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The role of the cerebellum for feedback processing and behavioral switching in a reversal-learning task

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ABSTRACT

Previous studies have reported cerebellar activations during error and reward processing. The present study investigated if the cerebellum differentially processes feedback depending on changes in response strategy during reversal learning, as is conceivable given its internal models for movement and thought. Negative relative to positive feedback in an fMRI-based reversal learning task was hypothesized to be associated with increased cerebellar activations. Moreover, increased activations were expected for negative feedback followed by a change in response strategy compared to negative feedback not followed by such a change, and for first positive feedback after compared to final negative feedback before a change, due to updating of internal models. As predicted, activation in lobules VI and VIIa/Crus I was increased for negative relative to positive feedback, and for final negative feedback before a change in response strategy relative to negative feedback not associated with a change. Moreover, activation was increased for first positive feedback after relative to final negative feedback before a change. These findings are consistent with updating of cerebellar internal models to accommodate new behavioral strategies. Recruitment of posterior regions in reversal learning is in line with the cerebellar functional topography, with posterior regions involved in complex motor and cognitive functions.

1. Introduction

Our understanding of the role of the cerebellum for behavior has recently seen a fundamental paradigm shift. The cerebellum is no longer thought of as solely involved in motor functions. Rather, its role for both movement and cognition is now widely accepted even though comparatively little is known about the actual mechanisms underlying cerebellar contributions to non-motor, cognitive functions (for a review, see recent consensus paper, Koziol et al., 2014). It has been proposed that the cerebellum generates internal models for the coordination of movement and thought (Ito, 2008; Wolpert, Miall, & Kawato, 1998) which allow prediction of sensorimotor events, feedback and/or thought, and behavioral outcomes. In dynamic or volatile environments, these predictions constantly have to be revised based on past experiences, stressing the need for continued monitoring of action/perception-outcome associations in order to ensure successful goal-directed behavior.

The notion of cerebellar internal models puts the cerebellum at the interface of motor behavior and cognition, ascribing a pivotal role for performance monitoring and adaptive behavior (for a recent review, see Peterburs & Desmond, 2016). In this regard, performance monitoring refers to a diverse set of cognitive and affective functions underlying adaptive behavior, e.g., processing of (external and internal) performance-related feedback, on-line error detection, inhibition of conflicting response tendencies, allocation of attentional resources, and regulation of emotional responses to specific response outcomes such as rewards or punishment. Evidence for cerebellar involvement in performance monitoring is provided by an ever-growing number of studies including work on animals as well as human subjects, clinical studies (in patients with cerebellar damage or cerebellar disease), behavioral paradigms, and functional neuroimaging. For instance, simple spike activity of cerebellar Purkinje cells has been shown to both predict and track motor errors during manual tracking of moving targets, a finding that is consistent with cerebellar forward and inverse models (Popa, Hewitt, & Ebner, 2013, Popa, Streng, Hewitt, & Ebner, 2016). Saccadic errors have been associated with activations in cerebellar lobules VIII-X, presumably representing visual error signals used to maintain saccadic accuracy (van Broekhoven et al., 2009). Moreover, cerebellar

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encoding of sensory prediction errors has also been shown for unexpected absence or presence of force pulses following reaching movements (Schlerf, Ivry, & Diedrichsen, 2012). Last, single-pulse transcranial magnetic stimulation (TMS) of the cerebellum has been shown to directly modulate frontal theta oscillations, a cortical signature of cortico-limbic routines implicated in error monitoring (Schutter & van Honk, 2006).

A functional magnetic resonance imaging (fMRI) study applying Granger causality mapping has recently established a functional link between cerebellar and ventrolateral prefrontal cortex activations during behavioral adjustments (Ide & Li, 2011), further highlighting the role of the cerebellum for monitoring of overt behavior and processing of erroneous responses. In line with this, altered neural responses (but intact behavior) in the context of saccadic updating and saccadic error processing have been reported in patients with post-acute focal vascular lesions of the cerebellum (Peterburs et al., 2011, Peterburs et al., 2013). In contrast, patients with progressive cerebellar degeneration showed behavioral impairments that were paired with altered neural responses (Peterburs et al., 2015), emphasizing the importance of plasticity and functional reorganization (or lack thereof) in patients with cerebellar damage.

With regard to non-motor aspects of adaptive behavior, the cerebellum has been linked to emotional and cognitive associative learning (for a review, see Timmann et al., 2010). Interestingly, lateral regions of the cerebellar hemispheres (Crus I and II) have also recently been implicated in learning of higher order rules, i.e., rules that specify the application of second-order rules and thus do not involve integration of sensory information with motor effectors (Balsters, Whelan, Robertson, & Ramnani, 2013). Lastly, the cerebellum is also involved in reward learning, with activations in Crus II in response to unexpected (monetary) rewards (Ramnani, Elliott, Athwal, & Passingham, 2004), and with altered neural responses to performance-related feedback in a probabilistic reward-learning task in patients with cerebellar lesions (Rustemeier, Koch, Schwarz, & Bellebaum, 2015). On the behavioral level, however, patients showed rather subtle deficits of reward-based reversal learning but not feedback-based learning per se (Rustemeier et al., 2015; Thoma, Bellebaum, Koch, Schwarz, & Daum, 2008). Moreover, the cerebellum has also been implicated in the coding of reward prediction errors (O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003).

