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RESEARCH NOTE

The internal structure of stopping as revealed by a sensory detection task

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Abstract An important aspect of everyday behaviour is the ability to cancel a prepared movement. In Experiment 1, subjects prepared a response, and then either executed it in response to a subsequent Go signal, or cancelled the movement if a NoGo signal occurred. Subjects had to detect weak shocks, which were delivered after the signals on some trials. Results were compared to a prior instruction condition in which subjects knew at the start of the trial if they should move or not. We found that detection rates on move trials were lower than on non-move trials, consistent with sensory suppression. There was no difference between conditions in detection for move trials. However, detection rates for non-move trials were significantly lower in the NoGo than in the prior instruction condition, suggesting an element of sensory suppression associated with actions, which are prepared, but then inhibited before execution. In Experiment 2, the delay between the NoGo signal and shock was varied. Detection rates improved monotonically as the interval increased from 0 up to 200 ms. The recovery from sensory suppression offers a new way of measuring the processes triggered by a NoGo signal. Our results suggest that when a prepared movement is inhibited the dismantling of the sensory consequences of the motor command takes at least 200 ms.

Keywords Action · Sensory suppression · Movement · Inhibition

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Introduction

Self-generated movements typically lead to an attenuation of sensation from the moving body part (Chapman et al. 1987). This effect may be centrally or peripherally mediated (Haggard and Whitford 2004; Duysens et al. 1995). Recent studies suggested an important peripheral component to this attenuation. Cutaneous inputs were presynaptically inhibited to the level of the spinal cord prior to voluntary arm movements in monkeys (Seki et al. 2003). Other single-unit and somatosensory evoked-potential studies have demonstrated that the transmission of cutaneous information through the dorsal column-medial lemniscal pathway projecting to primary somatosensory cortex is attenuated during movement (Chapin and Woodward 1982; Rushton et al. 1981). In addition, reafferent feedback from body movements may produce decreases in detection of test stimuli by backward masking (Duysens et al. 1995).

Sensory suppression also involves central signals related to the preparation and dispatch of motor commands. Chapman and colleagues (Williams et al. 1998) tested detection of cutaneous stimuli during the simple reaction time (RT) to a visual Go signal. Detection of stimuli applied to the moving finger was significantly reduced relative to detection when the finger was at rest. Detection began to decline 120 ms before movement onset [70 ms before electromyographic (EMG) activity] and was greatest just before EMG onset. This anticipatory suppression cannot be due to peripheral effects because the muscle had not yet been activated. Recently, Voss et al. (2006) found further evidence for a central mechanism of sensory suppression. They delayed the dispatch of the motor command in a simple RT task using transcranial magnetic stimulation (TMS) over motor cortex. Shock detection during the delay period was no different from

no-TMS trials, suggesting the signals controlling suppression originate prior to motor cortex.

The above studies focus on sensation during preparation and execution of movement. However, withholding a prepared action is also a critical aspect of voluntary control (De Jong et al. 1995). If preparation and execution of action result in sensory suppression, one might ask what happens to sensory systems when a prepared movement is inhibited. Two closely related paradigms, the stop-signal and the Go/NoGo paradigms, are commonly used to explore inhibitory control. In the latter, subjects generate a motor response upon presentation of a Go signal, and attempt to inhibit the response on occasional NoGo trials. Logan et al. (1984) conceptualised cancellation processes as a horse-race between a process for movement execution and another for movement cancellation. If the go process wins, then the movement is executed; but if the stop process wins then the movement is successfully inhibited. The outcome depends heavily on when the stop signal is given. Success in cancelling a movement is more likely when the signal to stop is given early in the trial. In keeping with the horse-race analogy, action ("going") and inhibition of action ("stopping") are thought to be distinct processes with different neural pathways (Aron and Poldrack 2006). Going is relatively slow, but selective for the specific action prepared. Stopping is relatively fast, and acts in an all-or-none, non-specific way (Coxon et al. 2007). The stopping process has proved difficult to study since stop and NoGo trials often do not produce overt behaviour (however, see Morein-Zamir et al. 2006, 2007). The main focus in behavioural studies has been the estimation of the internal latency of stopping (the stop-signal reaction time or SSRT) which can be inferred mathematically from models such as the horse-race model. In the current study, we propose a behavioural method, which reveals the internal latency of stopping on trials where no movement or muscle activity is involved.

