Post-error speeding after threat-detection failure

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Abstract

Cognitive control enables individuals to rapidly adapt to changing task demands. To investigate error-driven adjustments in cognitive control, we considered performance changes in post-error trials, when participants performed a visual search task requiring to detect angry, happy, or neutral facial expressions in crowds of faces. We hypothesized that the failure to detect a potential threat (angry face) would prompt a different post-error adjustment than the failure to detect a non-threatening target (happy or neutral face). Indeed, in three sets of experiments we found evidence of post-error speeding, in the first case, and of post-error slowing, in the second. Previous results indicate that a threatening stimulus can improve the efficiency of visual search. The results of the present study show that a similar effect can also be observed when participants fail to detect a threat. The impact of threat-detection failure on cognitive control, as revealed by the present study, suggests that post-error adjustments should be understood as the product of domain-specific mechanisms that are strongly influenced by affective information, rather than as the effect of a general-purpose error-monitoring system.

Keywords: Cognitive control, Post-error slowing, Faces, Emotion, Threat, Visual search, Anger-superiority effect

1. Introduction

A fundamental aspect of cognitive control is the ability to monitor the outcomes of our actions in order to correct our errors. A common finding in choice-reaction time tasks is that response latencies tend to increase on trials following errors. This post-error adjustment is generally referred to as post-error slowing (PES; Rabbitt, 1966; Laming, 1979).

PES is a robust phenomenon that has been observed in a great variety of different tasks, including Stroop (Gehring & Fencsik, 2001), flanker (Cavanagh, Cohen, & Allen, 2009; van Veen & Carter, 2002), simple forced-choice and go/no-go (Jones, Cho, Nystrom, Cohen, & Braver, 2002), Simon (Fan, Flombaum, McCandliss, Thomas, & Posner, 2003), and categorization (Jentzsch & Dudschig, 2009) tasks. Despite the large number of studies, however, the cognitive and neural mechanisms involved in PES are still debated. As pointed out by Gehring et al. (2012), one problem in the study of PES is identifying the function of slowing.

Functional accounts, such as the conflict monitoring theory (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Cohen, & Carter, 2004), the inhibition account (Marco-Pallares et al., 2008; Ridderinkhof, 2002), and the reinforcement learning theory (Holroyd & Coles, 2002), share the common idea that PES

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reflects a strategic increase in control aimed at reducing the probability of an error (for a discussion, see Houtman and Notebaert, 2013). Because the literature indicates that post-error behavioral adjustments correspond to an increase in the reaction times (RTs) and to an increase, or (more often) to a non-decrease, in accuracy, then in general error reactivity is understood as an increase in response caution.

However, PES might not necessarily be the expression of an adaptive mechanism aimed at improving performance. Instead, PES might occur because error processing has a detrimental effect on subsequent information processing. In fact, non-functional accounts of PES predict a decrement in performance after an error (longer RTs and a decrease in accuracy), because error monitoring subtracts cognitive resources from a capacity-limited central information processor (bottleneck error-monitoring theory; Dudschig & Jentzsch, 2009; Jentzsch & Dudschig, 2009) or because errors, being infrequent and salient events, divert attention toward them (orienting account; Notebaert et al., 2009). Also the non-functional accounts of PES, therefore, predict a decrement in performance after an error.

In their review, Danielmeier and Ullsperger (2011) point out that there is evidence for both functional and non-functional accounts of error reactivity and that these accounts are not mutually exclusive. The available evidence thus indicates that error reactivity comprises different components and it is not always an adaptive response.

In the present study we will focus on the adaptive component of error reactivity. According to the functional accounts of error reactivity, the prolonged reaction times subsequent to errors reflect an increase in response caution. But do reaction times always slow down after an (infrequent) error[2]?

To determine whether error reactivity leads necessarily to an increase in response caution, we used an experimental design that differs in three main respects from the vast majority of studies on error reactivity. Almost all studies on error reactivity make use of neutral stimuli void of affective components, employ experimental designs based on speeded RT tasks that usually produce sub-second response times, and use short response-stimulus intervals (RSI). In order to emphasize the strategic planning that may occurs in natural settings after an error (which may differ from the responses elicited by the aforementioned methods), in our experiments we used affective stimuli that have a motivational significance, a visual search task that requires relatively long response times (*e.g.*, the search for one angry face in a crowd of happy faces), and longer RSIs.

In the present visual-search experiments, the presence/absence of a threat in the target item was the key factor that was manipulated in the attempt to activate adaptively different post-error adjustments. In a visual search task in which the target is a valenced face (angry, happy, or neutral), an error corresponds to the failure to detect either a nonthreatening (happy or neutral) or a threatening (angry) target. In general, these two errors have very different potential consequences for the individual.

The failure to detect a nonthreatening target mimics a situation that is void of

[2]It has been shown that the sign of the post-error adjustments (slowing vs. speeding) depend on the frequency of errors in the experiment. When the proportion of errors is low, post-error slowing is observed; when the proportion of errors is high, post-error speeding is observed. This result has been explained by the orienting account by arguing that frequent errors are not surprising and, therefore, they do not orient attention toward them and away from the task (Desmet, Fias, Hartstra, & Brass, 2011; Notebaert et al., 2009).

aversive consequences for the individual. In functional terms, this kind of error is similar to the errors that are studied in the literature on PES. For this kind of errors, increasing post-error response caution to improve future performance is an adaptive behavioral adjustment. In fact, there is no cost if the individual fails to react quickly.

