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Inhibitory motor control based on complex stopping goals relies on the same brain network as simple stopping

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ABSTRACT

Much research has modeled action-stopping using the stop-signal task (SST), in which an impending response has to be stopped when an explicit stop-signal occurs. A limitation of the SST is that real-world action-stopping rarely involves explicit stop-signals. Instead, the stopping-system engages when environmental features match more complex stopping goals. For example, when stepping into the street, one monitors path, velocity, size, and types of objects and only stops if there is a vehicle approaching. Here, we developed a task in which participants compared the visual features of a multidimensional go-stimulus to a complex stopping-template, and stopped their go-response if all features matched the template. We used independent component analysis of EEG data to show that the same motor inhibition brain network that explains action-stopping in the SST also implements motor inhibition in the complex-stopping task. Furthermore, we found that partial feature overlap between go-stimulus and stopping-template led to motor slowing, which also corresponded with greater stopping-network activity. This shows that the same brain system for action-stopping to explicit stop-signals is recruited to slow or stop behavior when stimuli match a complex stopping goal. The results imply a generalizability of the brain's network for simple action-stopping to more ecologically valid scenarios.

Introduction

The ability to stop ongoing behaviors after they have been initiated is a cognitive mechanism that is part of everyday life. Much research has used the stop-signal task (SST; Logan et al., 1984; Verbruggen and Logan, 2009) to investigate the factors that affect stopping, and how stopping is implemented in the brain. Stopping in the standard SST recruits an interconnected network of fronto-subcortical brain regions (the 'stopping-network') including the pre-supplementary motor area (pre-SMA), the right inferior frontal cortex (rIFC), and the basal-ganglia, with downstream effects on M1 (for reviews, see: Aron et al., 2014; Bari and Robbins, 2013; Chambers et al., 2009; Ridderinkhof et al., 2011; Stinear et al., 2009; Wiecki and Frank, 2013). Activity within this stopping network has been found across several brain imaging modalities. In the human scalp electroencephalogram (EEG), time–frequency analyses show a signature of successful action-stopping at fronto-central scalp sites, specifically within the theta- (5–8 Hz) and delta-frequency bands (1–4 Hz) (Lavallee et al., 2014; Nigbur et al., 2011; Schmiedt-Fehr and Basar-Eroglu, 2011; Wessel and Aron, 2013; Yamanaka and Yamamoto, 2010).

Yet it is important to ask whether this 'stopping network' for the standard SST generalizes to stopping in more realistic scenarios. Arguably, instances in which behaviors need to be canceled following explicit stop-signals (as in the standard SST) are relatively rare in the real world. Instead, stopping must be exerted in more complex situations such as the one given in the abstract, in which someone has to stop their step into the street when a car is bearing down. The stopping goal in that situation presumably consists of a complex template of features, which include the size of an object, its trajectory, velocity, and its distance. This stopping-template is presumably represented in working memory, and the stopping system is turned on if all or many features of a given situation match it.

Here, we developed a new behavioral paradigm that models action-stopping to more complex, realistic, stopping goals. In this task, participants had to quickly respond to arrow stimuli, just like in the standard SST. However, unlike the standard SST, we now used arrow-stimuli that differed perceptually along five different dimensions: color, position, number of arrows, arrow style, and print (outline or bold). Before every sequence of stimuli, a unique combination of these five features was presented to the participants as a 'stopping-template', which they had to maintain in memory. Participants then had to respond as quickly as possible to a sequence of arrow-stimuli, *unless* all five dimensions of the current stimulus matched the dimensions of the stopping-template. In that case, the action had to be stopped.

We hereafter refer to this new task as the 'complex-stopping task' (CST). Note that while the task is more akin to a go/nogo task (where the signal to nogo occurs at the same time as the go stimulus) than a classic stop-signal test (where the signal to stop occurs later than the

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go stimulus), our task is set up to also elicit a clear-cut stopping situation similar to the standard SST. This was done by creating a highly prepotent go-response on all trials, through having relatively few stop/nogo-trials, and by requiring relatively fast reaction times on go-trials. The prepotency of the go-response was measured by the number of failed stop/nogo-trials that is clearly attributable to failed motor inhibition (see below). Note also that this task is clearly more ecologically valid than the SST. This is because participants now have a more complex, multidimensional stopping goal in mind. As they are about to respond, they must match the features of the stimulus (a proxy for context) to their stopping goal. A partial match does not constitute a stopping scenario. This is similar to the situation in which a car is bearing down on a pedestrian with the correct trajectory to be potentially stopping-relevant, but is not moving fast enough to necessitate a stop. Of course, the CST is again a laboratory-based model of control that involves sequential trials with relatively simple stimuli, but it is clearly a closer model of realistic situations than the standard SST.

In a behavioral pilot (Experiment 1), we first established that the go response did have prepotency (similar to the standard SST): participants often failed to successfully stop, despite recognizing that stopping was needed. Interestingly, we further observed that partial matches between the go-stimulus and the stopping-template lead to slowed responding: when some (but not all) of the features of the go-stimulus matched the stopping template, go RT was increased. While the slowing could relate to many potential factors (Jahfari et al., 2010), we hypothesized that it could reflect partial recruitment of the stopping system, something we have referred to elsewhere as 'braking' (Swann et al., 2013; Wessel et al., 2013).

