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Action-stopping refers to the ability to stop planned or ongoing actions and can be deployed in different modes to meet one's current goals. For example, action-stopping may be engaged partially, to briefly pause an action and re-evaluate its appropriateness, or fully, to cancel an action altogether. The selectivity with which the stop-process is triggered by changes in the environment can also vary, such that it is triggered only by goal-relevant stimuli (e.g. a red traffic light) or else by any salient stimulus, even goal-irrelevant ones (e.g. a text message notification while driving). While a prefrontal-basal-ganglia-thalamocortical network has been implicated in action-stopping (Wessel & Aron, 2017), how we toggle between the above modes of control and whether they rely on precisely the same network remains unclear. A recent article in this journal provides some clues, whilst also raising a number of pertinent questions (Giarrocco et al., 2021).

In the experiment, two non-human primates performed a variant of the classic stop signal task. They responded to a 'go' signal by reaching to a target. Occasionally a 'stop' signal presented after the go required them to attempt to stop their response. In other trials, an 'ignore' signal was presented instead of a stop, and required them to continue responding as planned. Interestingly, the subjects' behavior on ignore trials differed across different sessions, consistent with the use of different strategies: (i) a selective discriminate-then-stop strategy (DTS), wherein the stop signal led to a complete behavioral interruption, but the ignore signal had no effect on behavior; and (ii) a non-selective stop-then-discriminate (STD) strategy, wherein stop and ignore signals led to complete (cancellation) or partial interruptions (pause), respectively (Bissett & Logan, 2014).

The authors recorded neural activity from dorsal premotor cortex (dPM) to examine the neural correlates of these strategies. They reasoned that, since neural activity in dPM can reflect chosen actions before they are executed (Mark M. Churchland et al., 2006; Kaufman et al., 2016), it might reflect changes in activity during action-stopping. Using a state-space approach they contrasted trajectories of the population-level activity in go, stop and ignore trials when the subjects adopted a DTS vs. STD strategy. The first key contrast focused on how population activity in stop trials differed compared to that in go trials, and highlighted the presence of a stop-process irrespective of which strategy was used. The second key contrast focused on differences in stop and ignore trials, and showed that the presence of a stop-process on ignore trials depended on the strategy employed. We discuss these contrasts one-by-one before turning to the broader theoretical implications.

Behavioral strategy had no effect on either behavioral stopping performance, quantified as the latency of stopping (stop signal reaction time), or the trajectory of dPM activity in stop trials. For both DTS and STD strategies, the trajectory in stop trials initially followed the same path as on go trials, but later diverged from the go-trial trajectory (Giarrocco et al., 2021). This began within ~100 ms of the stop

signal. The change in trajectory in stop trials might reflect the influence of a stop-process that acts on dPM to shift the population activity away from a movement-promoting state, so as to cancel the movement. Indeed, the timing of the stop-related changes in dPM activity are consistent with the timing of changes in activity/excitability of primary motor cortex in non-human primates and humans (100-150 ms after a stop signal; Jana et al., 2020; (Jerjian et al., 2020). These changes are thought to reflect the activation of the action-stopping network, whose function is to suppress output from primary motor cortex to the spinal motor neurons (Wessel & Aron, 2017).

In contrast to stop trials, behavioral strategy had a stark effect on both behavior and the trajectory of dPM activity in ignore trials. Manual response times were slower in ignore trials (compared to the go trials) when using a STD but not DTS. One possibility is that the delayed responses in STD sessions reflect a brief 'pause' in behavior. Of course, the term 'pause' here could be purely metaphorical or else could reflect some physiological process which acts on the motor system to inhibit or delay movement. dPM activity was consistent with the latter, since for the STD strategy it initially took a similar path as in the stop trials (i.e. diverged from go trials) but after this brief divergence, returned to the trajectory of go trials. Meanwhile, activity in ignore trials when using the DTS strategy simply followed that on go trials, consistent with the lack of behavioral difference between trial types. The fast, but brief, divergence of dPM activity when using a STD strategy hints at the automatic, but partial, recruitment of a stop-process, which acts as a pause whenever a salient stimulus is detected. This partial recruitment could be 'ramped-up' if the stimulus is subsequently identified as a stop signal.

