Journal Club

Editor's Note: These short, critical reviews of recent papers in the *Journal*, written exclusively by graduate students or postdoctoral fellows, are intended to summarize the important findings of the paper and provide additional insight and commentary. For more information on the format and purpose of the Journal Club, please see http://www.jneurosci.org/misc/ifa_features.shtml.

Distinguishing between Types of Errors and Adjustments

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Review of Navarro-Cebrian

How the brain detects and reacts to errors has become a central question in cognitive neuroscience research (Gehring et al., 2012). As such, many studies using event-related brain potentials (ERPs) and functional magnetic resonance imaging (fMRI) have focused on the underlying neural mechanisms of error detection and adjustments that take place following errors. Much of this research suggests that errors initiate cognitive control mechanisms that serve to improve subsequent performance (Holroyd and Coles, 2002). However, the evidence for such post-error improvements is not entirely straightforward, because other studies indicate errors actually hinder performance on later trials (Notebaert et al., 2009). Understanding the contexts in which errors recruit neural and behavioral adjustments is becoming increasingly important as researchers frequently use these measures to capture cognitive processing abnormalities in psychopathology (Pizzagalli, 2011).

There are likely multiple reasons why conclusions regarding error adjustments are mixed. One reason is that all errors are not alike: whereas some errors are merely "action slips" that occur at the time of the response, other errors are caused by encoding failures at the time of the stimulus (i.e., before the response is made). Recent research suggests error adjustments depend on the type of error (Maier et al., 2011; van Driel et al., 2012). For instance, some errors might enhance selective attention leading to improved performance, whereas others may detract attention resulting in poorer performance. A separate line of work suggests that post-error adjustments require the subjects' conscious awareness of having made a mistake (Nieuwenhuis et al., 2001). That is, errors might initiate greater cognitive control on subsequent trials only if the errors are consciously detected. Yet, these lines of research have occurred in parallel, with no studies simultaneously examining how both the source of error and the conscious recognition of errors contribute to post-error adjustments.

A study recently published in *The Journal of Neuroscience* by Navarro-Cebrian et al. (2013) examined different error types (stimulus encoding failure or action slip), the subjective consciousness and certainty of having made an error, and how these factors relate to the dynamics of error detection and subsequent post-error compensations. Subjects indicated whether a target face stimulus was upright, upside down, or whether they were uncertain about the orientation. Subjects then rated the accuracy of their response after each trial (correct, incorrect, or uncertain). In terms of error detection, the authors focused on two well studied ERPs related to error processing, the error-related negativity (ERN) and error positivity (Pe), as well as ERPs related to stimulus encoding—the N170 and P1—to unravel the neural dynamics of the different error types (aware vs unaware vs uncertain and stimulus vs response). They found that both the ERN and Pe were larger for aware errors compared with both unaware errors (when the response was incorrect but rated as correct) and responses the participants rated as uncertain. Moreover, uncertain responses were associated with reduced N170 and P1, indicative of a stimulus encoding failure.

In terms of post-error compensations, Navarro-Cebrian et al. (2013) focused on two neural adjustments that occur after errors: 1) error-related alpha suppression (ERAS; Carp and Compton, 2009), which refers to the reduction of oscillations in the alpha frequency band (a frequency band associated with mental fatigue) in the intertrial interval after an error relative to a correct response; and 2) phase coherence between medial frontal cortex electrode sites (FCz) and presumably task-relevant visual processing area electrode sites (PO7, O1, O2, PO8). Both types of error adjustments were limited to aware error trials, suggesting that post-error compensations in neural processing occur only when participants are aware and certain of their errors.

However, a critical piece that is missing from the Navarro-Cebrian et al. (2013) study is the consideration of behavioral adjustments that occur after errors and how they relate to error awareness and certainty. Post-error behavioral adjustments, such as post-error slowing or post-error accuracy, reflect the degree to which participants actually change their overt responses in a task following errors,

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and therefore offer essential insight into the dynamics of error monitoring (Danielmeier and Ullsperger, 2011). Most importantly, post-error behavioral adjustments serve as an indicator of the "adaptiveness" of response strategies. Post-error accuracy is an arguably more adaptive behavioral adjustment (accuracy is almost always desired), whereas the adaptiveness of post-error slowing seems to depend on task-specific variables such as the length of time between trials and cognitive demands. Post-error slowing is not always correlated with post-error accuracy (Danielmeier and Ullsperger, 2011), and the recent "orienting account" of post-error slowing suggests it reflects off-task processing of the novel event of an error (Notebaert et al., 2009). Thus, not all post-error behaviors are adaptive in every context.

Although Navarro-Cebrian et al.'s (2013) task design prevented the analysis of post-error behavior because of the prolonged interval between trials, the exclusion of such data limits some of the possible conclusions one can make about neural compensations. Specifically, the extent to which ERAS following aware errors was compensatory is unclear. Indeed, previous work has found that ERAS predicts post-error slowing, but not post-error accuracy (Carp and Compton, 2009) such that, like post-error slowing, ERAS reflects the degree to which the participant is aroused to an unexpected event following an error trial. Moreover, a recent study found higher ERAS was associated with self-reported depression and less adaptive emotion regulation strategies (Compton et al., 2013). Thus, ERAS is not necessarily adaptive in terms of task performance and self-regulation.

This alternative notion, that ERAS reflects off-task processing, points to a different set of conclusions. Specifically, it suggests that error awareness in some tasks may hinder post-error performance insomuch as participants become more physiologically vigilant (reduced alpha) without a concomitant increase in accuracy. This compensatory effort following errors may be considered to be inefficient, as more resources are devoted to off-task processing following an error without a benefit in accuracy.

To understand the adaptiveness and flexibility of the brain in terms of error monitoring, it will be important for future research to tease apart the conditions under which these adjustments are truly adaptive. This understanding will be facilitated by examining both the neural and behavioral phenomena that surround errors. This will not only have implications for cognitive neuroscience research, but will also enhance our knowledge of potential individual differences variables used for psychopathology studies and clinical assessment (Pizzagalli, 2011).

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