In the main study (Experiment 2), we used EEG to test whether the observed stopping and 'braking' in the CST is subserved by the same motor inhibition network that explains stopping to explicit stop-signals in the standard SST. We recorded scalp EEG during the CST (the main task of interest) and also for the SST (which was used as a functional localizer for the stopping-system). We used independent component analysis (ICA, Jutten and Herault, 1991) to decompose each participant's observed scalp EEG signal mixture into its underlying temporally independent source signals (independent components, IC). As done previously (Wessel and Aron, 2013), we identified ICs in each subject that represented a typical EEG signature of successful stopping from the SST. We then tested whether this independent network showed increased activity during outright stopping and/or braking in the CST. We predicted that activity within the stopping-ICs identified in the SST should be increased following action-stopping in the CST (stopping hypothesis). Furthermore, if the RT slowing on partial feature match trials is explained by partial recruitment of the brain's motor inhibition network (i.e., 'braking'), then the activity within the stopping-ICs should increase when partial matches induce increased RT slowing (braking hypothesis).

Materials and methods

Participants

Experiment 1

17 right-handed participants (mean age: 21 y, sem: .37, range: 18–24; 12 female) performed the task in exchange for course credit. They provided written informed consent according to a local ethics protocol. Data from two participants were excluded, one due to high error rates (pressed wrong buttons on 46% of trials), and one due to high miss rates (did not respond to go-stimuli on 16% of trials), leaving a sample of 15 participants.

Experiment 2

11 right-handed participants (mean age: 20.9 y, sem: .87, range: 18–28; 9 female) provided written informed consent according to a local ethics protocol and performed the task in exchange for $15/h. These participants were different participants from Experiment 1.

Materials and procedure

Experiment 1

Stimuli were displayed on a 17 in. iMac personal computer (Apple, Inc., Cupertino, CA) running MATLAB 2009b (the MathWorks, Natick, MA) and Psychtoolbox 3 (Brainard, 1997). Responses were registered through a standard Apple USB keyboard. Participants performed the complex-stopping task first, then performed a working memory task, and then a standard stop-signal task (results from these latter two tasks are not discussed).

Experiment 2

After the EEG caps were attached and prepared, participants were seated in an electromagnetically-shielded and sound-attenuated room. Stimuli were displayed on an electromagnetically shielded CRT monitor (NEC MultiSync FB2141SB; NEC Corporation, Japan) connected to an IBM-compatible personal computer running MATLAB 2009b and Psychtoolbox 3. Viewing distance was 70 cm. Responses were registered through a custom USB keypad. Participants performed the complex-stopping task first, then a working memory task (results not discussed), and then the standard stop-signal task.

Complex-stopping task (CST), experiments 1 and 2

Each trial consisted of a template-encoding phase followed by a stop/go phase (Fig. 1). The template-encoding phase began with a fixation screen showing the word "MEMORIZE!" and three pairs of horizontal lines, which were arranged on three vertical positions on the screen. After 1000 ms of fixation, the stopping-template appeared, which consisted of squares that varied along five perceptual dimensions: color (red, blue, green), vertical position (as indicated by the horizontal lines), number (1, 2, or 3 squares), print (filled or outline), and style (either simple squares or squares with additional horizontal lines on both sides; this feature indicates whether the arrows in the stop/go phase would consist of arrowheads only, or of arrowheads with lines attached to them). This stimulus was on the screen for 3000 ms, and the participants were instructed to memorize all five features. Then, the word 'Go!' appeared for 500 ms, followed by a blank screen of 500 ms, which started the stop/go phase.

The stop/go phase consisted of a series of arrow stimuli that were displayed on the screen, which varied along the same five dimensions as the stopping-template. These stimuli could match the stopping-template anywhere between 0 and all 5 dimensions. These stimulus types will henceforth be denoted M0 (0 matches with the stopping-template), M1 (1 match), M2 (2 matches), M3 (3 matches), M4 (4 matches), and MSTOP (all five dimensions match; i.e., those trials are stop-trials). Participants were instructed to respond as fast as possible to the direction of the arrow using a finger of their right hand (right arrow key for right, left arrow key for left), *unless* the stimulus on the screen matched the stopping-template in all five dimensions (MSTOP-stimuli). In that case, the participants had to stop their response. In order to increase the stopping demand of the task, an adaptive deadline algorithm ensured that RT remained fast throughout the experiment.[1] After the response was made, the stimulus on the screen disappeared. The ITI was set so that the stimulus-onset asynchrony between two subsequent go-stimuli was exactly 2000 ms. Importantly, in order to

[1] This was done as follows: The initial deadline was set to 1000 ms. After the first 2 trials (a trial denotes a full sequence of template-encoding followed by the stop/go-phase), it was adapted online, based on the performance on all go-stimuli within the last 2 trials: if the miss rate (no response made before the deadline on go-stimuli) and the error rate (wrong button pressed) were both below 10%, the deadline would decrease by 50 ms. If either error rate or miss rate exceeded 10%, the deadline would increase by 50 ms. A minimum for the deadline was set at 600 ms.