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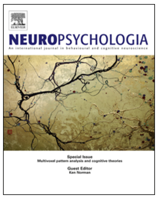

The inhibitory control reflex[☆]

Frederick Verbruggen[*], Maisy Best, William A. Bowditch, Tobias Stevens, Ian P.L. McLaren

School of Psychology, University of Exeter, Exeter EX4 4QG, UK

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ABSTRACT

Response inhibition is typically considered a hallmark of deliberate executive control. In this article, we review work showing that response inhibition can also become a 'prepared reflex', readily triggered by information in the environment, or after sufficient training, or a 'learned reflex' triggered by the retrieval of previously acquired associations between stimuli and stopping. We present new results indicating that people can learn various associations, which influence performance in different ways. To account for previous findings and our new results, we present a novel architecture that integrates theories of associative learning, Pavlovian conditioning, and executive response inhibition. Finally, we discuss why this work is also relevant for the study of 'intentional inhibition'.

1. Introduction

Few seem to doubt the importance of response inhibition for optimal and goal-directed behaviour. Without the ability to stop habitual or no-longer relevant actions, we would be slaves of our past; we would be impulsive creatures that respond to any potentially relevant stimulus that presents itself; and we would not be able to respond adequately to changes in the environment. Quite often, this would lead to terrible outcomes. One could even say that we would be doomed without inhibition… At least, it seems this way when you look at the pivotal role of response inhibition in current theories of self-control. There is a vast amount of cognitive and neuroscience literature that suggests that response inhibition is one of the core 'executive' or 'cognitive control' functions (Logan, 1994; Miyake et al., 2000; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004; Verbruggen & Logan, 2008d). Furthermore, work in psychiatry and clinical psychology suggests that deficits in response inhibition are associated with various clinical disorders (Bari & Robbins, 2013; Chambers, Garavan, & Bellgrove, 2009). It is not always obvious whether the response inhibition deficit is the cause or a consequence of the disorder, but some longitudinal studies suggest that the ability to stop one's actions can influence behavioural and substance addictions later in life (e.g. Nigg et al., 2006). In this article we will not dispute that response inhibition is a critical aspect of cognitive and emotional functioning. However, we will question the general idea that response inhibition is always a deliberate act of control. We will demonstrate that learning to stop can lead to automatisation of response inhibition. We focus primarily on 'external' or 'stimulus-driven' response inhibition, but also consider briefly how this work can have implications for the study of 'intentional' inhibition (Brass & Haggard, 2007, 2008; Filevich, Kühn, & Haggard, 2012). We will review previous research on 'automatic' inhibition and related topics, and present new empirical material that speaks to the issues of what is learned and how it is learned.

2. Response inhibition in the laboratory

Popular paradigms to study top-down or deliberate response inhibition include the go/no-go paradigm and the stop-signal paradigm. In the go/no-go paradigm, subjects are presented with a series of stimuli and are told to respond when a go stimulus is presented and to withhold their response when a no-go stimulus is presented (e.g. press the response key for a square but do not press the response key for a diamond). In the stop-signal paradigm, subjects usually perform a choice reaction task on go trials (e.g. press the left response key for a square and press the right response key for a diamond). On a random selection of the trials (stop trials), a stop signal (e.g. an auditory tone or a visual cue, such as the outline of the go stimulus turning bold) is presented

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[*] Corresponding author.
E-mail address: f.l.j.verbruggen@exeter.ac.uk (F. Verbruggen).

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after a variable delay (stop-signal delay; SSD), which instructs subjects to withhold the response to the go stimulus on those trials. Popular variants of the stop-signal paradigm include the countermanding task, in which eye movements have to be cancelled (Schall & Boucher, 2007), and the stop-change task, in which the cancelled response has to be replaced by another response (Verbruggen & Logan, 2009b).

Performance in response inhibition paradigms can be modelled as an independent "horse race" between a go process, which is triggered by the presentation of a go stimulus, and a stop process, which is triggered by the presentation of the no-go stimulus or the stop signal (Logan & Cowan, 1984; Logan, Van Zandt, Verbruggen, & Wagenmakers, 2014; Verbruggen & Logan, 2009b). When the stop process finishes before the go process, response inhibition is successful and no response is emitted (*signal-inhibit*); when the go process finishes before the stop process, response inhibition is unsuccessful and the response is incorrectly emitted (*signal-respond*). The latency of the stop process (stop-signal reaction time or SSRT) is covert, but it can be estimated in the stop-signal task (Logan & Cowan, 1984). SSRT has proven to be an important measure of the cognitive control processes that are involved in stopping (but see Verbruggen, Chambers, & Logan, 2013, for a cautionary note).

