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Temporal dynamics of error-related corrugator supercilii and zygomaticus major activity: Evidence for implicit emotion regulation following errors

David Dignath¹, Anja Berger², Iris M. Spruit⁴ & Henk van Steenbergen^{4,5},

¹ University of Freiburg, Germany

² University of Regensburg, Germany

⁴Institute of Psychology, Leiden University, The Netherlands

⁵Leiden Institute for Brain and Cognition, The Netherlands

Correspondence concerning this article should be addressed to

Henk van Steenbergen

Wassenaarseweg 52

2333 AK Leiden

The Netherlands

Phone number: +31 (0)71 527 3655

Fax number: +31 (0)71 527 3783

E-mail address: HvanSteenbergen@fsw.leidenuniv.nl

Abstract

According to feedback control models, errors are monitored and inform subsequent control adaptations. Despite these cognitive consequences, errors also have affective consequences. It has been suggested that errors elicit negative affect which might be functional for control adaptations. The present research is concerned with the temporal dynamics of error-related affect. Therefore, we ask how affective responses to errors change over time. Two experiments assessed performance in a Stroop-like task in combination with online measures of facial electromyography that index affective responses specific for muscles that are associated with the expression of negative (corrugator supercilii) and positive affect (zygomaticus major). After errors, corrugator activity first increased relative to correct trials but then decreased (below correct trials) for later time bins. Zygomaticus activity showed a concomitant inverse pattern following errors, such that an initial decrease was followed by a later increase relative to correct trials. Together, this biphasic response in both facial muscles suggests that early negative responses to errors turn into increasingly more positive ones over time. Error-triggered electromyography did marginally predict behavioral adjustments following errors at the inter-individual, but not at the intra-individual level, providing only limited evidence for a functional role of error-related affect for immediate changes in behavior. However, the dynamics of error-related electromyography points to the role of implicit emotion regulation during task performance. We propose that this process helps to maintain homeostasis of positive and negative affect which in the long term could facilitate adaptive behavior.

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Keywords: errors; post-error slowing; performance monitoring; EMG; affect; cognitive control

Highlights

▶ We assessed the temporal dynamics of error-related affect

► We used facial electromyography to index affective responses specific for muscles involved in the expression of negative (corrugator supercilii) and positive affect (zygomaticus major)

Results suggest that an initially negative valence response to errors (relative to correct trials) changed into increasingly positive valence for later time bins

EMG responses to errors did marginally predict behavioral adjustments following errors at the inter-individual but not the intra-individual level

► The dynamics of error-related affect point to a role of implicit emotion regulation to maintain adaptive homeostasis of positive and negative affect

When people make an error, corrective mechanisms are needed that prevent future lapses and optimize behavior according to one's goals. Not surprisingly, error detection and correction are central to theories of performance monitoring (for an overview, see Schuch, Dignath, Steinhauser, & Janczyk, 2018; Ullsperger, Danielmeier, & Jocham, 2014). At the neural level, the monitoring of errors and error antecedences (i.e., response conflict) has been linked to the dorsal anterior cingulate cortex (ACC) (Buzzell et al., 2017; Holroyd et al., 2004; Keil, Weisz, Paul-Jordanov, & Wienbruch, 2010). Error monitoring is also reflected in a specific event-related brain potential (ERP) signature of the human EEG. The error-related negativity (ERN) refers to a negative deflection which peaks around 80 ms after an incorrect response (Falkenstein, 1990; Gehring, Liu, Orr, & Carp, 2012) and is independent of a specific motor response (Holroyd, Dien, & Coles, 1998), favoring an interpretation of the ERN in terms of a cognitive control signal (Ullsperger et al., 2014).

Errors also have a strong affective quality and evidence suggests a crucial role of affect for error monitoring (e.g., Luu, Collins, & Tucker, 2000). For instance, the ACC codes not only for errors, but also for negative events like pain (Rainville, Duncan, Price, Carrier, & Bushnell, 1997), social stress (Eisenberger, Lieberman, & Williams, 2003) and negative affect in general (Shackman, Salomons, Slagter, Fox, Winter, & Davidson, 2011). Furthermore, the ACC is part of a larger network with close connections to 'emotional hotspots' like the amygdala and the anterior insula (Pourtois et al., 2010; Craig, 2009). In line with this affective interpretation of ACC activity, it has been suggested that the ERN reflects an affective response to errors (Pailing et al., 2002; Gehring & Willoughby, 2002). Theoretically, this is of interest since recent research suggested that conflict and error-triggered affect is not only epiphenomenal, but has a functional role as a driving force for

control adjustments (Inzlicht et al., 2015; van Steenbergen, Band, & Hommel, 2009; van Steenbergen, 2015; Dignath et al., in press). This speculation is supported by studies showing that errors (and conflict between responses more generally) lead to negative affective evaluations (Aarts, De Houwer, & Pourtois, 2012; Maier, Scarpazza, Starita, Filogamo, & Làdavas, 2016), trigger avoidance motivation (Dignath & Eder, 2015; Hochman et al., 2017) and are accompanied by physiological changes which are typical for negative, high arousing affect (Hajcak, McDonald & Simons, 2003; Spruit, Wilderjans, & van Steenbergen, 2018; Hajcak & Foti, 2008).

