The Anterior Cingulate Cortex:

Regulating Actions in Context

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Luu, P., & Pederson, S. M. (in press). The anterior cingulate cortex: regulating actions in context. In M. I. Posner (Ed.), *Cognitive neuroscience of attention*. New York: Guilford Publication, Inc.

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Prior to the advent of non-invasive neuroimaging technologies, knowledge about human cognitive functions and how they mapped onto neuroanatomy had to be gleaned primarily from animal studies and studies of patients with known cerebral lesions. In the 80s and 90s availability of non-invasive neuroimaging technologies, such as Positron Emission Tomography (PET) and functional Magnetic Resonance Imaging (fMRI), allowed precise localization of cognitive functions in the intact human brain (see (Posner & DiGirolamo, 1998; Posner, Petersen, Fox, & Raichle, 1988). Of particular interest to this volume is a series of PET studies examining regions involved in word reading, which suggested that the anterior cingulate cortex (ACC) is involved in a form of attention that is referred to as *attention for action* (Posner & Dehaene, 1994; Posner et al., 1988).

Attention for action describes cognitive operations that allow for voluntary (i.e., controlled) processes to override or exert influence over automatic processes (Posner, 1978). This attention system is not sensory or cognitive operation specific. Attention for action has been described as executive attention (Vogt, Finch, & Olson, 1993). Consistent with the idea of attention for action, executive attention is thought to be engaged when routine functions are insufficient or ongoing behavior must be adjusted to meet environmental demands (Posner & DiGirolamo, 1998).

In this chapter we describe our current understanding of ACC function and attention for action based upon research using dense-array EEG technology. Dense-array EEG technology is relatively new, being in common use only within the past decade. Traditionally, event-related potential (ERP) technology was valued for its direct reflection of neuronal function, unlike fMRI and PET methodologies, which rely on indirect measures of neuronal activity. However, unlike these hemodynamic-based technologies that provide precise spatial localization of cognitive functions, traditional ERP methods have poor spatial resolution. With dense-array ERP technology, localization is improved and has been shown to be both accurate and capable of discriminating nearby sources (see (Cuffin, Schomer, Ives, & Blume, 2001; Laarne, Tenhunen-Eskelinen, Hyttinen, & Eskola, 2000; Lantz, Grave de Peralta, Spinelli, Seeck, & Michel, 2003; Luu, Tucker, Derryberry, Reed, & Poulsen, 2003).

Using ERP methodologies, we study a particular component of executive attention of the ACC: action monitoring. In action monitoring, the appropriateness of an action must be monitored within a given context. Inappropriateness of the response, defined as errors, is evaluated relative to the context of the action. Violations of action relative to action context are essentially expectancy violations, and the detection of these violations is understood as a core component of attention for action.

The Error-Related Negativity: An Index of Action Monitoring

The error-related negativity (ERN) or the error negativity (Ne), was first reported in the early 90s by Falkenstein et al. (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991) and Gehring et al. (Gehring, Goss, Coles, Meyer, & Donchin, 1993). The ERN is recorded as a negative deflection in the ongoing EEG with a peak negativity approximately 50-150 ms after an erroneous response (see Figure 1). The ERN has a mediofrontal distribution, and using dense-array EEG recordings Dehaene and colleagues (Dehaene, Posner, & Tucker, 1994) localized the source generator of the scalp recorded ERN to the ACC. This important localization finding was later confirmed both in other dense-array EEG (Luu, Collins, & Tucker, 2000; Miltner, Braun, & Coles, 1997) and fMRI studies (Kiehl, Liddle, & Hopfinger, 2000; Menon, Adleman, White, Glover, & Reiss, 2001; Ullsperger & von Cramon, 2001).

Functional significance of the ERN remains controversial, and there exists at least three competing functional theories. The first theory claims that the ERN reflects the output of an error detection system (Holroyd & Coles, 2002). Rather than reflecting error detection per se, the conflict monitoring theory claims that the ACC's detection of conflict produces the ERN, and that errors are merely associated with increased conflict (Carter, Botvinick, & Cohen, 1999; Carter et al., 1998). Incorporating the vast human and animal literatures, we propose that the ERN is not merely a reflection of the evaluation of an error or of conflict, but instead reflects the affective consequence of expectancy violations (Luu & Tucker, in press; Luu et al., 2003). We do not perceive our proposal to be inconsistent with the error or conflict monitoring theories. Rather in our theory the limbic functions of the ACC are emphasized; error or conflict within a particular task induces affective evaluations of expectancy violations.