A very different situation arises if the target represents a potential threat (*e.g.*, an angry face), given that the failure to detect a threat is a serious risk to an individual's safety. From an evolutionary perspective, individuals must rapidly identify the source of a threat and act effectively to avoid potential danger (Mathews, 1990). Several lines of evidence suggest that threatening events generate defensive reactions which mobilize the defensive motivational system of the organism (Bradley 2000; Cuthbert et al. 2000; Lang, Bradley, & Cuthbert, 1997; Weinberg, Riesel, & Hajcak, 2012). A defensive reaction typically increases attention and readiness for action in order to cope with the threat.

The fact that failing to detect a threatening or a nonthreatening target produces different consequences for the individual has led us to hypothesize that error reactivity may also take on different forms in the two cases. We propose that the failure to detect a threatening target in a visual search task may prompt a defensive reaction also in the laboratory, thus producing a transient enhancement in visual search efficiency in the following trial (*i.e.*, a RTs decrease in the post-error trial without an accuracy cost), compared to the search efficiency after a correct trial, or after failing to detect a non-threatening target. As a consequence, we hypothesize that the failure to detect a threatening target may lead to a reduction of PES, or even to post-error speeding. This result would be important for the theories on error reactivity because it would question the idea that error reactivity necessarily leads to an increase in response caution.

1.1. Threat-relevant stimuli: increased alertness and processing efficiency

Ethologically oriented psychologists have advanced the notion of a "defense system" concerned with the detection and amelioration of both physical and social potential threats to security (*e.g.*, Marks & Nesse, 1994; Masterson & Crawford, 1982; Trower, Gilbert, & Sherling, 1990). Indeed, several lines of evidence suggest that stimuli with threat significance are processed in a privileged manner (Maior et al., 2012). (1) Angry faces are more effective as conditioned stimuli for aversive unconditioned stimuli than happy and neutral faces. Moreover, responses to angry conditioned faces are more resistant against extinction than happy or neutral conditioned faces (Öhman & Dimberg, 1978). (2) Stimuli such as angry faces, spiders, or aversive pictures induce behavioral effects even when subjects are unaware of them (Gelder, Morris, & Dolan, 2005; Morris, Öhman, & Dolan, 1998, 1999). (3) In visual-search tasks, the search for threatening targets requires smaller reaction times (RTs) than the search for nonthreatening targets (Öhman, Flykt, & Esteves, 2001; Flykt, 2005). (4) The presentation of a threat-relevant stimulus can facilitate early vision. For example, contrast sensitivity improves after the presentation of a threatening face, but not after the presentation of a neutral face or an upside-down threatening face (Phelps, Ling, & Carrasco, 2006).

It has been argued that visible and abstract potential threats elicit different responses (Eilam, Izhar, & Mort, 2011). The defensive behavior elicited by a perceptible threat takes on three forms: freezing (to hide from the enemy's attention), fleeing (to increase the distance from the danger) or fighting (to dissuade the enemy). The defense response elicited without an identifiable triggering threat, instead, manifests itself in the form of as an increased vigilance with the purpose of gathering information about the potential threat, in order to produce an optimal response.

We hypothesize that the awareness of having failed to detect the presence of a threat may act as an internal cue (*i.e.*, a not identifiable triggering threat) that elicits a defensive reaction. This defensive reaction may make the individual more vigilant and alert, thus facilitating response preparation and/or decision making in order to select an appropriate action (Keil et al., 2010; Lang, Bradley, & Cuthbert, 1997). For example, in a recent study by Fernandes et al. (2013), the activation of defensive response strategies was triggered by emotional stimuli depicting a threat directed either toward or away from the observer (*i.e.*, by pictures of a man pointing a gun toward the observer or away from him). Participants were instructed to judge the orientation of two peripheral bars, while ignoring the task-irrelevant central image (a threatening image or a neutral image). Fernandes et al. found faster RTs in the bar orientation discrimination task when the threat was directed toward the observer than in the control condition, with no decrease in accuracy. Conversely, when the threat was directed away from observer, RTs were slower than in the control condition.

In summary, several lines of evidence indicate that the presence of a threat, because of its social and biological relevance, can induce specific attention, learning, and visual advantages. The signals of an imminent threat can be external or internal. The purpose of the present study is to determine whether the awareness of the failure to detect a threat, because of its risks for the individual, and because of the necessity of locate the source of a potentially persisting danger, can induce a defensive behavior. According to the defense cascade model (Fanselow, 1994; Lang, Bradley, & Cuthbert, 1997), the defensive behavior is characterized by cognitive changes "that are consistent with threat-unspecific hypervigilance to all stimuli in the environment" (Weymar, Keil, & Hamm, 2013).

We therefore expect that, for the failure to detect a threatening target, error reactivity may take on the opposite form than PES, that is, it may manifest itself as post-error speeding.

1.2. The anger superiority effect

The use of a visual search task requiring to detect a discrepant face in crowds of faces is particularly suited to study the modulation of cognitive control after an error. With such a task, in fact, the failure to detect a threatening or a nonthreatening target calls for opposite post-error adjustments.