Of particular relevance for the present research are studies that indirectly assessed the valence of affective reactions following errors using facial electromyographic activity (EMG). EMG has been shown to index affective changes with high temporal resolution (e.g., Dimberg, Thunberg, & Elmehed, 2000). Although it might be difficult to completely dissociate negative/positive valence for EMG, because facial muscles most likely track an integrated, bipolar representation of valence (Lang et al., 1993; Larsen et al., 2003), there is consensus that the corrugator supercilii (frowning) muscle is activated by negative and deactivated by positive stimuli (Heller, Lapate, Mayer, & Davidson, 2014; Larsen, Norris, Cacioppo, 2003; Topolinski, Likowski, Weyers, & Strack, 2009). While it is less clear whether the zygomaticus major (smiling) muscle is sensitive to bipolar valence (Larson et al., 2003) it is sensitive to positive affect with increased activation for positive stimuli (Larsen et al., 2003; Williams, Leong, Collier, & Zaki, 2019; Winkielman & Cacioppo, 2001). For instance, a recent study provided evidence that zygomaticus activity during presentation of positive (but not negative) movie scenes was highly correlated with subjective ratings of participants, but also closely tracked dynamic changes of positive affect in the movies over

time (Golland, Hakim, Aloni, Schaefer, & Levit-Binnun, 2018). Interestingly, when performing a simple response-interference task (and without any affective stimuli presented), Lindström and colleagues showed stronger EMG over the corrugator supercilii muscle within 200 ms following an error relative to a correct trial (Lindström, Mattsson-Mårn, Golkar, & Olsson, 2013). This finding has been replicated by two subsequent studies using the Go/No-Go and the flanker task providing converging evidence that errors elicit negative affect as indicated by increased corrugator activity (Elkins-Brown, Saunders, He, & Inzlicht, 2017).

Emotion regulation after errors

Affective responses often have a relevant signaling function for future behavior (cf. Frijda, 1986). At the same time, the frequent experience of a specific affective state runs the risk of perseveration and escalation (cf. Rothermund, 2003). Therefore, regulatory mechanisms are warranted that counteract the current affective state and maintain adaptive homeostasis between positive and negative affect. Emotion regulation refers to a set of mechanisms that fulfill this function. Often emotion regulation has been described as an explicit control process and research has shown that explicit emotion regulation strategies modulate affective responses to conflict (Yang, Notebaert, & Pourtois, 2019; Moser, Most, & Simons, 2010) and errors (for ERN evidence, see Wang, Yang, & Wang, 2014; Hobson, Saunders, Al-Khindi, & Inzlicht, 2014; Levson & Bartholow, 2018; for ACC evidence, see Ichikawa et al., 2011)

However, emotion regulation can also proceed implicitly (Braunstein, Gross, & Ochsner, 2017; Gyurak, Gross, Etkin, 2011). For instance, attention is automatically drawn towards stimuli of opposite valence to the current affective state (Rothermund, 2003),

implicate goals modulate goal pursuit (Braunstein et al., 2017) and implicit reappraisal changes the evaluation of affect (Wang et al., 2017). Support for this comes from research showing that participants can regulate their affective responses without conscious supervision or explicit intention (Williams, Bargh, Nocera, & Gray, 2009; Schwager & Rothermund, 2014; Etkin, Egner, Peraza, Kandel, & Hirsch, 2006). Here, we suggest that similar implicit affect regulation mechanisms modulate affective responses to errors. More specifically, we hypothesize that initial negative affect following an error changes into more positive affect with increasing time (cf. Solomon & Corbit, 1974). Such an implicit emotion regulation would prevent participants from becoming frustrated and paralyzed after too many errors.

Adaptive changes in behavior following errors

In theory, monitoring of errors serves subsequent behavioral adjustments (Yeung, Botvinick, & Cohen, 2004). For instance, RTs following an error are often slower than RTs following correct trials and this post-error slowing (PES) effect is predicted by the amplitude of the ERN (Debener, et al., 2005; see also Marco-Pallarés, Camara, Münte, & Rodríguez-Fornells, 2008). However, there has been a controversy about whether PES reflects beneficial or detrimental aspects of post-error behavior. While some studies observed adaptive changes following an error (King, Korb, von Cramon, & Ullsperger, 2010; Steinhauser, Maier & Steinhauser, 2017; Steinhauser & Andersen, 2019), others reported maladaptive effects (Purcell & Kiani, 2016; Jentzsch & Dudschig, 2009; Buzzell et al., 2017). Thus, it is currently unclear how error monitoring influences subsequent behavior. Interestingly, a series of recent proposals suggested that error and conflict-induced affect is functional for behavioral adjustments (Dreisbach & Fischer, 2015; Inzlicht, et al., 2015; see

also Notebaert & Verguts, 2008). While some of these accounts focus on negative affect (triggered by conflict and errors) as a driving force for control (Botvinick, 2007; Dreisbach & Fischer, 2015), others suggest that conflict/errors trigger a transition from negative to positive affect and that later positive affect might act as a learning signal for control (Silvetti Seurinck, & Verguts, 2011; Schouppe et al., 2015; Fritz & Dreisbach, 2015).