Action in Context: Expectancy Violations

There is a large body of literature on brain responses to context violations (see (Pritchard, Shappell, & Brandt, 1991). These studies have examined effects of context violation at different levels (e.g., stimulus feature discrepancies, semantic violations, etc.). In this chapter we limit our brief review of context violations to situations in which violations are immediately relevant to action control, i.e., context is established to direct appropriate behaviors.

Initially, it was believed that the elicitation of the ERN required explicit recognition that an error has been committed (Dehaene et al., 1994). If an error response is not recognized as such, an error feedback is required, which is adequate for the elicitation of a mediofrontal, stimulus-locked negativity thought to be equivalent to the ERN (Kopp, Rist, & Mattler, 1996; Miltner et al., 1997; Ruchsow, Grothe, Spitzer, & Kiefer, 2002). The feedback provides information regarding violation of the task context and thus elicits a negativity with a peak latency between

250 and 400 ms post-stimulus that we refer to as the medial frontal negativity (MFN, see (Gehring & Willoughby, 2002; Tucker, Luu, Frishkoff, Quiring, & Poulsen, in press). Interestingly, this finding of error feedback inducing a mediofrontal response was anticipated by the findings of Gevins et al. (Gevins et al., 1989) who reported a mediofrontal theta response, at about the same time as the MFN, after presentation of an error feedback. It is likely that the MFN is part of the N2 complex known to index both automatic and controlled detection of context violation (Pritchard et al., 1991), but this relation remains to be clarified.

Other studies have shown the MFN to be similar to the ERN in several ways. Kopp et al. (Kopp & Wolff, 2000) studied contingency learning in humans and found that when established contingencies are violated, a negative component over mediofrontal recording sites is observed. In sequence learning paradigms as subjects learn the sequence, violations of a position within the sequence elicit an N2 with a mediofrontal distribution, and this N2 response is larger as subjects learn the sequence (Eimer, Goschke, Schlaghecken, & Stürmer, 1996; Schlaghecken, Stürmer, & Eimer, 2000). These findings suggest that as subjects learn the context of appropriate action, violations of that context elicit larger ACC responses.

Using an old/new memory paradigm, Nessler and Mecklinger (Nessler & Mecklinger, 2003) found that an MFN-like component indexes correct recognition of new, but semantically similar items (i.e., lures) in this recognition test of previously learned items. The authors found that the correctly rejected lures elicited a larger MFN-like response than items that were correctly recognized as old (i.e., previously studied) or lures that were incorrectly classified as old (i.e., falsely recognized).

Based on the view that all learning occurs in a context defined by the specific features of the task at hand (Balsam, 1985), one interpretation of this finding is that the larger MFN in the presence of lures reflects the ACC's detection of a context violation. Explicitly stated in the context of this recognition paradigm, the lures violate the background context of previously encountered items. To the extent that this context violation is detected—as indexed by a larger MFN—the more likely the lures will be correctly recognized as newly presented items. The failure of this detection—as evidenced by a lack of or smaller MFN—results in the erroneous identification of the lures as old.

Schnider and colleagues (Schnider, Valenza, Morand, & Michel, 2002) used a memory paradigm to investigate brain responses to suppression of irrelevant stimuli—as defined by the current context of the study—that had been previously encountered. Examining the responses to non-target items revealed that as subjects were exposed to a second run of non-target items, the ERP to these items were differentiated from the target items by a lack of an MFN. Similar to Nessler and Mecklinger's (2003) findings, targets appear to be defined electrophysiologically, and perhaps cognitively, by how they "standout" from the context of the task.

Protection Against Negative Outcomes as a Context for Action

In monkeys and humans, the cingulate motor area (CMA) is activated when a change of behaviors is required due to reductions of an expected reward (Bush et al., 2002; Shima & Tanji, 1998). Shima and Tanji observed that cells in the rostral CMA (CMAr) are activated only when reduction of reward is associated with a corresponding "corrective" response. Bush et al. extended these results to humans, adding that a non reward-related behavioral switch signal was not sufficient to activate the CMA. These studies confirm the role of the ACC in compensatory behaviors when expectations are violated.