A rich literature has tried to understand whether, in a visual-search task, there is a processing advantage for angry as opposed to happy faces. The typical finding is that angry faces are detected more efficiently than happy faces among a crowd of distractors (Hansen & Hansen, 1988; Öhman, Lundqvist, & Esteves, 2001). The most recent literature, however, has challenged this "anger superiority effect" (ASE) by pointing out that it strongly depends on the presence of low-level visual features, which naturally co-occur with the expression of anger (Becker, Anderson, Mortensen, Neufeld, & Neel, 2011). A recent study, for example, has concluded that "prior reports of anger or happiness superiority effects in visual search are likely to reflect on low-level visual features associated with the stimulus materials used, rather than on emotion" (Savage, Lipp, Craig, Horstmann, & Becker, 2013, p. 758).

Another important consideration is that most studies on the ASE have used static displays whereas, in natural settings, emotional expression can only be transmitted through motions resulting from face deformations (Arsalidou, Morris, & Taylor, 2011; Pilz, Vuong, Bülthoff, & Thornton, 2011). In a previous study, which investigated the ASE under both static and dynamic conditions, we indeed found evidence for an ASE when using dynamic displays of facial expressions, but not when the emotions were expressed by static face images (Ceccarini & Caudek, 2013).

If the dynamics of facial emotions facilitate the ASE, then it is important to use dynamic stimuli to study the control adjustments that take place after participants fail to detect a threatening target. For this reason, in the present study the post-error adjustments were investigated using dynamic faces.

2. Experiment 1

In Experiment 1, participants completed a visual search task for angry, happy, or neutral expressions in crowds of discrepant faces (angry, happy, or neutral). Each face image simulated the rigid three-dimensional (3D) rotation from the view of the individual's profile to the full frontal view of the face (Figure 1A). A rigid rotation about the *y*-axis does not produce ecologically valid dynamic expressions. Such a display, in fact, has the properties of a static image, while also providing dynamic cues (although unrelated to the unfolding of facial expressions). The stimuli of Experiment 1, therefore, are not optimal for observing the ASE and the expected post-error adjustments. If we find evidence that, also in these conditions, post-error adjustments are modulated by the presence/absence of a threat, that would strengthen our argument.

——— Please insert Figure 1 about here ———

2.1. Method

2.1.1. Participants

A total of 17 undergraduate students from the University of Florence participated in the experiment. All participants were naïve to the purpose of the study and had normal or corrected-to-normal vision. Participation was voluntary.

2.1.2. Apparatus

Stimulus presentation and data acquisition were conducted using a PC-compatible computer (Dell Precision PWS690, Intel Xeon X5355 at 2.66 Ghz, NVIDIA Quadro FX 4600) connected to a 19-inch video monitor (Philips Brilliance 109P4) operating at 75 Hz. A custom Visual C++ program was used for stimulus presentation and response recording.

2.1.3. Stimuli

Twelve caucasian facial identities (six males and six females) were generated with the FaceGen software. For each facial identity, we create 3 three-dimensional (3D) models, each with a different facial expression (angry, happy, and neutral). These 36 facial models were then processed with the 3dStudio Max software in order to equate illumination intensity and illuminant direction in each face. For each 3D face model, we generated 30 images representing the face orientations after successive 3° rotations about the *y*-axis. Such images were then transformed into video sequences (30 fps) with the Flash CS5 software. The duration of each video sequence was 1000 ms.

Each stimulus display presented 12 dynamic faces rotating in synchrony from the view of the individual's left profile to the full frontal view of the face. The positions of the face images within the stimulus displays were determined randomly on each trial, with the constraint that the minimum distance between the (200 $\times$ 200 pixels) regions containing each face was at least 10 pixels (Figure 1D).

Visual feature confounds. Becker et al. (2011) provide a number of methodological recommendations for studying the ASE. They suggest to vary set sizes to compare search efficiency between stimulus types, to keep constant the content of the distractor crowds across different targets types, to require participants to consciously search for a particular kind of expression, and to use dyshomogenous distractors. In particular, they stress the necessity to rule out the possibility that low-level visual features could account for the effect (see also Horstmann & Bauland, 2006; Pinkham, Griffin, Baron, Sasson, & Gur, 2010; Purcell, Stewart, & Skov, 1996; Purcell & Stewart, 2010; Savage et al., 2013). To address this latter issue, we measured the bottom-up visual salience of the full frontal views of the face images by means of Itti and Koch's model of visual attention (Itti & Koch, 2000, 2001; Koch & Ullman, 1985). The model analyzes natural images by extracting low-level features such as intensity, color, and orientation at a range of spatial scales. The maps generated for each image feature are then combined to create a saliency map, with locations of higher salience being more likely to be fixated (Parkhurst, Law, & Niebur, 2002).

By using the last frame of the 36 video sequences (full frontal view of the twelve facial identities, each with an angry, happy, or neutral expression), we generated 8640 images comprising one target face and eleven distractors. Each image was divided into an evenly spaced 4 $\times$ 3 grid, with each cell covering 320 $\times$ 256 pixels. Each facial identity (target), with an angry, happy, or neutral emotional expression, was positioned (in different images) within each cell of the grid; the eleven remaining facial identities (distractors), having a discrepant but homogeneous facial expression, were randomly positioned in the remaining grid cells (Figure 2A). These images were then processed with the SaliencyToolbox 2.2 software for MATLAB, with the standard settings (Walther and Koch, 2006; `http://www.saliencytoolbox.net/`). For each image, we computed the total activation within the cell containing the target face (Calvo & Nummenmaa, 2008; Ceccarini & Caudek, 2013; Humphrey, Underwood, & Lambert, 2012). On average, the angry and happy target faces did not differ in terms of their bottom-up salience, $t_{2879} = 0.46$, $p = .6459$. The neutral target faces, instead, had a lower bottom-up salience relative to both angry ($t_{2879} = -347.71$, $p = .0001$) and happy ($t_{2879} = -324.17$, $p = .0001$) target faces.

