

Neural dynamics of error processing in medial frontal cortex

Rogier B. Mars,^{a,b,*} Michael G.H. Coles,^a Meike J. Grol,^{a,c} Clay B. Holroyd,^d
Sander Nieuwenhuis,^e Wouter Hulstijn,^b and Ivan Toni^{a,b}

^aF.C. Donders Centre for Cognitive Neuroimaging, P.O. Box 9101, NL-6500 HB Nijmegen, The Netherlands

^bNijmegen Institute for Cognition and Information, Radboud University, P.O. Box 9104, NL-6500 HE Nijmegen, The Netherlands

^cHelmholtz Institute, P.O. Box 80125, NL-3508 TC Utrecht, The Netherlands

^dDepartment of Psychology, University of Victoria, P.O. Box 3050 STN CSC, Victoria, BC, Canada V8W 3P5

^eDepartment of Cognitive Psychology, Vrije Universiteit, Van der Boerhorststraat 1, 1081 BT Amsterdam, The Netherlands

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Adaptive behavior requires an organism to evaluate the outcome of its actions, such that future behavior can be adjusted accordingly and the appropriate response selected. During associative learning, the time at which such evaluative information is available changes as learning progresses, from the delivery of performance feedback early in learning to the execution of the response itself during learned performance. Here, we report a learning-dependent shift in the timing of activation in the rostral cingulate zone of the anterior cingulate cortex from external error feedback to internal error detection. This pattern of activity is seen only in the anterior cingulate, not in the pre-supplementary motor area. The dynamics of these reciprocal changes are consistent with the claim that the rostral cingulate zone is involved in response selection on the basis of the expected outcome of an action. Specifically, these data illustrate how the anterior cingulate receives evaluative information, indicating that an action has not produced the desired result.

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Introduction

To survive in changing environments, an organism must be able to adapt its behavior to the situation at hand. This flexibility can be achieved by evaluating response outcomes and adjusting behavior accordingly (Dickinson, 1985). In this regard, error signals provide important evaluative information, since they indicate that a behavior was inadequate given the current context and that, in future, a different response needs to be selected (Holroyd and Coles, 2002).

* Corresponding author. F.C. Donders Centre for Cognitive Neuroimaging, P.O. Box 9101, NL-6500 HB Nijmegen, The Netherlands. Fax: +31 24 3610989.

E-mail address: rogiar.mars@fcdonders.ru.nl (R.B. Mars).

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Existing data on the neural substrates of action selection indicate that the medial frontal cortex plays a crucial role in selecting actions on the basis of their outcomes (Matsumoto and Tanaka, 2004) and subsequent monitoring of response outcomes (Holroyd et al., 2004a; Ridderinkhof et al., 2004). Rather than attributing a single role to this vast cortical expanse, recent studies have started to associate different functions to the different anatomical structures that lay within the medial frontal cortex (Picard and Strick, 2001; Rushworth et al., 2004). In this context, an anterior portion of the cingulate cortex, the rostral cingulate zone anterior (RCZa), has been specifically associated with processing of error information and selecting appropriate behavioral adjustments (Holroyd and Coles, 2002; Rushworth et al., 2004; Fiehler et al., 2004).

These inferences on the neural bases of error processing have been obtained in the context of a “static” experimental environment, in which the organism knows the behavior that is appropriate for the current situation. Thus, a given response can be evaluated immediately against an internal representation of the correct stimulus–response relationship. Should the response be incorrect, error information is available from an internal error-detection process at the time of the response (Gehring et al., 1993; Holroyd et al., 2005). However, in a novel environment, with as yet unknown stimulus–response associations, error information is not available until the delivery of external performance feedback. This implies that, during the learning of stimulus–response associations by trial and error, the time at which error information is available will change. Prior to learning, error information will not be available until external performance feedback is delivered, but after learning, error information will be available earlier from internal sources at the time of the response itself. Thus, a neural structure that adjusts behavior as a function of the evaluation of response outcomes should dynamically shift its responsivity as a function of learning, from external sources provided by error feedback to internal sources associated with the error response itself. We predicted that, following error feedback, activity in the anterior

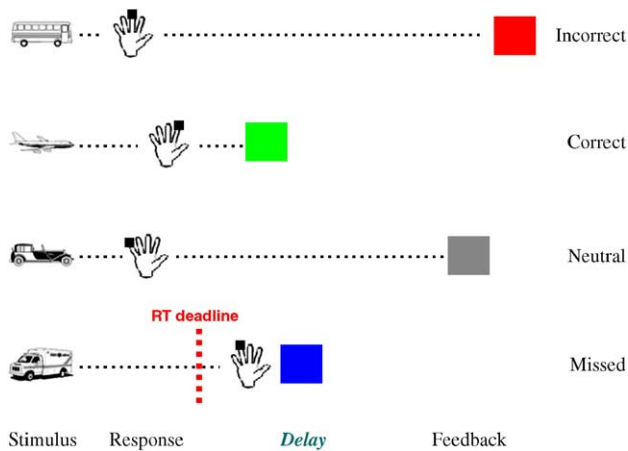


Fig. 1. Task setup. Participants had to learn, by trial and error, arbitrary associations between visual stimuli and motor responses. After a variable delay, visual feedback (red/green square) was provided, indicating correct and incorrect responses. On 50% of the trials, feedback consisted of a non-informative gray square. When responses occurred after the reaction time deadline (750 ms), immediate feedback (blue square) was provided.