Further evidence of MFN reactivity to motivational consequences of context violation comes from studies investigating MFN responses to affective feedback. Gehring and Willoughby

(Gehring & Willoughby, 2002) found that rather than responding to a correctness of a response, the MFN was sensitive to loss, with MFNs larger on trials following loss trials than those following gain trials. We used a delayed feedback paradigm to investigate brain responses to evaluative feedback (Luu et al., 2003). Each trial began with a feedback stimulus (a letter grade), based on performance from five trials previous, which indicated both speed of response and the correctness of the response. Similar to Gehring and Willoughby's findings, the MFN was sensitive to feedback type and of larger amplitude for feedback indicating negative feedback, which was not necessary indicative of errors. Extending this finding, the larger MFN to negative feedback was also not necessarily indicative of a loss of points. In other studies, we have found MFNs that differentiated between good and bad target locations, which signaled whether points could be earned or lost, respectively (Tucker, Hartry-Speiser, McDougal, Luu, & deGrandpre, 1999), and good and bad self-descriptive trait words (Tucker et al., 2003). These findings are consistent with the concept of attention for action, suggesting that there is a bias in context-action representations and that this bias is for prevention of loss or negative evaluation. Core to this bias is evaluation of expectancy violations along a negative affect dimension.

There is increasing evidence that ERN amplitude varies with negative affect (Gehring, Himle, & Nisenson, 2000; Johannes, Wieringa, Nager, Dengler, & Münte, 2001; Luu, Collins et al., 2000; Pailing & Segalowitz, in press). It is possible that the violation of context representation (i.e., expectancy) is inherently aversive and that mechanisms originally developed for evaluating the unpleasantness of physical and psychological pain are also used for the evaluation of context violations (Luu, Collins et al., 2000; Luu & Tucker, 2002, in press), which is consistent with the role of the ACC in pain evaluation (Rainville, Duncan, Price, Carrier, & Bushnell, 1997).

Action Regulation: Evaluating Action Against Context

When an MFN in response to error feedback was first recorded, it was assumed to be equivalent to the response-locked ERN. We recently investigated this possibility using the delayed feedback paradigm described above (Luu et al., 2003). This paradigm removes response control properties associated with immediate feedback presentation while preserving affective responses that can influence subsequent performance, thus providing access to both ERN and MFN measures in the same subject.

Based on extensive cytoarchitectural, lesion, electrophysiology, and imaging evidence that the ACC can be functionally differentiated by cognitive (dorsal) and affective (rostroventral) subdivisions (for a review see (Bush, Luu, & Posner, 2000), we first estimated the ERN sources using one dipole in the region of the dorsal ACC and a second dipole in the rostral extent of the ACC using BESA (2000) software (see Figure 2). We then applied the same source model to the MFN. Surprisingly, when the ERN model was applied to the MFN, only the dorsal ACC source was active. van Veen and Carter (van Veen & Carter, 2002) have also reported a dorsal ACC source for both ERN and N2 (i.e., MFN) components. Therefore, it appears that when an actual error is committed the rostral ACC is additionally engaged.

Because the rostral ACC source appears to be active only after error commission and is best seen in response-locked data, we speculated that the rostral ACC is involved in response monitoring. In contrast, because the MFN is locked to the stimulus and is active when either an error is committed or a feedback is presented, we proposed that the dorsal ACC may be involved in monitoring the action context (Luu et al., 2003). Consistent with the cognitive-affective division, the dorsal ACC tracks parameters of the task (such as feedback and conflicting task demands), and the rostroventral ACC tracks the affective evaluation of response outcomes.

Similar results have been obtained using fMRI methodologies. For example, Elliot and Dolan (Elliot & Dolan, 1998) found dorsal ACC activity when subjects had to formulate a hypothesis about what would constitute a correct response given a set of stimuli. In contrast, the rostral ACC was active only when subjects made a choice.