Here, we have compared sensory attenuation on Go and NoGo trials to investigate processes of movement preparation and cancellation. We combined a sensory suppression paradigm (Williams et al. 1998) with the Go/NoGo paradigm. In Experiment 1, in a prior instruction condition, each trial was preceded by a verbal instruction (to move or not to move). Shock detection rates for move and non-move trials were compared with a Go/NoGo version of the same task. In the prior instruction condition, subjects knew in advance whether they would move on any given trial, and thus there was no need to prepare actions on non-move trials. In the Go/NoGo condition, subjects had to prepare a motor command and wait for a signal before deciding whether to execute the movement or cancel it. Experiment 2 investigated the time-course of events triggered by the NoGo signal. On NoGo trials, when the prepared movement must be cancelled, we charted the dismantling of the now obsolete motor command by using weak cutaneous stimuli to reveal the time-course of sensory detection at different intervals after the NoGo signal.

Materials and methods

Experiment 1

Subjects

Thirteen paid subjects took part with ethical committee approval. The data from three subjects were excluded because their detection of cutaneous shocks at rest was unstable across the experiment (post-test detection varied more than ±15% from pre-experiment levels). Data from the remaining 10 subjects (4 female, 7 right-handed, mean age 33 years) were included in the final analysis.

Procedure

The subject's right hand was positioned with the index finger resting on a small pivoting plate (Fig. 1a) fixed to a potentiometer. Movement of the finger was mechanically limited to 20°. Surface EMG was recorded from the first dorsal interosseous (FDI) muscle using Ag/AgCL electrodes. A single 4 mm bipolar stimulating electrode was mounted on the dorsum of the middle phalange of the index finger. A square wave pulse of 10 mA fixed amplitude was delivered by a neuromuscular stimulator. A black cardboard sheet over the subject's right hand prevented vision of their hand. A simple staircase procedure (Levitt 1971) first established the shock intensity at which approximately 80% of stimuli delivered to the resting finger were detected. Intensity was varied by adjusting stimulator pulse-width. This intensity level was then used throughout the experiment. Occasionally, it was necessary to fine-tune the intensity level of the stimulus during a practice block. Stimulus intensity then remained constant throughout the experimental blocks. The staircase procedure was repeated at the end of the experiment.

In the prior instruction task, a verbal instruction "move" or "do not move" was given by the experimenter at the start of each trial (Williams et al. 1998). After 1,000 ms, a Go signal (a green LED for half the subjects and a red LED for the remainder) was presented for 700 ms. This acted as a response window encouraging fast responses, and thus allowing shock delivery in the critical interval for sensory suppression effects just prior to movement. The shock was delivered 50 ms before each subject's mean reaction time (the onset of EMG activity served as a measure of the reaction time in both experiments) from the practice block. Subjects made speeded right index finger abductions in

