanual experiment [$Left FDI, F_{(2,18)} = 4.8, P < 0.05$; $Right FDI, F_{(2,18)} = 7.5, P < 0.05$]. Post hoc comparisons are shown in Fig. 5.
Effect of a preceding Stop All trial on Go trial lift time

For unimanual, LT averaged across effectors was $8.3 \pm 1.5$ ms for Go trials and $11.2 \pm 2.8$ ms for trials that followed Stop All ($P > 0.2$). For bimanual, LT was $9.3 \pm 2.1$ ms for Go trials and $14.1 \pm 2.8$ ms for trials that followed Stop All ($P > 0.1$).

Asynchrony of lift times between effectors

For unimanual, LTA was $2.2 \pm 1.3$ ms for Go trials, with the index finger lifting slightly before the middle finger. For bimanual, LTA was $7.9 \pm 2.2$ ms for Go trials, with the right index finger lifting slightly before the left index finger. There were no significant differences between the lift times of the effectors.

**TABLE 1.** EMG burst onsets and electromechanical delay

<table>
<thead>
<tr>
<th></th>
<th>Unimanual</th>
<th>Bimanual</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EIP Onset, ms</td>
<td>EMD, ms</td>
</tr>
<tr>
<td></td>
<td>Mean SE</td>
<td>Mean SE</td>
</tr>
<tr>
<td>Go</td>
<td>$-47.1 \pm 5.0$</td>
<td>$-58.9 \pm 3.2$</td>
</tr>
<tr>
<td>Stop 300</td>
<td>$-22.4 \pm 7.7$**</td>
<td>$-23.4 \pm 7.6$***</td>
</tr>
<tr>
<td>Stop 240</td>
<td>$10.6 \pm 6.6$***</td>
<td>$2.3 \pm 7.2$***</td>
</tr>
<tr>
<td>Stop 180</td>
<td>$-18.3 \pm 10.3$***</td>
<td>$-30.2 \pm 10.1$**</td>
</tr>
<tr>
<td>Stop 120</td>
<td>$-50.2 \pm 6.2$</td>
<td>$-62.5 \pm 3.6$</td>
</tr>
</tbody>
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EMG burst onsets and electromechanical delay (EMD) for the responding effector on Go trials and selective Stop trials. EMG onset is reported relative to the target (i.e., $0$ ms = Target). EIP, responses initiated by the index finger, prime mover extensor indices proprius, to stop the left indicator during Stop Middle trials. ED, responses initiated by the middle finger, prime mover extensor digitorum, to stop the right indicator during Stop Index trials. Left FDI, responses initiated by the left index finger, prime mover first dorsal interosseus, to stop the left indicator during Stop Right trials. Right FDI, responses initiated by the right index finger, prime mover first dorsal interosseus, to stop the right indicator during Stop Left trials. Planned contrasts with Go trials are shown as $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$. Error bars: SE.
was a main effect of Condition for both experiments [unimanual, $F_{(3,27)} = 15.8$, $P < 0.001$; bimanual, $F_{(3,27)} = 4.0$, $P < 0.05$]. For unimanual, there was a significant difference between Go and Stop Index ($P < 0.05$) with the index finger lifting after the middle finger on Go trials that followed Stop Index trials (Fig. 6A). LTA was greater after Stop Index than Go trials at 300 ms ($P = 0.01$), 240 ms ($P < 0.05$), and 180 ms ($P < 0.001$), with the index finger lift occurring after the middle finger lift (Fig. 6B). LTA was also greater after Stop Middle than Go trials at 300 ms ($P < 0.01$), with the middle finger lift occurring after the index finger lift.

For bimanual, there was a significant difference between Go and Stop Right ($P < 0.05$) with LTA reduced after Stop Right trials (Fig. 6C) and further reduced for Stop Right trials at 300 ms ($P < 0.01$) (Fig. 6D).

**DISCUSSION**

As predicted, selective inhibition of both unimanual and bimanual movement was harder to perform than nonselective inhibition (Fig. 2). During selective inhibition trials, LTs were delayed by $\leq 100$ ms in both unimanual and bimanual movement contexts (Fig. 3). These delays indicate that the mechanism involved in rapidly preventing movement operates in a nonselective way to temporarily “brake” intended motor output and is likely to be generated upstream from primary motor cortex. In addition, Stop trials had persistent effects on the motor system. Although there were no after-effects of Stop All trials in the present study, performing selective inhibition induced an asynchrony in lift time between the digits on subsequent Go trials (Fig. 6). This suggests that selective inhibition differentially alters the gain of motor representations for an extended duration.