We (Makeig, Luu, & Tucker, 2002) further investigated this response monitoring/action context duality using independent components analysis (ICA). ICA decomposes the multichannel EEG data by "blind" separation of the single-trial data into independent components that contribute separate information to the data. Makeig et al. found that the ERN is the sum of several components, with one component varying with the actual response and the second varying with the parameters of the task, (i.e., being responsive to target onset, response deadline, and feedback presentation). Although the number of components contributing to the ERN varies between subjects, they generally can be separated along this response tracking versus context division.

Thus, it appears that the ACC is involved in associating an appropriate response within a given context, monitoring the outcome of the action, and switching behaviors when outcomes are not as expected. We refer to these functions as action regulation. As such, the ERN is expected to index basic learning processes. Current direct evidence for the role of the ERN in learning is limited but the indirect evidence is compelling. We have reviewed this possibility extensively elsewhere (see (Luu & Tucker, 2002, in press) and provide a brief summary below.

Action Regulation and Learning

Electrophysiological evidence for the involvement of the theta rhythm (4-7 Hz for humans) in learning comes from animal studies. Adey (Adey, 1967) found that in early stages of learning, when animals were trying to learn the association between a conditioned stimulus and reward, a theta rhythm was prominent and phased-locked to the auditory cue. As the animals' performance marked proficiency on the task, theta amplitude decreased, and this was due to either a loss of phase-locked activity or a modulation of the frequency. However, when the cue was reversed, theta activity reappeared and was again phase-locked to the stimulus.

Buzsáki et al. (Buzsáki, Grastyán, Tveritskaya, & Czopf, 1979) observed similar effects. When an animal has to remember whether the current stimulus is the same or different from a previous stimulus in order to determine which response to make, Givens (Givens, 1996) found that theta recorded in the dentate gyrus became phase-locked to the stimulus. However, when performing a much simpler, well-learned task of stimulus-response mapping, theta was not phase-locked to the stimulus.

How to integrate these animal findings with the ERN literature has been difficult until we discovered that the ERN reflects that part of the theta rhythm that is phase-locked to the response (Luu & Tucker, 2001). We reported that when the ERN data are filtered with a 4-7 Hz bandpass, it is clear that the ERN is but one part of an ongoing midline oscillation, and that when errors are committed this midline oscillation alternates with potentials recorded over the motor cortex, which are also oscillatory in nature. Examining single-trial data, the theta origin of the ERN becomes quite clear: the ERN reflects the phase-locked component of the midline theta rhythm (Luu, Tucker, & Makeig, submitted). When phase-locked data are subtracted from total theta activity, leaving non-phase locked activity, differences between error and correct trials are still observed.

When a theta source model, based on the two midline sources identified as necessary to account for a frontal midline theta process (Asada, Fukuda, Tsunoda, Yamaguchi, & Tonoike, 1999), was fitted to the ERN data the source distribution and phase relation between the sources were almost identical to those obtained for midline theta rhythm (Luu et al., 2003). Neurophysiologically, it has been proposed that the theta rhythm is the mechanism by which distant cortical structures exchange information of local networks (Miller, 1991). If the ERN is integrally related to ongoing theta rhythms, the ERN may index basic learning mechanisms of limbic networks. That is, rather than reflecting the functions of a single ACC region, the ERN may reflect theta coordination of the broader action-regulation functions of the limbic system.

Action Regulation and Awareness

The role of executive attention in awareness was previously discussed by Posner (Posner, 1994). Here we briefly discuss the electrophysiological evidence regarding the role of awareness in error commission and expectancy violation. Awareness in this context is defined by subjects' report of being aware of either making an error or of the presence of an action-context violation. As noted previously, it was thought that a subject must be aware of making an error at the time of error commission in order to elicit an ERN (Dehaene et al., 1994), and later studies showed that if a subject is not aware of making an error, presentation of an error feedback generated an ERN-like response (Miltner et al., 1997).

Addressing this issue directly, Scheffers and Coles (Scheffers & Coles, 2000) asked subjects to rate the degree to which they believed a response was correct or in error. These authors found that when subjects rated a correct response as being erroneous, the ERN associated with this response was much larger than ones associated with responses rated as correct. Similarly, those incorrect responses rated as correct elicited smaller ERNs than those error responses rated as incorrect. We attempted to address this issue by examining late responses, i.e., responses that are executed correctly but are too late according to an imposed RT deadline (Luu, Flaisch, & Tucker, 2000). We divided the responses into three levels of lateness, with the logic being that as subjects become increasing late they also become aware of the status of the late response. For example, those responses that barely exceed the RT deadline will not be easily perceived as erroneous compared to those responses that are very late. We found that as subjects became increasingly late in their response, the ERN increased in amplitude. However, the latest responses still elicited a smaller ERN than an ERN associated with an error of commission. This later finding is consistent with subjective experience because in speeded response tasks subjects are immediately aware of committing the wrong response.