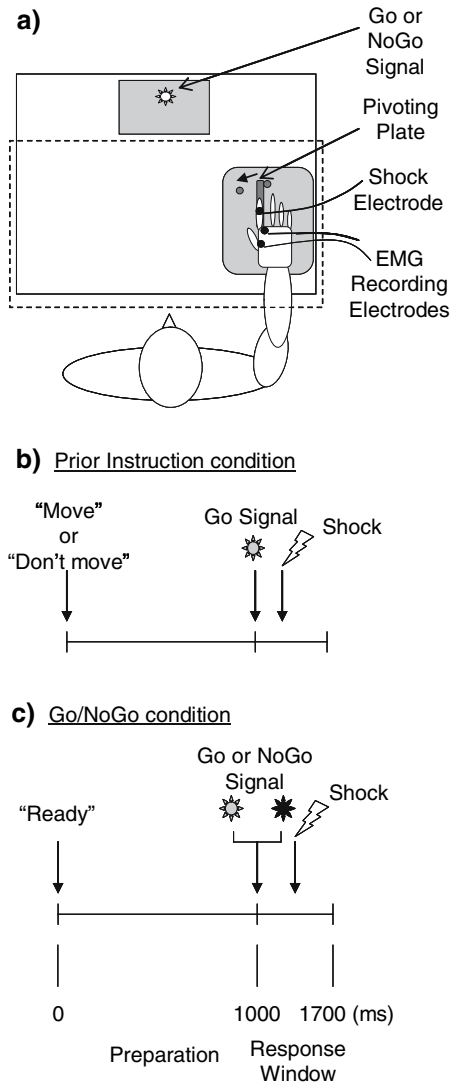

Fig. 1 **a** Experimental **s**et-up. Subjects placed their right index finger on a pivoting plate. The signal was presented via an LED in front of the subject. Direct vision of the hand was prevented. **b** Experimental design for Experiment 1. In the prior instruction condition, the experimenter gave an instruction at the start of each trial, either "move" or "do not move". The Go signal was presented after 1,000 ms. Subjects either moved or did not move their index finger during the 700 ms response window. **c** In the Go/NoGo condition (Experiment 1), the experimenter said "ready" at the start of each trial. Subjects waited for and responded to the Go signal, but withheld movement following the NoGo signal. In both conditions, the shock was delivered at 50 ms before each subject's mean reaction time

response to the "Go" signal on "move" trials, but no response on non-movement trials.

In the Go/NoGo task, the start of each trial was announced by the experimenter saying "ready". The green LED 1,000 ms later signalled "Go" for five subjects and the red light signalled "NoGo", while for the remaining subjects this order was reversed. After each trial, subjects reported verbally ("yes"/"no") whether they perceived a shock stimulus. No feedback was given. The experimenter then initiated the next trial after an intertrial interval of at least 1 s.

Subjects performed a practice block of 44 trials, followed by 4 experimental blocks of 44 trials. Each block consisted of 30 movement trials and 10 non-movement trials yielding a 3:1 Go to NoGo ratio. Previous (unpublished) results from our lab, suggest that the level of sensory suppression on NoGo trials is inversely proportional to the frequency of NoGo trials. A ratio of 3:1 Go to NoGo trials was a trade-off between the requirement for high levels of motor preparation on the one hand, and the requirement for a good estimate of sensory suppression on the other. A further 4 catch trials with no shock stimulus were divided equally between Go and NoGo trials. The order of the blocks was interleaved for condition and the order of the trials was randomised.

Experiment 2

Subjects

Fourteen new subjects took part in the study. The data from 3 subjects were excluded because of unstable detection rates (post-test detection varied more than ±15% from pre-experiment levels). Data from the remaining 11 subjects (7 female, 3 left-handed, mean age 23 years) were included in the final analysis.

Procedure

After a practice block, subjects completed 6 experimental blocks of 54 trials. Each block consisted of 36 Go trials and 12 NoGo trials. A further 6 catch trials (no shock stimulus) were divided equally between Go and NoGo trials. The order of trials was randomised. Shock stimuli were delivered either at the Go or NoGo signal, or after a 100 or 200 ms delay. In all other respects, Experiment 2 was identical to the Go/NoGo condition of Experiment 1.

Results

Experiment 1

On catch trials lacking any shock stimulus only 1.25% false positive detections were recorded, indicating that subjects used a very conservative response strategy. There was no difference in the number of false positives on catch trials between tasks ($P = 0.343$). Errors of commission (i.e. when a non-movement trial was accompanied by EMG activity) were 3.0 and 5.5% for the prior instruction and Go/NoGo tasks respectively. Electromyographic activity was sometimes observed in the agonist FDI muscle in the absence of

an overt finger movement. Errors of omission (i.e. movement trials without movement during the response window) occurred on 1.8% of movement trials. Both types of error trials were excluded when measuring the effects of sensory suppression. The pre- and post-experiment staircases showed similar shock intensity thresholds (mean pulse-widths = 20.8 and 19.7 μs: $t(9) = 1.819$; $P = 0.102$).

Because sensory attenuation follows a precise time-course leading up to movement onset, the interval between shock and the onset of EMG activity must be similar across tasks if detection rates are to be compared. RTs for each subject were therefore trimmed to ±2 SD (excluding 3.8% of movement trials) and subjected to a one-way ANOVA. The mean RTs for the Go/NoGo and prior instruction tasks were 331 and 230 ms, respectively. This difference was significant $F(1,9) = 76.417$; $P < 0.0001$. However, the mean duration between shock and EMG activity did not differ significantly $F(1,9) = 0.218$; $P = 0.651$, suggesting that our adjustment of shock to each subject's mean RT was successful.