————— Please insert Figure 2 about here —————

2.1.4. Procedure

Each trial began with the presentation of a fixation cross (500 ms) followed by the presentation of a random arrangement of twelve dynamic faces (1000 ms). Each face was shown as rotating about a vertical axis from the sideway position to the full frontal view. All faces were removed from the screen after they completed the 90^0 rotation and the screen remained blank until the participants' response. Participants were free to respond also after the stimulus had disappeared from the screen. The interval between successive trials was set to 2500 ms and was initiated by the participant's response. Participants were asked to indicate with a key-press whether all faces showed the same expression or whether one face showed an expression differing from the others. Participants were instructed to perform the task as quickly and accurately as possible. No feedback on correct or incorrect responses was provided. RTs were measured from onset of stimuli.

Each session consisted of two blocks of 162 trials presented in a random order and separated by a 10 minutes break. The first block of trials was preceded by 20 practice trials.

2.1.5. Design

There were nine different target-distractor combinations: *aTnD*, *aThD*, *hTaD*, *hTnD*, *nThD*, *nTaD*, *neutral*, *angry*, *happy*, where the lowercase letters *a*, *h*, and *n* denote "angry", "happy", and "neutral" faces, respectively; the uppercase letters *T* and *D* denote "target" and "distractor", respectively. So, the string *aTnD* denotes the trials with an angry target face in a neutral crowd. The conditions *neutral*, *angry*, and *happy* are the target-absent conditions with neutral, angry, and happy faces, respectively. In Experiment 1, each of the nine conditions was repeated 36 times, for a total of 324 trials per participant.

2.2. Statistical analyses

Post-error RT adjustments were computed as indicated by Dutilh et al. (2012), that is, as $PES_{robust} = RT_{N+1} - RT_{N-1}$, where N, $N+1$, and $N-1$ denote the trials in which an error is committed, and the following and the preceding trials, respectively. PES_{robust} describes the fluctuations in the RTs surrounding an error and is obtained by computing the difference $RT_{N+1} - RT_{N-1}$ within each triplet of successive correct/error/correct trials, and then by averaging the results over all triplets of trials with a similar structure. Instead, in the traditional method for quantifying the PES, the mean RT (MRT) of all post-correct trials is subtracted from the MRT of all post-error trials: $PES_{traditional} = MRT_{post\text{-}error} - MRT_{post\text{-}correct}$. PES_{robust} is more robust than $PES_{traditional}$ because it takes into consideration the fact that error trials are not evenly distributed across the time series (see Appendix A). In computing post-error RT adjustments, we only considered the sequences of trials in which $N-1$ and $N+1$ were correctly performed trials. For comparison purposes, the potential post-correct RT adjustments were also computed, in a similar manner to $\text{PES}_{\text{robust}}$, by considering all groups of three successive correct trials.

Statistical analyses of various effects were done by means of linear mixed-effects (LME) models (for RTs) and generalized mixed-effects (GLME) models with a binomial link function (for error rates) (Pinheiro & Bates, 2000). LME and GLME models allow to consider simultaneously the standard fixed-effects factors controlled by the experimenter and also the random-effects factors. For the LME and GLME models used in this study, random effects consisted of participants (modeling both slopes and intercepts) and stimulus ID (modeling intercepts only) (*e.g.*, Barr, Levy, Scheepers, & Tily, 2013; Caudek, 2013; Caudek & Domini, 2013; Caudek & Monni, 2013; Sica, Caudek, Chiri, Ghisi, & Marchetti, 2012). Models were fitted using Restricted Maximum Likelihood (REML). We used `R` (R Core Team, 2013), `lme4` (Bates, Maechler, Bolker, & Walker, 2014), `nlme` (Pinheiro, Bates, DebRoy, Sarkar & R Core Team, 2014), and `lmerTest` (Kuznetsova, Brockhoff, & Christensen, 2014). p-values were estimated by likelihood ratio tests of the full model with the effect in question against the model without the effect in question and by using the Satterthwaite and Kenward-Roger (KR) approximations of the degrees of freedom. The RT outliers (trials outside the range of the mean reaction time ± 2.5 standard deviations) were discarded (less than 1%). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality.

There are several advantages that comes from adopting mixed-effect linear models over the traditional ANOVA approach (Baayen, Davidson, & Bates, 2008; Gelman & Hill, 2007): LME models (1) allow correlated observations within a unit or cluster of observations; (2) provide a greater statistical power for the analysis of repeated observations; (3) allow to model heteroskedasticity and non-spherical error variance; (4) provide a flexible method of dealing with missing data. Given that the number of errors made by each participant is not under the experimenter's control, the data of the present experiments are necessarily unbalanced. Whereas LME models are robust in the analysis of unbalanced data, this situation is highly problematic for the traditional repeated-measures ANOVA.