Interestingly, fMRI studies frequently report cerebellar activations in concert with neocortical activations during error processing, reward learning, and reversal learning (e.g. Greening, Finger, & Mitchell, 2011; Linke et al., 2010; Remijnse, Nielen, Uylings, & Veltman, 2005; Waltz et al., 2013). Unfortunately, these activations are rarely discussed in detail. Reversal learning is particularly interesting for probing the above mentioned aspects of cerebellar function because during reversal learning rules have to be inferred from performance feedback and then applied in order to alter previously successful response strategies. More specifically, a reversal learning task creates a volatile environment because stimulus-response-outcome associations change without explicit notice. Consequently, constant updating of internal models for the prediction of reward based on cue-response associations is necessary to optimize behavior.

In line with cerebellar internal models for movement and thought, it is conceivable that the cerebellum differentially processes performance feedback depending on behavioral adaptation, i.e., on changes in response strategy during reversal learning. We re-analyzed fMRI data from a reversal task that was part of a larger investigation (Becker, Nitsch, Hewig, Miltner, & Straube, 2016) of the neural, and specifically cerebral, correlates of behavioral adaptation and value tracking in order to address this issue. In this study, participants performed an fMRI-based reversal-learning task in which they chose one of two visual stimuli and subsequently received feedback. Based on the literature, we expected the cerebellum, in particular its posterolateral regions, to show elevated activation to negative feedback relative to positive feedback, because monitoring requirements are higher if feedback signals the need to adapt behavior. Furthermore, we hypothesized that negative feedback followed by a change in response strategy (i.e., choice of the other, previously not rewarded stimulus on the subsequent trial) as compared to negative feedback not accompanied by a change in response strategy would identify cerebellar modules concerned with updating of internal models to incorporate the new behavioral strategy. Similarly, increased activations in these cerebellar modules were expected for the first positive feedback following a change in response strategy relative to the final negative feedback after a change in response strategy.

2. Materials and methods

The present study was part of a larger investigation of the neural correlates of reversal learning. While neocortical and subcortical activations with regard to reward prediction error and value tracking across trial sequences have been investigated and discussed extensively in a previous publication (Becker et al., 2016), the present work focuses exclusively on cerebellar involvement and presents new analyses and specific contrasts of interest for cerebellar activations during reversal learning.

2.1. Participants

31 healthy adult participants (10 females; mean age (± SD) = 28.4 years (± 6.6)) were recruited for participation from the Jena community via public announcement. All participants were right-handed according to self-report and had normal or corrected-to-normal vision. Exclusion criteria were history of or currently present neurological or psychiatric disorders, psychotropic medication within the last six months, and any contraindications for participation in an fMRI study (e.g., ferromagnetic implants, pregnancy, claustrophobia). The study conforms to the Declaration of Helsinki and was approved by the ethics committee of the University of Jena.

2.2. Experimental task

The fMRI-based reversal learning task (Cools, Clark, Owen, & Robbins, 2002) used in this study is reported in detail in (Becker et al., 2016). In brief, two symbols were presented simultaneously on a screen visible by a head mirror. One of the symbols was associated with a monetary reward (win of 10 cent displayed as '+10'), and one was associated with monetary loss (loss of 10 cent displayed as '−10'). In each trial, one symbol could be selected by pressing a button on an MRI-compatible response pad. In order to maximize the monetary gains, participants had to figure out the correct symbol. After a variable number of correct choices and unknown to the participants, the previously rewarded option became the new loss option and vice versa (reversal event). An average of 30.9 reversal events occurred during the entire experiment. Spurious loss feedback was given after some correct responses, following a probabilistic rule, to increase task difficulty.

For analysis of behavioral data, average response times (RT) for correct and incorrect responses were compared using a paired-sample *t* test. In addition, RTs for first correct responses reflecting a change in response strategy, for perserverative errors, and for incorrect responses immediately preceding a change in behavioral strategy (FNF) were compared using paired-sample t tests. A Bonferroni-corrected significance level of $p < .013$ was applied to account for multiple testing.

2.3. fMRI data acquisition, preprocessing and analysis

Functional magnetic resonance data were acquired at 3 T with a Siemens Magnetom Trio (Siemens, Medical Systems, Erlangen, Germany) scanner. Three runs of 384 volumes, each consisting of 35 slices (slice thickness = 3 mm; inter-slice gap = 0.50 mm; in-plane