Figure 2a shows shock detection rates in each condition. A repeated measures ANOVA showed a significant main effect of movement $F(1,9) = 141.211$; $P < 0.0001$, no main effect of condition $F(1,9) = 3.261$; $P = 0.104$, and a significant interaction between movement and condition $F(1,9) = 21.944$; $P = 0.001$. Post-hoc t tests showed that this interaction arose because non-movement trials showed poorer detection in the Go/NoGo task than in the prior instruction task ($t(9) = 3.920$; $P = 0.004$). Detection rates for movement trials were similar in both tasks ($t(9) = 0.761$; $P = 0.466$).

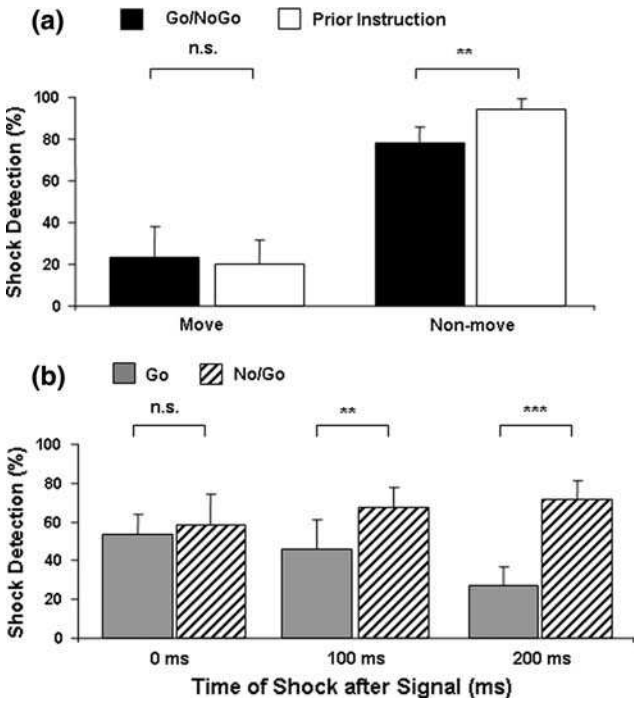

Fig. 2 **a** Experiment 1; the mean percentage of electrical stimuli detected for the Go/NoGo and prior instruction conditions. The stimulus was delivered at each subject's mean RT. **b** Experiment 2; the mean percentage of electrical stimuli detected for Go and NoGo trial types. The stimulus was delivered at 0, 100 or 200 ms after the Go or NoGo signal

Experiment 2

Only 2.2 and 3.1% false positive detections occurred for Go and NoGo catch trials, respectively. The number of false positives did not differ between conditions ($P = 0.411$). The overall error of commission rate was 5.1%. Errors of omission accounted for 1.4% of all Go trials. The pre-experiment shock intensity threshold did not differ from the post-experiment threshold (mean pulse-width = 22.0 μs). Prior to analysis, the RTs for each subject were trimmed as before, removing 4.6% of Go trials.

Shock detection rates were analysed with a repeated measures 2 × 3 ANOVA for the factors Go ("Go" vs. "NoGo") and stimulus timing (0, 100 or 200 ms after the Go/NoGo signal). The mean overall RT for Go trials was 291 ms (SD = 75 ms). On 97.9% of movement trials the shock stimulus was delivered prior to the onset of EMG activity and the remaining 2.1% of trials were discarded.

Figure 2b shows shock detection rates as a function of time. As expected, there was a significant main effect of movement $F(1,10) = 20.997$; $P = 0.001$. The main effect of stimulus timing was not significant $F(2,20) = 2.796$; $P = 0.102$, but the interaction between movement type and stimulus timing was significant $F(2,20) = 35.325$; $P<0.0001$. This interaction was explored by holding each factor fixed in turn, and investigating the simple effect of the other factor. ANOVAs revealed significant effects of stimulus timing for the Go trials $F(2,20) = 20.843$; $P<0.0001$ and interestingly, also for the NoGo trials $F(2,20) = 5.450$; $P = 0.015$. Comparisons between conditions at each time interval revealed no difference between Go and NoGo trials at 0 ms, $t(10) = 0.961$; $P = 0.359$. However, comparisons for the later 100 and 200 ms intervals revealed significant differences $t(10) = 3.376$; $P = 0.007$ and $t(10) = 7.514$; $P<0.0001$, respectively.