2.3. Results

Post-error and post-correct RT adjustments. The mean post-correct and post-error RT adjustments as a function of Condition (*aThD, aTnD, hTaD, hTnD, nTaD, nThD, angry, happy, neutral*) are shown in Figure 3, top panel. An LME model with participants and stimulus ID as random effects, and with fixed effects for Condition and Performance Accuracy (correct/incorrect trial) revealed a statistically significant effect of Condition on the RT adjustments, $\chi^2_1 = 41.05$, $p = .0001$. The effect of Performance Accuracy was not statistically significant, $\chi^2_1 = 1.80$, $p = .180$, and neither was the Condition × Performance Accuracy interaction, $\chi^2_8 = 9.83$, $p = .2770$. An angry target face in a happy crowd, $t_{3823} = 3.69$, $p = .0002$, and an angry target face in a neutral crowd, $t_{3823} = 3.21$, $p = .0013$, produced a statistically significant decrease in the RTs on the following trial. This post-threat speeding was not modulated by Performance Accuracy. A statistically significant increase in the RTs on the $N + 1$ trial was observed after a neutral target face in a happy crowd, $t_{3823} = 2.22$, $p = .0261$, and after a target-absent angry crowd, $t_{3823} = 2.48$, $p = .0131$. No significant effects were found in the other target/distractors combinations. Contrast analysis showed that the combined *aThD*, *aTnD* conditions produced a post-threat speeding of -124 ms (*S.E.* = 25 ms), t_{3830} = -4.87, p = .0001, and that participants took longer (164 ms) to respond on the $N+1$ trial after a happy target face in a neutral crowd than after an angry target face in a neutral crowd, z = 3.21, p = .0013.

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Sequence effects for post-error RT adjustments. For error trials, sequence effects were examined with an LME analysis with participants and stimulus ID as random effects, and with fixed effects for Condition on trial $N-1$ and Condition on trial N. The interaction $\text{Condition}_{\text{N-1}} \times \text{Condition}_{\text{N}}$ was not statistically significant, χ^2_{63} = 62.56, p = .4921. Likewise, a separate analysis showed that the interaction $\text{Condition}_{\text{N}} \times \text{Condition}_{\text{N+1}}$ was also not statistically significant, χ^2_{64} = 55.73, p = .7598.

Anger superiority effect. Figure 4, top-left panel, provides a description of the mean RTs for all the target-distractor combinations of Experiment 1. For target-present trials, an LME analysis with participants and stimulus ID as random effects, and with fixed effects for Condition indicated that Condition had a statistically significant effect on the response latencies, χ^2_5 = 21.51, p = .0006. Contrast analysis showed slower RTs for an angry target face in a neutral crowd than for a happy target face in a neutral crowd, z = 3.67, p = .0001; the average of the mean RTs for angry target faces was lower than the average mean RTs for all the other conditions, z = 3.72, p = .0001; the mean RTs for a happy target face in an angry crowd did not differ from the mean RTs for an angry target face in a happy crowd, z = 0.961, p = .651 (adjusted p values). Crowds of neutral distractor faces produced slower RTs than crowds of angry distractor faces, t_{1629}

= 2.571, p = .0102; no RTs difference was observed between crowds of angry distractor faces and crowds of happy distractor faces, t_{1629} = 1.55, p = .1213.

———— Please insert Figure 4 about here ————

Performance accuracy. The percentages of errors were 19%, 17%, and 8% for nonthreatening targets, threatening targets, and target-absent trials, respectively. False alarm rates were 7%, 7%, and 11% for target-absent trials in the *angry*, *happy*, and *neutral* conditions, respectively. We analyzed the errors by fitting a binomial logit random effects (GLME) model to the correct and incorrect responses, with participants and stimulus ID as crossed random effects. The error rates were not affected by the presence/absence of a threatening target face on trial N, $z = 1.25$, $p = .211$. Accuracy was significantly higher on target-absent trials than on trial with nonthreatening target faces, z = 4.77, p = .0001.

A further GLME model with participants and stimulus ID as random effects, and with fixed effects for Condition (*aThD, aTnD, hTaD, hTnD, nTaD, nThD, angry, happy, neutral*) and Performance Accuracy (correct/incorrect trial) showed that the probability of an error on trial $N + 1$ was not affected by any of these two variables, nor by their interaction, χ^2_{17} = 20.93, p = .2296 (see Figure 5, top panel).

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2.4. *Discussion*

Experiment 1 does not provide the optimal conditions for the ASE: Image motion was generated by a rigid 3D rotation rather than by a 3D deformation, the stimuli were synthetic face images rather than natural images, and we used all the nine possible combinations of angry, happy, and neutral faces for the target-distractor pairings (in order to minimize the possibility of anticipatory response strategies – see Becker et al., 2011), rather than an asymmetry design. In spite of these limitations, an ASE was found also within the present stimulus conditions and, importantly, we found new evidence for post-threat speeding, after both correct and error responses. Post-threat speeding can be interpreted as an enhancement of processing efficiency, given that post-threat accuracy remained constant (Figure 5). In these less-than-optimal conditions for the ASE, however, we did not find a heightened defensive behavior when participants failed to detect a threatening target, relatively to when they correctly localized the threatening target.

3. Experiment 2

In Experiment 2, we tried to isolate the best stimulus conditions for the ASE and, therefore, for observing a post-error enhancement of vigilance after the failure to detect a threatening target. Participants completed a visual search task for dynamic angry or happy expressions in crowds of neutral faces. The distractor crowd was held constant for the two targets, so that the search speed through the distractor crowds did not vary across target types. The dynamic stimuli were natural faces selected from the Radboud Faces Database (Langner et al., 2010).

4. Method

4.1. Participants

A total of 14 undergraduate students from the University of Florence participated in Experiment 2. All participants were naïve to the purpose of the study and had normal or corrected-to-normal vision. Participation was voluntary.