Here, we aim to differentiate between these accounts and test whether initial negative affect or later positive affect (i.e., due to affect regulation) after errors predicts subsequent behavioral adaptation in terms of PES. Previous research (Lindström et al., 2013) found a positive correlation between negative affect (amplitude of corrugator supercilii in EMG) and PES in a single-trial analysis but did not investigate the putative role of late error-related positive affect. Furthermore, research on PES suggests that maladaptive post-error effects are more often observed with shorter time intervals following an error, while adaptive adjustments have been mostly reported for longer time intervals following an error (for an overview, see Wessel, 2018). A possible mechanism related to affect regulation could account for this temporal dynamic: While initial negative affect might be maladaptive, later positive affect could inform more adaptive processes.

The present research

The present research used a Stroop-like task. Participants had to indicate a target that was preceded by an irrelevant distractor. To induce a large number of errors, distractors and targets could match in 50% of the cases (congruent trial), while in the remaining trials distractors incorrectly afforded the wrong response (incongruent trial). To probe the dynamics of affective responses we measured EMG while participants performed the task. Previous research measured post-error EMG activity for the corrugator supercilii

only (and reported statistical tests only for time bins until 300 ms after responses, but not for later time bins). In these cases, interpretation is limited to short variations of negative affect, but it does not necessarily allow to draw an inference regarding positive affect. Therefore, the present study measured both, activity of the corrugator supercilii and the zygomaticus major.

Our hypothesis of an implicit emotion regulation following errors predicts that activity in the corrugator supercilii should be higher for erroneous compared to correct trials immediately after the response and then reverse over time. In addition, we predicted that activity in the zygomaticus major should show an increase for erroneous compared to correct trials during the later time bins.

Previous research found stronger corrugator activity for errors relative to correct responses from the response until 300 ms post-response. Since we used a different task design and also a new DV (zygomaticus major), we did not make any predictions regarding the exact time course of the affective reversal. Furthermore, previous research used task protocols with (Elkins-Brown., 2017, Exp.2) and without error feedback (Elkins-Brown., 2017, Exp.1; Lindström et al., 2013). In order to compare the possible role of feedback for affective error-responses more systematically, we provided explicit error feedback in Experiment 1 but omitted feedback in Experiment 2. Finally, to assess the functional role of affect for post-error adjustments, we correlated the EMG peak amplitudes with PES both on the inter-individual and intra-individual level.

Materials and Method

Raw data and analysis scripts can be found on the Open Science Framework (https://osf.io/8t57n/). Methods and results of both experiments are reported simultaneously.

Participants

Participants were 68 (Experiment 1: 30; Experiment 2: 38¹) right-handed students of Leiden University aged between 18 and 30 years (M = 22.7, SD = 2.6; 8 males). They signed informed consent and participated in exchange for 5€ or partial course credit. Participants were debriefed after the experiment. Eleven subjects had to be excluded from analyses due to low EMG activation indicating a loose or broken electrode (ten from Experiment 2). Eight additional subjects were excluded because they did not meet the criterion recommended by Elkins-Brown et al., 2017 of having at least 14 artifact-free error segments. Finally, two additional participants were excluded because they made more than 20% of errors². This left us with a sample size of n = 23 for Experiment 1 (7 excluded) and n = 24 (14 excluded) for Experiment 2. Given these relatively small sample sizes, only the analyses collapsed across experiments are sufficiently powered to detect earlier reported error-related effects in EMG (Elkins-Brown, et al., 2017; Lindström et al., 2013). On the other hand, our analyses on the effect of feedback (between-subject comparison of Experiment 1 versus 2) are only sensitive to relatively large effect sizes.

Behavioral task

¹ While collecting data of Experiment 2 we identified that some data was not recorded correctly due to a broken electrode. We therefore run more participants for this experiment.

² The accuracy scores of these two participants were identified to be extreme outliers (more than 3 interquartile ranges below the 25th percentile). When including these participants, EMG analyses still showed the effects in the same direction although the effect of trial type in some time bins became marginally significant. The observed inter-individual relationship between EMG and behavior also remained significant. We employed a modified version of the Stroop-like conflict task that has been developed by Schmidt and Weissman (2014; see also Dignath, Johannsen, Hommel, & Kiesel, in press). Each trial presented a blank screen (1000 ms), a distractor (133 ms), a blank screen (33 ms), a target (133 ms), another blank screen (1383 ms) during which the response was recorded, and a feedback screen (200 ms; no text shown in Experiment 2). The distracter consisted of three identical direction words ('Left', 'Right', 'Up', or 'Down'; 48-point Courier New font) stacked vertically at the center of the display. The target was a single word at the center of the display ('Left, 'Right, 'Up' or 'Down'; 77-point Courier New font). We instructed participants to press a key on a computer keyboard as quickly and as accurately as possible to identify the target. In particular, we instructed participants to press F (left middle finger), G (left index finger), J (right middle finger) or N (right index finger), respectively, to indicate that the target was 'Left, 'Right, 'Up' or 'Down'. In Experiment 1, the word 'Error' or 'Too slow' (60-point Courier New font) appeared as feedback after incorrect responses or response omissions, respectively. In Experiment 2 this feedback was not presented during the test blocks. The task was presented on a 15-inch monitor (1280 x 1024 px @ 60 Hz) via E-Prime version 2.0 software (Psychology Software Tools, Sharpsburg, PA, USA). All stimuli appeared in black on a gray background. All odd-numbered trials used a congruent or incongruent pairing of the words Left and Right and all even-numbered trials used a congruent or incongruent pairing of the words Up and Down so that there was no possibility of direct or indirect stimulus/response repetitions that could complicate the ability to interpret trial-by-trial adaptations in cognitive control.