An interesting question (see Discussion) is whether the development of sensory suppression on Go trials is faster than recovery from suppression on NoGo trials. Absolute change in detection rates was compared for Go and NoGo trials, for the intervals 0–100 ms, and 100–200 ms post-signal. Over the early 0–100 ms interval, the change in sensory suppression on Go trials was of similar size to the dismantling of suppression on NoGo trials $t(10) = 0.452$; $P = 0.661$. However, the absolute change in detection rate for the later interval, 100–200 ms, showed that sensory suppression on Go trials developed more quickly than recovery of sensation following NoGo signals $t(10) = 2.272$; $P = 0.046$.

Discussion

In both experiments, weak cutaneous shocks were less likely to be detected just prior to a voluntary movement than when no movement occurred. This replicates sensory suppression effects previously reported (Williams et al. 1998). In Experiment 1, there was no difference in shock detection rates during movement trials between different instruction conditions. However, on NoGo trials, when a prepared movement was successfully cancelled, subjects detected significantly fewer shock stimuli than in non-movement trials of a prior instruction task when they presumably neither prepared actions in advance, nor inhibited them. This suggests that motor preparation contributes to sensory attenuation. Merely preparing a movement gates sensory input. Peripheral feedback cannot have played a role in this attenuation, since no actual movement occurred.

In Experiment 2, we studied the time-course of attenuation in the absence of overt movement. Interestingly, detection rates on NoGo trials improved monotonically as the interval between the NoGo signal and the shock was increased from 0 to 200 ms. We suggest that this recovery of sensation following a NoGo signal arises as follows. Up until the time of the NoGo signal, the movement is held in preparation and the sensory system is suppressed correspondingly (Voss et al. 2006). Once the NoGo signal is registered, the cortical motor pathway is gradually inhibited (stopping process), and the suppression of the sensory system is gradually released. We have used the term "dismantling the motor command' to refer to these processes together. The release from sensory suppression following the NoGo signal offers a new way to measure the stopping process. Our Experiment 2 suggests that stopping is not a single discrete event, but rather is a process that develops gradually and monotonically over time, taking approximately 200 ms. The resulting view of stopping is consistent with studies using other methods, such as stop-signal reaction time (SSRT; Band et al. 2003). We have studied the stopping process by assessing how action-related suppression of sensation is dismantled as a result of a signal instructing cancellation of a prepared action.

As going and stopping are thought to involve independent processes according to the horse-race model, one might ask whether these processes proceed at different rates. Methods such as the SSRT cannot measure these rates of progress directly. In contrast, we were able to test whether the development of sensory suppression following a Go signal occurred as rapidly as the dismantling of sensory suppression following a NoGo signal. For the first 100 ms, the attenuation after a Go signal and the dismantling of suppression following a NoGo signal proceed at similar rates. However, for the subsequent interval, 100–200 ms post-signal, the rate of movement-related sensory suppression on Go trials exceeds the rate of dismantling of suppression on NoGo trials. This rate difference could arise at a motor or a sensory stage. For example, a motor explanation based on horse-race models could hypothesise that the stop process operates more slowly than the go process. Alternatively, a sensory explanation could hypothesise that modulations of sensory cortex take longer to dissipate than to develop. Our own data do not allow us to distinguish between these two alternative hypotheses. Nevertheless, the stopping process may develop more slowly over time than the go process. Interestingly, this result contrasts with the assumption of psychological horse-race models of stopping, which assume that the stop process is faster than the go process (Logan et al. 1984; Coxon et al. 2007). Further investigation of this point would be a fruitful topic for future research.

In conclusion, the main findings of this study are firstly, that sensory suppression can occur due to the preparation of actions, even when they are not executed. Secondly, the recovery from sensory suppression can offer a new way of measuring the processes triggered by a NoGo signal. Our results suggest that fully dismantling a prepared motor command takes at least 200 ms.

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