4.1.1. Apparatus and stimuli

The apparatus was the same as in Experiment 1. Stimuli were 3D face models of nine different facial identities showing angry, happy, and neutral facial expressions (Figure 1, panel B). The stimuli were generated by following the procedure described by Ceccarini and Caudek (2013). From the Radboud Faces Database (Langner et al., 2010) – a standardized set of face images that display facial expressions based on prototypes from the Facial Action Coding System (FACS; Ekman, Friesen, & Hager, 2002) – we selected nine face identities, each with three emotional expressions, with similar ratings of intensity of the expression, clarity of the expression, and genuineness of the expression. Each image was cropped to remove hair and background. These 27 images were uploaded into Facegen in order to create a 3D model of each face with the PhotoFit SDK function. These 27 3D models were then processed with the 3dStudio Max software in order to equate illumination intensity and illuminant direction in each face.

In the Radboud database, the happy faces are represented with open-mouth smiles and the angry faces are represented with the mouth closed. Previous studies have shown that images of faces with an open mouth relative to close-mouthed faces yield a simple visual feature (visible teeth) that can drive efficient search (Becker et al., 2011; Purcell, Stewart, & Skov, 1996). To address this issue, following the same procedure described by Ceccarini and Caudek (2013), we modified the nine happy face images with the 3dStudio Max software in order to create 3D face models expressing happiness with a closed mouth.

The 3D face models were then transformed in video sequences (30 fps) by means of the Flash CS5 software. The frame sequences representing the temporal unfolding of the angry, happy, and neutral expressions were generated by a linear morphing between the untransformed images of the neutral faces selected from the Radboud database and the happy and neutral face images transformed as indicated above, or the fully-expressive untransformed angry faces. To generate dynamic faces with a neutral expression, we used the function PhotoFit SDK of the FaceGen software that allows to produce realistic images of the spoken phoneme /W/.

The duration of each video sequence was 1500 ms. Within this temporal window, a neutral face was displayed for 300 ms, followed by the morphing transition between the neutral face and the final expressive face (or the face with the spoken phoneme /W/) (533 ms), and by the final expression of the face (677 ms). This procedure allows a precise control of the timing of the change without sacrificing the realism of the expressive dynamics (*e.g.*, Becker et al., 2012). The duration of the temporal unfolding of facial expressions of emotion (533 ms) is in line with other experiments generating dynamic facial expressions with methods similar to the present study (*e.g.*, Arsalidou, Morris, & Taylor, 2011; Becker et al., 2012; Horstmann & Ansorge, 2009; Schultz & Pilz, 2009).

Bottom-up visual salience. By using the last frame of each of the 27 video sequences (full frontal view of the nine facial identities, each with an angry, happy, or neutral expression), we generated 1440 displays comprising one target face and seven distractors. The displays were divided into an evenly spaced 2×4

grid, with each cell covering 512×320 pixels. Each of the 18 expressive faces (9 angry and 9 happy) was positioned (in different displays) within each cell of the grid. Seven neutral faces (distractors) were randomly selected (for each display) from the remaining eight facial identities and were randomly positioned in the remaining grid cells. These displays were processed with the SaliencyToolbox 2.2 software for MATLAB (with the standard settings) and, for each display, we computed the total activation within the cell containing the target face. On average, the angry and happy target faces did not differ in terms of their bottom-up salience, $t_{1439} = 0.14$, $p = .8882$.

Intensity of emotional expressiveness. The facial expressions of the 27 selected face identities were analyzed by means of the FaceReader software (Noldus Information Technologies, 2012). This analysis showed that, for all the selected images, the emotional expressiveness was greater than 0.95.

Amount of image motion. We measured the amount of image motion in order to insure that it was approximately the same across the three emotional expressions (angry, happy, and neutral faces; see Horstmann & Ansorge, 2009). Following the same procedure described by Ceccarini and Caudek (2013), image motion was evaluated by comparing the first (neutral) and the last (full emotion or the face with the spoken phoneme /W/) frame of the video sequence, for each face identity and each expression. An ANOVA indicated that the average amount of image motion did not differ significantly depending on whether the motion sequences displayed the temporal unfolding of an angry emotion, of a happy emotion, or of the spoken phoneme /W/, $F_{2,24} = 0.09$, $p = .914$.

4.1.2. Procedure

The procedure was the same as in Experiment 1. No feedback on correct or incorrect responses was provided. Each session consisted of four blocks of 180 trials presented in a random order and separated by a 10 minutes break. The first block of trials was preceded by 20 practice trials.

4.1.3. Design

There were three different conditions: angry target with neutral distractors (*aTnD*), happy target with neutral distractors (*hTnD*), target-absent trials with only neutral distractors (*neutral*). For each participant there were 180 trials for each of the two target-present conditions, and 360 trials for the target-absent condition.

4.2. Results

Post-error and post-correct RT adjustments. In examining post-error and post-correct adjustments, it is important to consider the stimulus conditions on trials $N-1$ and $N+1$ (Steinhauser & Yeung, 2012). Because of the larger number of trials per subject and the smaller number of conditions, in Experiment 2 this control was possible. Therefore, we examined the post-correct and post-error RT adjustments for matched target/distractors combinations on trials $N - 1$ and $N + 1$. The mean post-correct and post-error RT adjustments as a function of Condition are shown in Figure 3, middle panel.