Participants performed a single block of 24 practice trials (about 48 seconds) with feedback (both in Experiment 1 and 2) and eight blocks of 96 test trials (each block lasted about 3

minutes; feedback in Experiment 1, no feedback in Experiment 2). Each block was followed by a self-paced break.

EMG Data Acquisition and Preprocessing

The participants' skin was gently cleaned above the left corrugator supercilii (frowning muscle) and left zygomaticus major (smiling muscle) and on the forehead (ground signal) in order to prepare these areas for fEMG signal recording. Five surface Ag/AgCl electrodes filled with electrode gel were applied to these regions. The EMG signal was acquired at 2000 Hz using a BIOPAC MP150 combined with the EMG2-R BioNomadix receiver. Stimulus and response onset markers were conveyed from the E-Prime program via a parallel port and saved into an event marker channel. Data was stored using AcqKnowledge software (BIOPAC Systems Inc., Goleta, CA).

The EMG data were preprocessed with BrainVision Analyzer software (Brain Products Inc., Gilching, Germany). After filtering the data using a 20 Hz low cutoff filter, a 500 Hz high cutoff filter and a 50 Hz notch filter, we calculated the Root Mean Square (RMS) over 100-ms time bins locked to the response. Artifacts were detected using a combination of methods described earlier (Achaibou, Pourtois, Schwartz, & Vuilleumier, 2008; Lindström et al., 2013). To specify, we rejected outliers in which a) absolute activity for a given time-bin and/or b) its difference with the following time-bin exceeded 3.5 standard deviations of its mean value. Mean and standard deviation for these absolute and difference RMS values were calculated separately across time bins (for each trial separately) and across trials (for each bin separately). Artifacts were detected for each condition and subject separately in a time window from -300 ms to 1500 ms relative to the response. In order to directly compare behavioral post-error slowing to the EMG response, data were segmented separately for

error trials and correct trials, provided both types of trials were preceded and followed by a correct response. For the correct triplets, an average of 15.7% of trials (range: 8.4% - 36.1%) contained artefacts, whereas for the error triplets, an average of 22.2% of trials (range: 4.8% - 43.8%) contained artefacts. On average, this resulted in 501 (range: 316-615) artifact-free trials for the correct triplets and 36 trials (range: 14-74) for the error triplets. The data were baseline corrected by subtracting the mean activity from 200 ms to 100 ms prior to the response from the activity in the rest of the bins (Elkins-Brown et al. 2017). We then exported the data into IBM SPSS Statistics 23 and analyzed the EMG response in the time window -100 ms to 1000 ms for each 100-ms time bin and each trial. Note that we did not z-score the data because we were interested in individual peaks in the dynamic development of the EMG response over time and the shape of this waveform could be distorted by standardization methods.

Analyses

For the main behavioral analyses, we calculated post-error slowing using the optimized method described by Dutilh and colleagues (Dutilh et al., 2012). This method yields a measure that is not confounded by global fluctuations in task performance over time (e.g., due to motivation or attention). More specifically, we isolated triplets of trials in which errors were preceded and followed by a correct trial. Individual mean post-error slowing scores were then calculated as follows: PES = RT post-error minus RT pre-error. Post-error accuracy was calculated by comparing mean accuracy after errors to mean accuracy after correct trials using trials from the entire data set: PEA = Accuracy post-error minus Accuracy post-correct.

The preprocessed EMG data was submitted to a repeated-measures ANOVA with the factors Feedback (feedback in Experiment 1 versus no feedback in Experiment 2), Time (11 100-ms time bins), and Trial Type (Error versus Correct).

To test the relationship between facial EMG (mean baseline-corrected EMG response across a given interval) and post-error slowing we performed analyses at the intra-individual and inter-individual level. Following the method recommended by Lorch and Myers (1990), the intra-individual analyses used regression analysis on individual error trials, for each subject separately. For each significant interval (see Results), this regression used the (baseline-corrected) mean EMG response across the time bins per trial to predict post-error RT (expressed as a difference score relative to the RT of the corresponding pre-error trial). For each significant interval, the regression coefficients were then submitted to ANOVAs with the factor Feedback to determine whether regression slopes reliably differed from zero across subjects (Intercept) and between Experiment 1 and 2 (factor Feedback). For the inter-individual scores of post-error slowing and average EMG activity (error minus correct) for each significant interval (see Results). If significant, this was followed-up by a linear regression that included the factor Feedback and the interaction between Feedback and the predictor variable.

As per reviewer request, we repeated the analyses above in a supplementary analysis on two subsets of the data. In the first subset, data were segmented separately for error trials and correct trials, provided that both types of trials were incongruent and that they were preceded and followed by a correct response. The second subset used the same selection criteria and the additional criterion that participants during incongruent errors selected the key associated with the distractor of that trial (distractor errors). Although the existing fEMG studies (Elkins-Brown., 2017; Lindström et al., 2013) have not analyzed their data using these strict criteria, they allow to dissociate the effects of congruency from errors (subset 1) and to test whether distractor errors show more distinct fEMG responses (subset 2), as has been suggested in a recent study on error types and pupil dilation (Maier, Ernst, & Steinhauser, 2019). The results of these analyses are reported in the supplement.