**Neurophysiological determinants of selective inhibition**

In support of our hypothesis, subjects were more likely to inadvertently respond during selective Stop conditions than Stop All conditions. This was observed in both unimanual and bimanual movement contexts and is thus generalizable to some
extent. For unimanual movements, both mechanical and neural factors constrain the degree of digit individuation (Schieber 2001; Schieber and Santello 2004) especially for the middle and ring fingers, which are the least independent (Hager-Ross and Schieber 2000). However, given the small-amplitude movement required to release the key in the present study, mechanical coupling is unlikely to be a major constraint (Lang and Schieber 2004). In the bimanual experiment there was no mechanical coupling, yet selective stopping was still more difficult than nonselective stopping. Therefore we consider neural factors to be the primary constraint on selective prevention of movement in this context.

We propose that an inhibitory neural pathway from prefrontal cortex, by the basal ganglia, nonselectively “brakes” M1, by suppressing ongoing excitatory input to the corticomotor pathway, preventing overt movement. Engaging the nonselective “brake” leads to delayed responses by the other digit when selective inhibition is required. Both EMD and EMG peak rate of change increased for the responding digit on selective inhibition trials. EMD reflects the time from when EMG is first detected to when the response is detected. Thus these combined results may reflect initial suppression of input to the corticomotor pathway followed later by a release of neural inhibition that is specific to the responding digit. In support of this interpretation, it was previously demonstrated that Stop signal tasks specifically engage the right inferior frontal gyrus (rIFC) of the prefrontal cortex, projecting to basal ganglia to inhibit prepared movement (Aron and Poldrack 2006; Aron et al. 2003, 2004; Band and van Boxtel 1999). This projection includes a hyperdirect pathway between rIFC and the subthalamic nucleus (STN) (Aron and Poldrack 2006; Aron et al. 2004; Poldrack et al. 2006) and an indirect pathway by the striatum (Alexander et al. 1990; Mink 1996). For both pathways, excitatory input to STN reduces thalamic output and, consequently, the output of M1 (Mink 1996; Nambu et al. 2002). Excitability of M1 decreases roughly 140 ms after presentation of a stop cue for nonselective inhibition tasks (Coxon et al. 2006; Hoshiyama et al. 1997; Sohn et al. 2002). The present results suggest this nonselective mechanism is engaged during unimanual and bimanual selective inhibition. This explanation fits nicely with a neural network model of the basal ganglia (STN in particular) in decision making (Frank 2006).

There was a higher probability of responding, and longer SSRTs, in selective inhibition trials. However, if a nonselective neural inhibition mechanism is invoked in both selective and nonselective trials, one might expect SSRTs to be equivalent between these conditions. A possible explanation for this is that selective inhibition is signaled by an apparent conflict, where one indicator stops but the other does not. This conflict

FIG. 6. Group results for Go trial lift time asynchrony (LTA). Positive LTA indicates that Middle/Right leads the Index/Left. Stop conditions indicate the LTA of Go trials that immediately followed a Stop trial. Unimanual (A) and bimanual (C) experiment LTA for Go trials and Stop conditions collapsed across stop time. Unimanual (B) and bimanual (D) experiment LTA for selective Stop conditions as a function of stop time. Go trial LTA is shown in white. Black bars reflect the LTA of Go trials that immediately followed a Stop Index/Left trial. Gray bars reflect the LTA of Go trials that immediately followed a Stop Middle/Right trial. Asterisks indicate results of planned comparisons comparing selective Stop trials with Go: *P < 0.05; **P < 0.01; ***P < 0.001. Error bars: SE.
signal requires a more complex decision to achieve incongruent responses (stopping the correct effector while responding with the other). The added complexity in these trials imposes a time delay not only for the required response, but also on the (nonselective) stop command. These findings indicate that nonselective neural inhibition and the neural disinhibition required for response overlap in time to some extent, clearly by independent mechanisms. These results are also consistent with the findings of De Jong et al. (1995), where SSRTs were longer in a conditional stopping paradigm than during nonconditional stopping.

### Coupling and decoupling

Go trial performance required that both digits move in the same direction at the same time. This coupling was most likely produced by synchronized neural activity between cortical movement representations. Cortical activity is strongly correlated between sites within M1 during unimanual movement preparation (Donoghue et al. 1998; Murthy and Fetz 1996; Sanes and Donoghue 1993) and between primary motor cortices bilaterally during bimanual movements (Murthy and Fetz 1996). Therefore selective inhibition requires a rapid deconstruction of the coupling between motor representations. A failure to uncouple representations within or between hemispheres could explain the reduced ability to selectively inhibit unimanual or bimanual responses, respectively.