An LME model with participants and stimulus ID as random effects, and with fixed effects for Condition (*aTnD*, *hTnD*, *neutral*) and Performance Accuracy (correct/incorrect trial) showed that the Condition × Performance Accuracy interaction was statistically significant, $\chi^2_2 = 86.87$, $p = .0001$. To interpret this interaction, a model with a "cell design" was used to test the hypotheses of a nil effect on the RT adjustments in each of the six levels defined by the Condition × Performance Accuracy interaction. For correct trials, we found no effects on the RT adjustments (*aTnD*: $t_{20.77}$ = 0.73, p = .4739; *hTnD*: t_{21} = -1.11, p = .2774; *neutral*: $t_{6.8}$ = -1.481, p = .1833). For error trials, instead, we found post-error speeding in the *aTnD* condition, $t_{235.64}$ = -3.23, p = .0014, and post-error slowing in the *hTnD*, $t_{114.91}$ = 8.07, p = .0001, and *neutral* conditions, $t_{38.07}$ = 3.20, p = .0027.

Sequence effects for post-error RT adjustments. An LME model with participants and stimulus ID as random effects, and with fixed effects for Condition in trial $N-1$ and Condition in trial N showed that the interaction $\text{Condition}_{\text{N-1}}\times$ $\text{Condition}_{\text{N}}$ was not statistically significant, χ_4 = 4.98, p = .2889. Likewise, a separate analysis showed that the $\text{Condition}_{\text{N}}\times$ $\text{Condition}_{\text{N+1}}$ interaction was also not statistically significant, χ_4 = 8.53, p = .0740.

Anger superiority effect. Figure 4, top-right panel, shows the mean RTs as a function of Condition. For target-present trials, an LME analysis with participants and stimulus ID as random effects, and with fixed effects for Condition indicated that the response latencies were modulated by Condition, χ^2_1 = 12.21, p = .0005. Contrast analysis indicated that the RTs for an angry target face in a neutral crowd were, on average, 317 ms faster than for a happy target face in a neutral crowd, $t_{16.72}$ = 4.104, p = .0008. RTs in target-absent trials were, on average, 661 ms slower than for a happy target face in a neutral crowd, $t_{47.34}$ = 4.03, p = .0002.

Performance accuracy. The percentages of errors were 12.8%, 6.7%, and 2.1% for nonthreatening targets, threatening targets, and target-absent trials, respectively. False alarm rates were 2% for target-absent trials (neutral distractors). A binomial logit GLME analysis showed that accuracy was higher on trials with a threatening target than on trials with a nonthreatening target, $z = 4.49$, $p = .0001$ (*i.e.*, less errors were made in trials with an angry face target). Moreover, accuracy was significantly higher when the target was absent then it was when the target was nonthreatening, $z = 4.53$, $p = .0001$. A further analysis showed that Performance Accuracy (correct/incorrect trial) on trial N was not affected by Performance Accuracy on trial $N - 1$, $z = 0.74$, $p = .46$. A final analysis showed that Performance Accuracy on trial $N + 1$ was not affected by Condition (*aTnD, hTnD, neutral*) and Performance Accuracy in trial N, nor by their interaction, $\chi^2_5 = 2.90$, $p = .7149$.

4.3. Discussion

Experiment 2 provided ecologically valid emotional stimuli, with natural dynamic facial expressions. Moreover, in Experiment 2, participants consciously searched for an expressive face in a neutral crowd (even though they could not predict whether the target was angry or happy), whereas in Experiment 1 such search strategy was not possible because target and distractors could take on any of three possible expressive values (angry, happy, or neutral). Within such stimulus conditions, which better support the ASE, participants showed post-error speeding for threatening targets and post-error slowing for nonthreatening targets, while maintaining similar levels of post-error accuracy in the two cases. Differently from Experiment 1, we found no evidence of post-threat speeding for correct responses. In sum, the results of Experiment 2 confirm our hypothesis that the failure to detect a threatening target promotes enhanced post-error processing.

5. A re-analysis of the data from Ceccarini and Caudek (2013)

A further test of the hypothesis that post-error reactivity takes on qualitatively different forms, depending on the presence/absence of a threat in the error trial, is provided by the re-analysis of the data from Ceccarini and Caudek (2013). In that previous study, an asymmetry design was used in four visual-search experiments requiring to detect angry or happy facial expressions in crowds of faces. The displays were static or dynamic (the dynamic displays were generated as in Experiment 2, see Figure 1, panel C). After removing the outlier responses, the combined data of the 51 participants totaled 10,831 trials, with 411 error trials embedded in sequences where $N-1$ and $N+1$ were correctly performed trials.

Ceccarini and Caudek (2013) examined four target-distractor combinations: happy target face in an angry crowd (*hTaD*), angry target face in a happy crowd (*aThD*), angry-face distractors (*angry*), and happy-face distractors (*happy*). Each condition was repeated 54 times, for a total of 216 trials per participant.

5.1. Results

Post-error and post-correct RT adjustments. The mean post-correct and post-error RT adjustments as a function of Condition are shown in Figure 3 bottom panel. An LME model with participants and stimulus ID as random effects, and with fixed effects for Condition (*aThD, hTaD, angry, happy*) and Performance Accuracy (correct/incorrect trial) showed that the Condition × Performance Accuracy interaction was statistically significant, $\chi^2_3 = 10.58$, $p = .0142$. For error trials, contrast analysis indicated that the response on trial $N + 1$ was faster in the *aThD* condition than in the combined *hTaD*, *angry*, and *happy* conditions, $z = 3.01$, $p = .0052$; for correct trials, instead, a similar analysis did not produce a statistically significant result, $z = 0.66$, $p = .7614$ (adjusted p values).