For all analyses, Greenhouse-Geisser correction was applied when assumptions of sphericity were violated. In these cases, we reported corrected p-values and uncorrected degrees of freedom. All significant effects (p < 0.05) are reported.

Results

Behavioral analyses

The overall behavioral results confirmed that in comparison to congruent trials, incongruent trials led to slower RTs (447 vs 365 ms), F(1,45)=569.84, p<.001, MSE=278.4, eta²p=.927. Compared to congruent trials, incongruent trials also lowered accuracy (89.6% vs 95%), F(1,45)=85.33, p<.001, MSE=0.001, eta²p=.655. Feedback did not influence RT and accuracy (*p*s < .130). Descriptive statistics of the behavioral data using the triplet approach are presented in Table 1. For the correct triplets, an average of 594 trials (range: 391-700) was obtained, whereas, for the error triplets, an average of 47 trials (range:16-99) was obtained. The task produced the expected post-error slowing effect, such that RTs after error trials were slower than before error trials, F(1,45)=33.55, p<.001, MSE=2741.7, eta²p=.427. In addition, accuracy after errors was also numerically higher than after correct trials, but this effect was not statistically significant, F(1,45)=1.25, p=.270, MSE=0.0,

eta²p=.027. Feedback did not have an effect on post-error slowing and post-error accuracy (ps > .175).

Facial EMG analyses

Mean corrugator and zygomaticus EMG activity over time are presented in Figure 1. ANOVAs on the corrugator muscle revealed effects of Time, F(10,450)=6.41, p<.001, MSE=0.3, eta²p=.125, Trial Type, F(1,45)=3.28, p=.077, MSE=3.0, eta²p=.068, and their interaction, F(10,450)=10.28, p<.001, MSE=0.2, eta²p=.186. Feedback did not have an effect (all ps > 0.126). Likewise, ANOVAs on the zygomaticus muscle revealed effects of Time, F(10,450)=3.88, p=.044, MSE=0.7, eta²p=.079, Trial Type, F(1,45)=6.84, p=.012, MSE=4.7, eta²p=.132, and their interaction, F(10,450)=4.16, p=.035, MSE=0.6, eta²p=.085. Again Feedback did not have an effect (all ps > .134). Post-hoc comparisons between error and correct trials revealed an initial significant error-related increase in corrugator activity (0-200 ms after response) accompanied by a decrease in zygomaticus activity (100-200 ms after response). Importantly, this pattern was followed by a reversal of activity later on in which error-related corrugator activity decreased and zygomaticus activity increased (300-1000 ms after response).

Relationship between facial EMG and post-error slowing

To assess the intra-individual relationship between the facial EMG response to errors and post-error slowing we ran trial-by-trial regression analyses. We extracted the mean EMG response using the time intervals that showed significant effects in the analyses described above (corrugator: 0-200 ms and 300-1000 ms after response; zygomaticus: 100-200 ms and 300-1000 ms after response). None of the extracted EMG responses were found to be

predictive of intra-individual variation in post-error slowing (ps > .357) and Feedback did not moderate the effect (ps > .607).

For the inter-individual relationship between facial EMG and post-error slowing, we used the time intervals for the two muscles as indicated above (see Table 2). Analyses revealed only a significant effect for the late (300-1000 ms) error-related decrease in corrugator response. As illustrated in Figure 2, error-related decrease in the corrugator muscle predicted increased post-error slowing (r = -.289, p = .049; Spearman's rho = -.320, p = .029). A linear regression on Post-Error slowing predicted by the factors EMG response, Feedback and the interaction between Feedback and EMG response revealed similar effects of EMG response (t = -1.99, p = .052) and did not reveal significant main or moderating effects of Feedback (ps > .765). Inspection of the normal predicted probability plot and the scatter plot of the relationship between predicted values and residuals revealed that the assumption of normal distribution of the error variance and the assumption of homoscedasticity were met.

As per reviewer request, we also performed correlation analyses on the traditional measures of PES (correct RT after error versus correct trial) as the optimized method reported above could overestimate PES, due to the effect of pre-error speedup (Dudschig & Jentzsch, 2009) and a different distribution of pre-error versus post-error congruency. Correlations are reported in Table 2, right column. Although both measures of PES correlated substantially (r = .835), the only significant Pearson correlation observed using the traditional method was a positive correlation between the late zygomaticus response and PES (r = .343, p = .018) which was no longer significant when using a robust regression method (Spearman's rho = .267, p = .070).

Discussion

The present study tested the temporal dynamics of affective responses to errors. Analyses on error-related EMG activity replicated previous findings of an initial increase in the corrugator supercilii within 200 ms after response onset, consistent with an initial negative affective response (Elkins-Brown et al., 2017; Lindström et al., 2013). Going beyond previous research, we also demonstrated that this initial increase in corrugator activity was followed by a subsequent reversal, indicating that negative affect is reduced and/or positive affect is subsequently increased in comparison to correct trials. This observation was corroborated by the analysis of the zygomaticus major showing a concomitant inverse response. Together, these results suggest that affective responses to errors change dynamically which could reflect a regulation of affective responses following errors in order to maintain homeostasis between negative and positive affect.