Using an antisaccade task and asking subjects to rate whether they were aware of making a saccadic error, Nieuwenhuis et al. (Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001) showed that unperceived errors elicited an ERN, a finding that is at odds with the previous two studies. However, it is possible that awareness is not the binary phenomenon Nieuwenhuis and colleagues conceived. It is also possible that awareness of an error is not necessary for eliciting the ERN but that awareness modulates the mediofrontal response to violations of expectancies.

Eimer and colleagues' studies of implicit and explicit serial learning (Eimer et al., 1996; Schlaghecken et al., 2000) help to shed light on this issue. In this task, subjects were required to make rapid responses to letter stimuli that were each mapped to a unique finger response. Participants were not informed of the appearance of a regular series of stimuli, but were later sorted into those who reported the existence of a regular sequence of stimuli and those who did not. Periodically, a position in the series was replaced with a deviant stimulus. Behaviorally, RTs on deviant trials and trials following deviant trials were longer than standard trials. The RT slowdown after a deviant trial is similar to the post-error slowing often observed in speeded response tasks. Subjects who did not report explicit knowledge of the stimulus sequence exhibited less of a slowdown after deviant trials, suggesting that they were less aware that a violation of the context had occurred. Comparing the electrophysiological response, these authors found that deviant stimuli elicited a larger N2 (i.e., MFN) than standard stimuli and that this response was larger in those subjects who were aware of a regular sequence. Thus, it appears that awareness of an error or context violation may not be necessary to elicit the ERN or MFN, but awareness does appear to modulate their amplitudes.

Conclusion

There are many theories of ACC function. Common to most theories is the belief that the ACC is engaged when rapid changes in behaviors are required. That is, contributions from the ACC are required when ongoing actions are inadequate or do not match up with current demands. The concept of attention for action is used to describe the cognitive processes that are engaged under situations that require control, although cognitive control may not be implemented by the ACC (see (Garavan, Ross, Murphy, Roche, & Stein, 2002; MacDonald, Cohen, Stenger, & Carter, 2000). The results from ERP studies of action monitoring reviewed in this chapter reveal that this concept is still appropriate for describing ACC functions, particularly because it emphasizes the role of action in cognition. It is likely that the ACC has evolved to regulate behaviors such that they are adaptive to sudden changes in the environment and should be important to early stages of learning. Indeed, in animal models of associative learning, the ACC is a critical component of a network responsible for rapid association between a stimulus and a required response (Gabriel, Burhans, Talk, & Scalf, 2002).

We use the construct of action regulation to describe ACC function because it emphasizes the role of the ACC in adapting behaviors to a given context. Recent evidence implicates the ACC in at least three processes involved in action regulation: (a) monitoring context violation (i.e., expectancy violation), (b) monitoring response relative to the context, and (c) evaluating the motivational or affective consequence of the expectancy violations. These basic functions support adaptive regulation of behaviors and are manifested as learning. The ACC is one structure within this circuit, with the amygdala, mediodorsal nucleus of the thalamus, and the basal ganglia making up the other key structures (Gabriel et al., 2002). The coordinating mechanism of activity between structures within this circuit remains to be elucidated, and we offer the theta rhythm as a strong candidate.

Figure Captions:

Figure 1. Scalp distribution of the ERN recorded with a 256-channel sensor array. View is top looking down with nose at the front. The ERN is observed at the top of the head (center of figure starting at channel 8 and extending caudally) as a negative deflection approximately 100 ms after erroneous button press. Also prominent in this figure is the Pe, the large positive deflection immediately after the ERN. The Pe spans an interval that approximately between 300 and 500 ms after erroneous button press.

Figure 2. The generators of the ERN as estimated by equivalent dipoles. The first dipole is located in the rostral ACC and the second dipole is located in the dorsal ACC/SMA.

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