The independent race model of Logan & Cowan (1984) assumes stochastic independence between the go and stop processes. However, complete independence between the go and stop processes is unlikely. Neuroscience studies indicate that going and stopping interact in the basal ganglia (note that for the inhibition of eye movements, the interaction seems to take place in the frontal eye fields and the superior colliculus; see e.g. Schall and Godlove (2012)). A motor response can be activated via the direct cortical-subcortical pathway (Nambu, Tokuno, & Takada, 2002). This involves the activation of 'Go' cells in the striatum, which inhibit the internal segment of the globus pallidus (GPi); this reduces inhibition of the thalamus, leading to the execution of a motor response. But the execution can be cancelled via activation of the indirect or hyperdirect pathways (Nambu et al., 2002). The indirect pathway involves the activation of 'No-go' striatal cells, which inhibit the external segment of the globus pallidus (GPe); this reduces tonic inhibition between GPe and the GPi, resulting in increased activity in GPi, and consequently, increased inhibition of the thalamus. It is thought that this can lead to the selective inhibition of a particular response (Aron & Verbruggen, 2008; Smittenaar, Guitart-Masip, Lutti, & Dolan, 2013). The downside of this pathway is that inhibition may be relatively slow (Aron, 2011; Aron & Verbruggen, 2008). Fast but global response inhibition could be achieved via a third pathway, namely the hyperdirect pathway (Aron et al., 2007; Wiecki & Frank, 2013). This involves activation of the subthalamic nucleus, which has in turn a broad effect on GPi, leading to global suppression of the thalamus. Computationally, the interaction between the go and stop processes can be described by the interactive race model (Boucher, Palmeri, Logan, & Schall, 2007). In this model, the go process is initiated by the go stimulus and a go representation is activated after an afferent delay. The stop process is initiated by the stop signal and a stop representation is activated after an afferent delay. Once the stop representation is activated, it inhibits go processing strongly and quickly. In this interactive race model, SSRT primarily reflects the period before the stop unit is activated, during which stop and go processings are independent, so its predictions correspond to those of the independent race model (Logan & Cowan, 1984).

Most research on response inhibition focuses on 'reactive' control processes after a no-go or stop signal is presented. However, successful performance in inhibition tasks requires finding a balance between going quickly on go trials and withholding a response on no-go or stop trials (Verbruggen & Logan, 2009c). Reaction time (RT) is typically longer in blocks in which stop signals can occur than in blocks in which no stop signals can occur. Several researchers have argued that this slowing reflects 'proactive' control adjustments: when subjects expect a no-go or stop signal, they adjust attentional settings, increase response thresholds, or proactively suppress all motor outputs to prevent premature responses (e.g. Aron, 2011; Jahfari, Stinear, Claffey, Verbruggen, & Aron, 2010; Verbruggen & Logan, 2009c; Verbruggen, Stevens, & Chambers, 2014; Zandbelt, Bloemendaal, Neggers, Kahn, & Vink, 2013). Inter- and intra-individual differences in proactive control may influence overall stopping performance. Therefore, proactive control is an important avenue for future research. But in this paper, we will highlight another aspect of response inhibition, namely the impact of priming and learning on performance.

3. Inhibition as a primed or prepared reflex

Most researchers assume that response inhibition in the go/no-go and stop-signal paradigms is a goal-driven and deliberate act of control. But in a series of studies, Van Gaal et al. demonstrated that response inhibition could be triggered by low-visibility primes in both the go/no-go and stop-signal paradigms. In their studies, they contrasted no-go or stop trials on which the briefly presented no-go or stop signal was masked, with go trials without a signal and with no-go or stop trials without a mask. Behaviourally, they found that the presentation of low-visibility no-go or stop-signals slowed down responding and increased the percentage of missed responses slightly (van Gaal, Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008; van Gaal, Ridderinkhof, van den Wildenberg, & Lamme, 2009; van Gaal, Ridderinkhof, Scholte, & Lamme, 2010; van Gaal, Lamme, Fahrenfort, & Ridderinkhof, 2011). They attributed this pattern to the 'unconscious' activation of the response inhibition network (but see Newell and Shanks (2014) for general concerns about procedures to assess consciousness)[1]. In the stop-signal experiments, the slowing seemed to increase over practice (van Gaal et al., 2009, 2011), suggesting that there was a learning component to the priming effect. The idea that the response inhibition network could be primed was further supported by a comparison between the low-visibility primes and the high-visibility no-go/stop signals. More specifically, the low-visibility primes elicited activation in frontal regions that are typically associated with deliberate, top-down inhibition (van Gaal et al., 2008, 2010), although it should be noted that there were some differences as well (van Gaal et al., 2011). Importantly, the activation of this 'unconscious inhibition network' correlated positively with the degree of slowing.

In one of our own studies we demonstrated that stopping could also be primed by task-irrelevant (highly visible) features (Verbruggen & Logan, 2009a). In a series of experiments, we presented the primes GO, ###, or STOP inside stimuli (circles or squares). In Experiment 1, subjects were instructed to respond to the shape (e.g. circle = left, and square = right) but to withhold the response when an auditory stop signal was presented. They were instructed to ignore the primes in the go stimulus. Even though the words were always irrelevant, we found that reaction times on go trials were significantly longer for STOP than for ### and GO primes; there was no reliable difference between ### and GO (Verbruggen & Logan, 2009a). In another experiment, GO, ###, or STOP were presented as stop signals. Subjects were told to inhibit the go response whenever any of these stimuli appeared. An

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[1] Newell and Shanks argued that identification or classification tasks, such as the ones used by Van Gaal et al., are not sensitive enough to assess awareness.