One limitation of the EMG measures employed is that it is challenging to determine the absolute intensity of the involved positive and negative affective states separately (Cacioppo, & Berntson, 1994). Corrugator activity has been shown to index an integrated bipolar representation of valence, so activity in corrugator could reflect increased negative affect, decreased positive affect, or a combination of both. On the other hand, zygomaticus recordings are sensitive to voluntary facial displays and cross-talk from adjacent muscles. In addition, zygomaticus activity has traditionally been linked to unipolar positive affect, while not being sensitive to negative affect (Larsen et al., 2003; cf. Golland et al., 2018; Heller et al., 2014). The late increase in zygomaticus together with the late decrease in corrugator rule out the possibility that the observed zygomaticus increase simply reflects a grimace (Bradley, Codispoti, Cuthbert, & Lang, 2001; Bradley & Lang,

2007), and instead is fully consistent with the assumed implicit emotion regulation process, such that the initial negative affective response to errors is compensated by subsequent positive affect (see also Burton, 2011). On the other hand, if zygomaticus activity reflects unipolar positive affect (cf. Larsen et al., 2003), the observed initial decrease in zygomaticus to errors might reflect decreased positive affect, but not necessarily increased negative affect. However, as has been argued by Larsen et al. (2003), the absence of zygomaticus decrease in response to negative affect could be due to low baseline values in their study, making it difficult to draw a strong conclusion about the specific involvement of positive and negative affective systems (Cacioppo & Berntson, 1994). In the remainder of this discussion we will, therefore, refer to positive and negative valence as the extremes of one bipolar valence dimension (Russell, 1980), while remaining agnostic about the contribution of qualitatively different affective states it might underlie.

Implicit affect regulation following controlled behavior

The affect-regulation interpretation proposed here fits well with research on the affective consequences of response conflict (without involving performance errors). For example, behavioral studies using affective priming paradigms have shown that passively viewing a conflicting stimulus (e.g. Stroop) leads to faster detection of negative relative to positive stimuli (Dreisbach & Fischer, 2012), while actively and correctly responding to conflict produced the reversed pattern with faster detection of positive relative to negative stimuli after conflict (Schouppe et al., 2015; Ivanchei et al., 2018). Similarly, while passive viewing of conflict stimuli for short durations led to more negative evaluations, increased viewing time led to more positive evaluations, suggesting that initial negative valence is counteracted by emotion regulation with sufficient time (Fritz & Dreisbach, 2015; see also

Pan, Shi, Lu, Wu, Xue, & Li, 2016, Exp. 2). The present research extends this line of research, by showing that similar affective dynamics can be observed for errors which have been theorized as a special case of conflict (cf. Yeung, Botvinick, & Cohen, 2004). However, we have to acknowledge that additional analysis which considered also the level of conflict-induced by stimuli (in addition to errors) provided only partial support for this claim (see supplement). Although results were descriptively similar to the main analysis reported above, corrugator EMG for early time intervals (i.e., initial negative valence) failed to reach the level of significance, which possibly could be due to reduced power. In any case, it would be informative for future research to provide a more fine-grained analysis of EMG responses to both conflict and errors (e.g., by differentiating between different types of errors for conflict and non-conflict trials, see Maier, Ernst, & Steinhauser, 2019).

In addition, future studies using other physiological measures might help to dissociate the corrugator response to negative valence from effects related to both physical and cognitive effort, which also have been shown to involve corrugator activity (Van Boxtel & Jessurun, 1993; Cacioppo, Petty, & Morris, 1985; de Morree & Marcora, 2010). Because effort is typically aversive (Kool, McGuire, Rosen, & Botvinick, 2010), it might be hard to separate their influences. However, effort does not always co-vary with negative valence (Inzlicht, Shenhav, & Olivola, 2018), so future studies might test whether EMG and more effort-specific measures such as task-evoked changes in the cardiac RZ-interval (Kuipers, Richter, Scheepers, Immink, Sjak-Shie, & van Steenbergen, 2017; Spruit, Wilderjans, & van Steenbergen, 2018) provide dissociable indices of these processes.

What are the mechanisms underlying such an implicit affect regulation following errors? Research on error commission showed that errors often lead to a fast and automatic correction (Rabbitt, 1966; Fiehler, Ullsperger, & von Cramon, 2005). Possibly, later positive valence could be due to the successful correction and goal competition. Future studies could directly test this hypothesis by measuring error correction and compare the time course of error correction and EEG components that track the evaluation of correction (Fiehler et al., 2005) with the time course of affective dynamics following errors and error correction. Alternatively, it has been suggested that errors trigger a motivational tendency to avoid the source of error (Dignath & Eder, 2015) and late positive valence could result from successful error avoidance. More specifically, Hochman and colleagues showed an acceleration of key release force after an error, indicating a stronger tendency to avoid the source of negative affect (Hochman et al., 2017). Again, this hypothesis could be tested by relating key release force with EMG activity during error trials. Finally, affect regulation could be related to disengagement from the error-associated, unsuccessful task (cf. Dignath, Kiesel, & Eder, 2015; Wessel, 2018) and an subsequent shift towards unrelated thoughts (e.g., mind wandering) triggered by negative affect (Smallwood, Fritzgerald, Miles, & Phillips, 2009; see Wang et al., 2017 for a similar idea related to reappraisal). Clearly, more research is needed to get a better understanding of affect regulation during task performance and errors.

