Biological Psychology 123 (2017) 250–268

Contents lists available at ScienceDirect

Biological Psychology

journal homepage: www.elsevier.com/locate/biopsycho

How to withhold or replace a prepotent response: An analysis of the underlying control processes and their temporal dynamics☆

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ARTICLE INFO

Article history:
Received 29 January 2016
Received in revised form
27 September 2016
Accepted 10 October 2016
Available online 15 October 2016

Keywords:
Action control
Response inhibition
ERP

ABSTRACT

The present study isolated and compared ERP components associated with flexible behavior in two action-control tasks. The 'withhold' groups had to withhold all responses when a signal appeared. The 'change' groups had to replace a prepotent go response with a different response on signal trials. We proposed that the same chain of processes determined the effectiveness of action control in both tasks. Consistent with this idea, lateral (Experiment 1) and central (Experiment 2) signal presentation elicited the same perceptual and response-related components in both tasks with similar latencies. Thus, completely withholding a response and replacing a response required a similar chain of processes. Furthermore, latency analyses revealed intra-individual differences: When the signal occurred in the periphery, differences between fast and slow change trials arose at early perceptual stages; by contrast, differences arose at later processing stages when signal detection was easy but stimulus discrimination and response selection were harder.

Changes in the environment or internal state often force us to update our actions or behavior in order to meet new requirements. In the laboratory, action control in response to an unexpected signal or cue has been studied using the stop-signal paradigm (e.g., Lappin & Eriksen, 1966; Logan, 1994; Verbruggen & Logan, 2008a), and the go/nogo paradigm (e.g., Donders, 1868/1969; Cattell, 1886; Luce, 1986; Wundt, 1880 for a review). The present study explored action control in different variants of these tasks.

1. The stop-signal and go/nogo paradigm

In the standard version of the stop-signal paradigm, subjects are instructed to respond to a go stimulus (e.g. press left for a left arrow and right for a right arrow), unless a stop signal appears after a variable delay. In the standard version of the go/nogo paradigm, subjects are instructed to respond when a go signal (e.g. 'O') appears, but to withhold their response when a nogo signal (e.g. 'X') appears. In the cued variant of the go/nogo task (Band, Ridderinkhof, & van der Molen, 2003; Bekker, Kenemans, & Verbaten, 2004; Bruin, Wijers, & van Staveren, 2001; Jonkman, Lansbergen, & Stauder, 2003; Randall & Smith, 2011; Smith, Jonstone, & Barry, 2006), a cue provides information about which response is probably required and subjects are asked to prepare this response (a key press with a left finger, a right finger, or no response). Whether or not the cued response is subsequently required is clarified by a second stimulus that follows after a variable delay.

In the literature, both stop-signal and go/nogo tasks have been used to study response inhibition. Neuroimaging studies suggest that both tasks require similar processes. ERP studies have shown that both nogo trials and stop-signal trials are associated with an N2 and a P3 (e.g., Simson, Vaughan, & Ritter, 1977; Pfefferbaum, Ford, Weller, & Kopell, 1985; Eimer, 1993; Donkers & van Boxtel, 2004; Lavric, Pizzagalli, & Forstmeier, 2004). Furthermore, fMRI studies found large overlap in the neural circuitry involved in stop-signal and go/nogo tasks. For example, the right inferior frontal cortex and the pre-supplementary motor area (pre-SMA) are activated on both stop-signal and nogo trials (for a meta-analysis, see Swick, Ashley, & Turken, 2011).

However, the meta-analysis of Swick et al. (2011) revealed some between-task differences as well, and they argued that the fronto-parietal control network was activated to a greater extent in the go/nogo task than in the stop-signal task. Furthermore, Eagle, Bari,

☆ This work was supported by a starting grant to FV from the European Research Council (ERC) under the European Union's Seventh Framework Programme (FP7/2007–2013)/ERC Grant Agreement No. 312445. FV is also FV is a Royal Society Wolfson Research Merit Award holder.

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http://dx.doi.org/10.1016/j.biopsycho.2016.10.005
0301-0511/

& Robbins (2008) reported only subtle neuroanantomical differences but large neurochemical differences. For example, serotonin seems to play an important role in inhibitory control on nogo trials but not on stop-signal trials. Finally, Schachar et al. (2007) found a dissociation between nogo performance and stop performance in children with ADHD but not in healthy control children.

Thus, the go/nogo and stop-signal tasks seem to require similar cognitive resources and neural pathways, but there appear to be some differences as well (especially in clinical populations and at a neurochemical level). The go/nogo task may place greater demands on action selection, whereas the stop-signal task may place greater demands on the motor inhibition system (Rubia et al., 2001). Furthermore, learning may play a greater role in standard go/nogo tasks than in stop-signal tasks (Verbruggen & Logan, 2008b).

2. Withholding vs. replacing a response

In daily life, people often have to replace the stopped or cancelled actions with a new action. To study this form of action control, variants of the stop-signal and go/nogo paradigm have been developed. In the stop-change paradigm (Logan and Burkell, 1986; Verbruggen & Logan, 2009), subjects are instructed to stop their initially planned response in the primary task (hereafter referred to as the go1 response) when a stop-change signal is presented, and replace it with a new response (hereafter referred to as the go2 response). Others have used a similar variant of the cued go/nogo task (e.g. Band et al., 2013; Randall & Smith, 2011). In these studies, subjects had to cancel a prepared go response and execute an alternative response instead.