For the unimanual experiment, index and middle digits had to be decoupled during selective Stop trials and this was most difficult when the middle finger was lifted in isolation. In humans, extensor digitorum (ED) consists of separate neuromuscular compartments that act to extend digits 2–5. Between-compartment synchronization suggests that divergent descending commands limit the extent to which extension of one digit can be performed independently of the others (Keen and Fuglevand 2003, 2004b). When attempting to selectively extend the middle finger, “motor overflow” to the index finger compartment of ED may have reduced the individuation of the movement. In contrast, selective index finger extension involves EIP, a dedicated index extensor. These neuromuscular factors explain the trend toward more successful decoupling during Stop Middle trials than during Stop Index trials.

Remarkably, LT was delayed by \( \leq 100 \text{ ms} \) on selective inhibition trials, with the extent of delay varying as a function of stop time. EMG onsets of the agonist musculature were similarly delayed, indicating that movement initiation was impeded. This discounts the possibility that the delay is induced by an increase of antagonist muscle activation. Neither LT nor EMG onset was significantly different from Go trials during Stop 120, when inhibition of the response was not possible. Participants always responded on these trials, stopping the indicators with the same accuracy as that during Go trials. This suggests that there was insufficient time to engage the inhibitory neural pathway and that movement preparation and initiation were uninterrupted. Importantly, these results demonstrate that participants did not wait for the stop cue and then produce a reactive movement. The responding digit was maximally delayed at selective Stop 240 when subjects only occasionally failed to prevent their response. Between 120 and 240 ms, the lift delay varied inversely with the probability of responding. This indicates that a nonselective inhibition strategy was present even though selective inhibition was required.

In the bimanual experiment, left LTs during Stop Right trials were delayed more so than right LTs during Stop Left trials. This occurred in the absence of differences in left and right EMG onsets or differences in the probability of responding for Stop Left and Stop Right. This potentially reflects left hemisphere dominance for coupled bimanual movements (Jancke et al. 1998; Serrien et al. 2003; Viviani et al. 1998). Stopping the right side involves braking left hemisphere movement preparation, which may also interrupt movement preparation for the left hand. The time required for additional engagement of the right hemisphere may delay left-hand movement in this situation.

Although others showed that responses can be delayed on trials that immediately follow a signal to prevent all movement (Barton et al. 2006; Mirabella et al. 2006), in the present study LTs after Stop All trials were not delayed. This may have been a result of the more complex design and number of Stop All trials in our study compared with previous work. Of interest was that LTA was significantly altered during Go trials after selective Stop trials and this depended on the type of selective Stop trial. For the unimanual experiment, the index finger lift preceded the middle finger on Go trials and this lead was amplified after a Stop Middle trial. However, after a Stop Index trial, the index finger was lifted after the middle finger. For the bimanual experiment, the right side preceded the left on Go trials. This LTA was reduced after Stop Right trials, especially at 300 ms when sufficient time was available for selective inhibition. It is worth repeating that these effects were observed on Go trials after selective Stop trials. The processes involved in selective inhibition of one digit or the other exerted a persistent and directional uncoupling of the fingers on subsequent Go trials.

There are a number of reasons to suspect that these LTA findings reflect intracortical function within M1. Animal studies demonstrate that GABAergic interneurons maintain the boundaries between M1 muscle representations (Jacobs and Donoghue 1991; Schneider et al. 2002). Human transcranial magnetic stimulation studies demonstrated that GABAergic inhibition of the prime mover representation is released leading up to (Reynolds and Ashby 1999) and during muscle contractions (Ridding et al. 1995). During tasks requiring selective movement, there is a simultaneous release of neural inhibition specific to the prime mover representation involved and active inhibition of surrounding M1 representations (Sohn and Hallett 2004; Stinear and Byblow 2003; Voller et al. 2005). In the present study, a cortical surround inhibition mechanism is likely to have prevented unwanted movement during (delayed) selective responding. During selective Stop trials, M1 corticospinal neuron firing to initiate the selective response probably counteracted earlier nonselective neural inhibition. Focused excitation and concurrent inhibition of surrounding/homologous M1 representations may induce a temporary gain differential between them, affecting subsequent behavioral Go trial performance. We consider this to be the most likely explanation for our LTA results.

In conclusion, our experiments demonstrate that selective inhibition of movement is more difficult to perform than nonselective inhibition. When selective inhibition is necessary, it comes at the cost of delayed initiation of movements that
need not be prevented. This is the case whether movements are prepared within or between hemispheres. Stopping behavior requires prefrontal–basal ganglia interactions to nonselectively “brake” M1 output and subsequent selective movement requires focal disinhibition of one movement representation. This induces an asymmetry of gain between the movement representations, thereby uncoupling the effectors for subsequent behaviors.

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