Relation between post-error affect and behavioral adjustments

We found limited evidence for a functional role of the affective response to errors for immediate adjustments in behavior. To specify, the only correlation observed was a marginally significant relationship between the late corrugator decrease to errors and increased post-error slowing. This finding could suggest that improved downregulation of negative valence could make people more cautious after an error. However, this finding did not survive correction for multiple comparisons and was not observed for the traditional measure of post-error slowing, thus requiring replication in future studies.

On the other hand, the present data did not show a correlation between affective responses to errors and PES at the intra-individual level. This is surprising because it has been suggested that these analyses are more sensitive to correlations between physiological measures and behavioral adaptation than analyses at the inter-individual level (see also Cavanagh & Shackman, 2015). Our finding also contrasts with recent work that did show a predictive role of other physiological measures including pupil dilation (van Steenbergen & Band, 2013) and cardiac effort (Spruit, Wilderjans, & van Steenbergen, 2018; cf. Kuipers, Richter, Scheepers, Immink, Sjak-Shie, & van Steenbergen, 2017) that do predict post-error adjustments at the intra-individual level. One obvious possibility is that it is more difficult to detect subtle relationships between variations in facial muscle activity and behavior because surface EMG measures are known to be noisier than other physiological signals (Tassinary, Cacioppo, & Vanman, 2007).

What is cognitive control without affect?

Not long ago, cognitive and affective processes have been cast as opposing forces on behavior (e.g. Metcalfe & Mischel, 1999; Muraven & Baumeister, 2000). However, more recent research emphasized the functional interaction of both (Pessoa, 2008). A particular strong version of such a close coupling between affect and control assumes a bidirectional role of affect and control: Affect follows from control demanding situations like conflict and errors; at the same time control follows from (negative) affect (Inzlicht et al., 2015; Dreisbach & Fischer, 2015; van Steenbergen, 2015). Our data clearly supports the first claim, showing that errors elicit an affective response. What about the second claim? An

attractive idea has been that affect (triggered by conflict or errors) is used as a signal to inform immediate behavioral adaptations (Botvinick, 2007). For instance, it has been suggested that changes in affect from one trial to the next modulate control adaptation following conflict (cf. van Steenbergen et al., 2009; but see Dignath, Janczyk, & Eder, 2017). Our data could not provide direct support for this claim concerning post-error control adaptations. This could implicate that error-triggered affect is only an epiphenomenon and not functional for control. However, the affective dynamics that we observed point towards an alternative interpretation in terms of implicit affect regulation following errors. Although affect regulation showed only limited immediate behavioral consequences, it might influence cognitive control more indirectly: Arguably, successful copying with error-related negative affect increases motivation and willingness to engage in demanding control operations in the future (Inzlicht & Schmeichel, 2012; Shenhav, Botvinick, & Cohen, 2013). In contrast, failed regulation of error-related affect might lead to a disengagement from the task because participants become frustrated (Aspinwall & Richter, 1999; Magno, Foxe, Molholm, Robertson, & Garavan, 2006; van Steenbergen, Band, & Hommel, 2015). It might be this regulation mechanism that is also impaired in mood disorders such as depression, that have been characterized by catastrophic responses to errors (Beats Sahakian, & Levy, 1996), which might be under opioid regulation (Beard et al., 2015; van Steenbergen, Eikemo, & Leknes, in press; van Steenbergen, Weissman, Stein, Malcolm-Smith, & van Honk, 2017). This perspective is in line with the expected value of control theory which describes cognitive control in terms of reward-based decision making (Shenhav et al., 2013). The decision to engage control is expressed as a utility function that weighs costs of control exertion against the expected value of associated outcomes. Possibly, positive affect that results from successfully coping with errors and the error-related initial negative affect might change the utility function towards control engagement and thereby increase persistence.

Summary

This research assessed how affective responses following errors change over time. Using physiological measures of facial muscles that track affective response with high temporal resolution and are associated with negative and positive valence, we showed that errors result in an initial negative valence that changes later into increasingly positive valence. Affective responses to errors did marginally predict behavioral adjustments following errors at the inter-individual but not the intra-individual level, providing limited evidence for an adaptive function of error-related affect for immediate changes in behavior. Our findings suggest that error-related change in affect involves implicit emotion regulation during task performance.

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Measure	Experiment 1 (N = 23) with feedback			Experiment 2 (N = 24) no feedback		
	Mean	SE	95% CI	Mean	SE	95% CI
RT pre-error (ms)	399	18	[362, 437]	365	11	[342, 389]
RT post-error (ms)	445	17	[409, 480]	409	16	[375, 442]
Post Error Slowing (ms)	45	12	[20, 71]	43	9	[24, 62]
Accuracy post-correct (%)	91.8	1.8	[95.6, 88.0]	94.8	0.8	[96.5, 93.1]
Accuracy post-error (%)	92.1	1.0	[94.2, 90.0]	92.8	0.6	[94.1, 91.5]
Post Error Accuracy (%)	-0.2	1.5	[-3.3, 2.9]	2.1	0.8	[0.4, 3.8]
Accuracy overall (%)	92.0	1.0	[94.2, 89.9]	93.0	0.6	[94.3, 91.7]