cingulate cortex would decrease as learning proceeds; conversely, following an erroneous response, activity in the anterior cingulate would increase as learning proceeds. These predictions can be derived from a neuro-computational model (Holroyd and Coles, 2002) that formally describes the relationship between neural systems involved in outcome evaluation with those involved in action selection.

To test these predictions, we asked human subjects to learn arbitrary visuomotor mappings (Wise and Murray, 2000; Toni et al., 2001), using performance feedback, while measuring their cerebral activity using functional magnetic resonance imaging (fMRI). Participants were presented with line drawings, each of which was associated with pressing one of four response buttons (Fig. 1). We manipulated the degree of learning achieved during the scanning session by varying the number of times a given visuomotor mapping was presented. For one condition (High Learning, HL), four distinct visuomotor mappings were presented 36 times each over the course of the scanning session, enabling the subject to fully learn the visuomotor associations. For a control condition (Low Learning, LL), 24 different mappings were presented 6 times each. A reaction time (RT) deadline ensured that participants made errors, even during learned performance. Crucially, by varying the delay between response and feedback, and by introducing neutral feedback on some of the trials, we were able to dissociate the hemodynamic responses elicited by response and feedback (see Experimental timing).

Materials and methods

Subjects

We studied eight right-handed male volunteers (mean age = 30.4 years, SD = 13.4) with normal or corrected-to-normal vision after obtaining informed consent according to institutional guidelines of the local ethics committee (CMO region Arnhem-Nijmegen, Netherlands). They were paid € 10 per hour for their participation. Imaging data from 5 additional subjects were discarded, since these subjects either failed to learn the appropriate

stimulus–response mappings adequately (2 subjects, less than 50% correct on post-scanning forced-choice recall task) or performed without any errors during the last part of the scanning session, indicating that the RT deadline was not tight enough for these subjects (3 subjects).

Experimental setup

Subjects lay supine in the scanner. Head movements were minimized by an adjustable padded head holder. Visual stimuli (visual angle of approximately 6°) were projected onto a mirror above the subjects' heads. Motor responses were recorded via an MR-compatible keypad (MRI Devices, Waukesha, WI), positioned on the right side of the subject's abdomen. Stimulus presentation and response collection were controlled by a PC running Presentation 0.51 (Neurobehavioral Systems, San Francisco, CA).

Behavioral procedure

Participants were asked to try to learn arbitrary associations between visual stimuli (black and white drawings of cars, airplanes, boats, etc.) and motor responses (pressing of one of four buttons with the fingers of the right hand) by trial-and-error using performance feedback (Fig. 1). We manipulated the degree of learning achieved during the experimental session by varying the number of times a visuomotor mapping was presented. For one condition (High Learning, HL), four distinct visuomotor mappings were presented 36 times each over the course of the scanning session, while for a control condition (Low Learning, LL), 24 different mappings were presented 6 times each. Trials enabling learning (HL) were pseudo-randomly intermixed and matched in number with trials in which learning was less likely to occur (LL). Participants received either performance feedback (green or red square) or neutral feedback (gray square, see Experimental timing) after each response, with a variable delay between these two events. To encourage error commission even during learned performance, a stringent reaction time deadline of 750 ms was enforced. When subjects responded after this deadline, immediate feedback (blue square) was provided and the trial ended. Subjects were instructed to try to avoid this at all costs. Subjects practiced the task in the scanner for 50 trials using a different stimulus set before the experimental session.

Following the scanning session, participants performed a forced choice recall test, in which all stimuli of the HL condition and a subset (50%) of the stimuli of the LL condition were presented 7 times each, randomly intermixed. Subjects were required to press the button corresponding to each stimulus, as during the scanning session. However, during the recall test, there was no reaction time deadline and no feedback was given, to allow for a reliable assessment of the learning of the stimulus–response mappings.

Imaging procedures

Images were acquired using a 1.5T Sonata scanner (Siemens, Erlangen, Germany). BOLD sensitive functional images were acquired using a single shot gradient EPI sequence (TR/TE 2.2s/40 ms, 28 transversal slices, interleaved acquisition, voxel size 3.5 × 3.5 × 3.5 mm). Following the experimental session, structural images were acquired using an MP-RAGE sequence (TR/TE/TI 2250 ms/3.93 ms/850 ms, voxel size 1 × 1 × 1 mm).

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