Behavioral and modeling work has tried to determine which processes are involved in replacing planned or prepotent responses. For example, Verbruggen, Schneider, & Logan (2008) introduced in a stop-change paradigm a delay between the stop signal and the go2 signal to examine whether the go1 response can be inhibited simply by activating the go2 response (go1 ⟵ go2) or whether it also requires a top-down inhibition process (go1 ⟵ stop + go2). The results of two experiments were consistent with models that included a stop process. This conclusion is further supported by computational modeling studies. For example, Camalier et al. (2007) used an oculumotor variant of the stop-change task (i.e. the double-step paradigm). They fitted three computational models to the data of both humans and macaque monkeys. The models including the stop process fitted the data better than the model without it, suggesting that a stop process was required to explain performance in the oculomotor stop-change task.

Some studies suggest that the same inhibitory processes are involved when stopping all actions (as in the stop-signal task) compared to stopping the primary response (go1) and implementing an alternative one (go2) (as in the stop-change task). Based on their review of behavioral and neurophysiological data, Band and van Boxtel (1999) argued in favor for a model consisting of a single inhibitory network, which involves multiple cortical and subcortical structures. The majority of subsequent fMRI studies support this view because both stop signals and stop-change signals activate the hyperdirect fronto-basal-ganglia stopping network (e.g., Mars, Piekema, Coles, Hulstijn, & Toni, 2007; Boecker et al., 2011; Kenner et al., 2010; for a review of the stop-signal and stop-change comparison see Boecker, Gauggel, & Drueke, 2013).

However, some findings suggest that there might be differences as well. For example, the estimated latency of the stop process (stop-signal reaction time; SSRT) is often longer in the stop-change paradigm than in the standard stop-signal paradigm (e.g. De Jong, Coles, & Logan, 1995; Logan & Burkell, 1986), which could indicate that different inhibitory processes are involved in the two paradigms. Furthermore, the ERP literature has provided conflicting results. In one of the first stop-signal versus stop-change task comparisons, De Jong et al. (1995) compared the lateralized readiness potential (LRP), which is a marker of motor preparation, on signal trials in the two tasks. They found below-threshold motor activation on signal trials in the stop-change task but not in the stop-signal task. This led them to conclude that a fast but non-selective inhibition mechanism is involved in the stop-signal task (consequently, responses could be suppressed at late, peripheral stages), whereas a slower but more selective mechanism is involved in the stop-change task (consequently, responses would be suppressed at central stages). Subsequent studies using different stop-change paradigms were not able to replicate De Jong et al.'s LRP results (Band et al., 2003; Krämer, Knight, & Münte, 2011). Nevertheless, Krämer et al. (2011) still argued that different inhibitory mechanisms were involved in both tasks because they observed a fronto-central N2 component on stop-signal trials but not on stop-change trials. Boecker et al. (2013) argued that these N2 differences might have been caused by the nature of the paradigm, which combined the Erikson flanker task with a stop/change-signal paradigm. Indeed, a recent ERP study (Rangel-Gomez, Knight, & Krämer, 2015) used a novel method (Laplacian transformation and independent component analysis, ICA) to disentangle activity elicited by the go stimulus from activity elicited by the stop and stop-change signals. This study found a bilateral parieto-occipital negativity around 180 ms and a fronto-central negativity around 220 ms for both stop-signal and stop-change trials, confirming previous fMRI results of a common inhibitory mechanism. Thus, an N2 can be observed when subjects have to withhold a response in the stop-signal paradigm and when they have to replace a response in the stop-change paradigm.

The cued go/nogo ERP literature also produced conflicting results. Some studies compared trials on which subjects had to cancel a planned go response (go/nogo) with trials on which they had to replace it (go/change) (e.g. Band et al., 2003; Randall & Smith, 2011). Band et al. (2003) observed an N2 in both conditions (although there were some subtle differences), and proposed that similar inhibitory mechanisms might be involved. Randall and Smith (2011) also observed an N2 in both conditions. However, compared with the go condition, they found a P3 in the nogo condition but not in the change condition. They proposed the N2 reflects conflict detection, whereas the P3 would reflect the cancellation of a planned response. In other words, they argued that inhibition was only involved in the go/nogo condition.

In sum, it is still unclear to what extent withholding a response and replacing a response require similar cognitive and neural mechanisms. We addressed this issue in the present study using ERPs.

3. The present study

The stop-signal task puts higher demands on motor inhibition than most variants of the go/nogo task. However, a methodological challenge of combining the stop-signal task with ERPs is the short succession of the go stimulus and the signal, which leads to an overlap of neural activity associated with the two stimuli (see Bekker, Kenemans, Hoeksma, Talsma, & Verbaten, 2005, for a discussion), complicating the interpretation of ERP modulations. Several procedures (which are discussed in more detail in the General Discussion) have been proposed to disentangle the activation patterns, but they can be complex. Furthermore, the refractoriness of ERPs could still lead to a false assessment of signal trial amplitudes (Woodman, 2010). To address these issues, the present experiments introduce a hybrid version of the stop-signal task and the cued go/nogo task (note that it also shares some features with the response-priming paradigm; see Schmidt, Haberkamp, &