Table 1. Behavioral results

Table 2. Inter-individual relationship between facial EMG and post-error slowing

Measure	Opti	mized PES	Traditional PES		
	Pearson's r	Spearman's rho	Pearson's r	Spearman's rho	
Early Corrugator response (0-200 ms)	161	120	016	.010	
Late Corrugator response (300-1000 ms)	289*	320*	097	138	
Early Zygomaticus response (100-200 ms)	.146	.251	.196	.357*	
Late Zygomaticus response (300-1000 ms)	.246	.248	.343*	.267	

(pooled across experiments, N = 47)

Note: * p < .05



Figures

FIGURE 1

time 0) for the corrugator and zygomaticus muscle, separately for Experiment 1 (feedback) and Experiment 2 (no feedback) (A) and pooled across experiments (B). Data show means ±1 standard error of the paired difference scores of error minus correct. Asterisk indicates significant differences of trial type per bin: p < .1, p < .05, ** p < .01.

FIGURE 2



Figure 2. Late corrugator EMG decrease (error minus correct; 300-1000 ms after response) predicts increased post-error slowing. The relationship is plotted separately for each experiment (A) and pooled across experiments (B). Data show fitted regression line with 95% confidence interval.

Supplementary Analyses

As per reviewer request, we repeated the analyses described in the main text on two subsets of the data.

Results facial EMG analyses: incongruent error versus incongruent correct trials

Data were segmented separately for error trials and correct trials, provided that both types of trials were incongruent and that they were preceded and followed by a correct response. Participants were only included if at least 14 artefact-free EMG trials per condition were retained. To partially compensate for the loss in statistical power, we included the two participants with high error rates. Data of 41 participants were included for this analysis.

Mean corrugator and zygomaticus EMG activity over time are presented in Figure S1. ANOVAs on the corrugator muscle revealed effects of Time, F(10,390)=4.34, p=.004, MSE=0.7, eta²p=.100, a trend effect of Trial Type, F(1,39)=3.78, p=.059, MSE=3.3, eta²p=.088, and most importantly a significant interaction, F(10,390)=7.84, p<.001, MSE=0.7, eta²p=.167. Feedback did not have an effect (all *p*s > 0.116). Likewise, ANOVAs on the zygomaticus muscle revealed effects of Time, F(10,390)=7.74, p<.001, MSE=0.3, eta²p=.166, a trend effect of Trial Type, F(1,39)=4.09, p=.050, MSE=0.7, eta²p=.095, and most importantly a significant interaction, F(10,390)=5.29, p=.004, MSE=0.2, eta²p=.119. Again Feedback did not have an effect (all *p*s > .212). The post-hoc comparisons indicated in Figure S1 revealed only a significant effect in the later time intervals in corrugator and zygomaticus, but not in the early time intervals, possible due to a lack of power.

Results facial EMG analyses: distractor errors versus incongruent correct trials

Data were segmented separately for error trials and correct trials, provided that both types of trials were incongruent and that they were preceded and followed by a correct response. Incongruent errors were only included when participants selected the key associated with the distractor of that trial (distractor errors, see Maier, Ernst, & Steinhauser, 2019). Participants were only included if at least 14 artefact-free EMG trials per condition were retained. To partially compensate for the loss in statistical power, we included the two participants with high error rates. Data of 38 participants were included for this analysis.

Mean corrugator and zygomaticus EMG activity over time are presented in Figure S2. ANOVAs on the corrugator muscle revealed effects of Time, F(10,360)=4.27, p=.005, MSE=0.7, eta²p=.106, an effect of Trial Type, F(1,36)=7.47, p=.010, MSE=2.9, eta²p=.172, and most importantly a significant interaction, F(10,360)=7.52, p<.001, MSE=0.7, eta²p=.173. Feedback did not have an effect (all ps > 0.180). ANOVAs on the zygomaticus muscle revealed effects of Time, F(10,360)=9.28, p<.001, MSE=0.3, eta²p=.205, no effect of Trial Type, F(1,36)=1.40, p=.245, MSE=0.9, eta²p=.037, and most importantly a significant interaction, F(10,360)=6.96, p=.001, MSE=0.2, eta²p=.162. Again Feedback did not have an effect (all ps > .186). The post-hoc comparisons indicated in Figure S1 revealed only a significant effect in the later time intervals in corrugator and to a lesser extent also in zygomaticus, but not in the early time intervals, possible due to a lack of power.

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FIGURE S1



Figure S1. EMG response locked to incongruent error and incongruent correct responses (vertical line indicates time 0) for the corrugator and zygomaticus muscle, separately for Experiment 1 (feedback) and Experiment 2 (no feedback) (A) and pooled across experiments (B). Data show means ±1 standard error of the paired difference scores of error minus correct. Asterisk indicates significant differences of trial type per bin: p < .1, * p < .05, ** p < .01.

FIGURE S2



Figure S2. EMG response locked to incongruent distracter error and incongruent correct responses (vertical line indicates time 0) for the corrugator and zygomaticus muscle, separately for Experiment 1 (feedback) and Experiment 2 (no feedback) (A) and pooled across experiments (B). Data show means ±1 standard error of the paired difference scores of error minus correct. Asterisk indicates significant differences of trial type per bin: $\dagger p < .1$, * p < .05, ** p < .01.