Incidentally, the idea of the stop-process being recruited automatically by infrequent stimuli, such as the stop signal, indirectly speaks to a long-standing debate about the role of the right inferior frontal cortex (rIFC) in action-stopping. The prefrontal-basal-ganglia-thalamocortical model of action-stopping proposes that information about the need to stop is fed to the right inferior frontal cortex, which initiates the stop-process via the basal ganglia, and ultimately suppresses thalamocortical drive to the motor areas of the brain (Aron et al., 2004; Jana et al., 2020; Wessel & Aron, 2017). Indeed, a recent slew of human electrophysiological and causal brain stimulation studies supports this view (Chen et al., 2020; Hannah et al., 2020; Jana et al., 2020; Schaum et al., 2021). However, Sharp et al. (2010), contested that activation of the rIFC following a stop signal was not specific enough to reflect a motor inhibitory process, since it could be triggered by occasional signals that did not require a stop (i.e. ignore signals). In return, Aron et al. (2014) pointed to the slowing of response times elicited by the ignore signals and argued that this reflected an automatic triggering of the stop-process, even when there was no requirement to stop, and that this was triggered via the rIFC. The changes in dPM neural activity on ignore trials in the study of Giarrocco et al. are broadly consistent with this notion of the automatic triggering of motor inhibitory processes by infrequent stimuli, conceivably initiated via rIFC, and fit with an emerging literature on the inhibitory influence of unexpected sensory events on the motor system (Wessel & Aron, 2017). However, the current work suggests that the theory regarding unexpected events may need to be extended to accommodate the use of different control strategies, because data from the DTS strategy suggest that the automatic recruitment of a 'pause' is not obligatory.

An open question is whether pausing and cancelling reflect a common process or two separate processes. One possibility is that when using a STD strategy, the pausing and cancelling of actions are sub-served by the

same stop-process: first recruited partially, and then fully if needed. If this were true, the distinct behavioral and neurophysiological responses across STD and DTS strategies in ignore trials might suggest that the automaticity with which the process is recruited can be toggled on or off. Moreover, it makes the prediction that stopping would be slower for a DTS strategy, because one first has to discriminate the meaning of the signal before initiating the stop-process (e.g. Bissett & Logan, 2014). However, stopping latency, and stop-related changes in neural activity, were equally fast regardless of the stopping strategy employed. The null findings here could reflect the limited statistical power of the study, since only two non-human primates were tested and one subject showed a preference for one strategy over the other (though see (Bissett et al., 2021), which questions the idea that different strategies necessarily result in different stopping latencies).

An alternative possibility is that two separate neuroanatomical systems are employed to pause and stop, and that the pause can be turned off independently of the stop. Indeed, separate lines of work have highlighted that distinct regions of rIFC and their connections with motor-related areas (Xu et al., 2017), as well as distinct sub-cortical pathways (Schmidt & Berke, 2017), may be involved in different sub-processes of action stopping. Specifically, the "pause-then-cancel" model of stopping (Schmidt & Berke, 2017) predicts that in stop trials, the divergence of trajectories in stop versus go trials should be sooner when using the STD strategy compared to DTS. However, the data here show that this divergence happens at approximately the same time for both strategies. This seems inconsistent with the idea of separate pause- and cancel-processes being recruited to stop actions. It is puzzling therefore that neither possibility seems to fit. Computational models (Boucher et al., 2007; Logan et al., 2015) based on earlier

neurophysiological data (e.g. Hanes et al., 1998) could therefore be adapted to incorporate newer data from other brain regions (e.g. premotor cortex, Giarrocco et al., 2021 and basal ganglia, Mallet et al., 2016) in order to generate new predictions about the mechanisms involved in pausing and cancelling actions. Future work might also seek to explore how it is that the pause can be toggled on and off, for example, whether it can be attributed to the one of the sub-domains of the rIFC already shown to be participate in outright stopping (Xu et al., 2017).

The study of Giarrocco et al. (2021) raises fundamental questions about the nature of executive control over actions, such as under what circumstances are stop-like processes triggered and what systems are used to control them. For example, understanding whether there are one or two neuroanatomical systems for stopping is clinically relevant to impulse control disorders, because if the latter is true, then different symptoms/disorders might dissociate to separate systems. This knowledge could inform treatment approaches, wherein treatment might be focused specifically on the dysfunctional system responsible for the particular behavioral deficit, e.g. the STN-mediated pause-process or the striatally-mediated stop-process (Schmidt & Berke, 2017). A broader question not tackled here concerns why subjects spontaneously adopted different strategies on different sessions and what brain mechanisms were used to toggle the switch between STD and DTS strategies (Bissett & Logan, 2014; Jana & Murthy, 2018; Sebastian et al., 2017). We look forward to future experiments seeking to further pin down the neurophysiological correlates of stopping for each strategy, as well as those that study the conditions that prompt switches of strategy and the mechanisms underlying such switches.

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