Sequence effects for post-error RT adjustments. An LME analysis with participants and stimulus ID as random effects, and with fixed effects for Condition (*aThD, hTaD, angry, happy*) in trial $N-1$ and Condition in trial N showed that the Condition$_{\text{N-1}}\times$ Condition$_{\text{N}}$ interaction was not statistically significant, χ_9 = 13.85, p = .1276. A separate analysis showed that the Condition$_{\text{N}}\times$ Condition$_{\text{N+1}}$ interaction was also not statistically significant, χ_9 = 3.22, p = .9548.

Anger superiority effect. By combining the data of the four experiments of Ceccarini and Caudek (2013), we examined the RTs as a function of Condition (threatening target, nonthreatening target, target-absent) and Stimulus Presentation (dynamic, static). The interaction Condition × Stimulus Presentation was statistically significant, χ^2_2 = 31.19, p = .0001. For dynamic displays (Figure 4, bottom left panel), the effect of Condition was statistically significant, χ^2_2 = 89.85, p = .0001. On average, participants were 171 ms faster on trials with a threatening target than on trials with a nonthreatening target, $t_{52.46} = -5.29$, p = .0001. Participants tended to be 403 ms slower on target-absent trials than on trials with a nonthreatening target, $t_{56.73}$ = 9.06, p = .0001. For static displays (Figure 4, bottom right panel), the effect of Condition was statistically significant, χ^2_2 = 92.03, p = .0001. However, the average RTs for trials with a threatening target and trials with a nonthreatening target were not significantly different from each other, $t_{50.89} = -0.67$, p = .506. Participants tended to be 567 ms slower on target-absent trials than on trials with a nonthreatening target, $t_{57.93}$ = 14.19, p = .0001.

Performance accuracy. The percentages of errors were 8.5%, 9.3%, and 2.1% for trials with a nonthreatening target, trials with a threatening target, and target-absent trials, respectively. False alarm rates were 4% and 1% for target-absent trials in the *angry* and *happy* conditions, respectively. A GLME analysis showed that error rate did not differ significantly as a function of whether the target was threatening or nonthreatening, $z = -0.73$, $p = 0.464$. Accuracy was higher when the target was absent then it was when the target was nonthreatening, $z = 5.99$, $p = .0001$. A further GLME analysis showed a statistically significant effect of response accuracy on trial $N - 1$: Participants were more accurate after a correct response (95% correct) than after an error (85% correct), $z = 2.70$, $p = .0069$. However, post-error accuracy did not differ depending on whether trial N provided a threatening (84% correct) or a nonthreatening (87% correct) target, $z = -0.38$, $p = .706$.

5.2. Discussion

Like in Experiment 1, the stimulus conditions of Ceccarini and Caudek (2013) are not optimal to study error reactivity after the failure to detect a threat. In fact, dynamic and static displays were randomly intermixed in half of the trials of their experiments, and an ASE was found for the dynamic displays only[3]. Nevertheless, also in those conditions, participants tended to show post-error speeding when they failed to detect a threatening target. No evidence was found for post-threat speeding after correct responses.

Differently from Experiments 1 and 2, in the data of Ceccarini and Caudek (2013) post-error accuracy was lower than post-correct accuracy. This result is consistent with several previous reports (Bombeke, Schouppe, Duthoo, & Notebaert, 2013; Houtman & Notebaert, 2013; Rabbitt & Rodgers, 1977; Fiehler,

[3]For the present analysis it was not possible to consider only the dynamic trials because, even though in two experiments the static/dynamic manipulation was blocked, in the remaining two experiments static and dynamic trials were randomly intermixed. Therefore, dynamic face images were used in all trials of an experimental block in only about one-fourth of the total number of trials.

Ullsperger, & Von Cramon, 2005) and it has been explained by the orienting account with the idea that errors act as "oddballs" that divert attentional resources from the task and, thus, impair subsequent performance. In spite of this overall post-error decrease in accuracy, the data of Ceccarini and Caudek (2013) show that a failure to detect a threatening target enhances post-error processing efficiency relative to the failure to detect a nonthreatening target. In fact, the first kind of error led to post-error speeding whereas the second produced post-error slowing, although the level of post-error accuracy was similar in both cases.

6. Analysis of combined experiments

To increase statistical power and to better examine sequential effects in error reactivity, we performed an additional set of control analyses by combining the data of all the experiments discussed above (*i.e.*, the data of Experiments 1 and 2, together with those of Ceccarini and Caudek, 2013) – see Supplemental Information. No significant post-correct RT adjustments were found in any conditions (Section S1.1 in Supplement 1). Instead, the data of the combined experiments showed that participants increased response speed after failing to detect a threatening target. This effect was stronger in Experiment 2 than in the other experiments, confirming our hypothesis that a defensive response, which improves processing efficiency after the failure to detect a threat, is more likely to be elicited within ecologically valid stimulus conditions (*i.e.*, natural dynamic expressions of emotions) (Section S1.2 in Supplement 1).

When considering only the target/distractors combinations in which angry faces were used as targets or as distractors, we found post-threat speeding on error trials; correct trials, instead, showed no effect (Table 1). Therefore, the analysis of the data of the combined experiments provides no evidence that post-correct adjustments ($RT_{N+1} - RT_{N-1}$) are modulated by the emotional content of the target on trial *N*. This suggests that the post-correct adjustments found in Experiment 1 do not generalize to different stimulus conditions (Section S1.3 in Supplement 1).

Trial *N*	Threat	Mean($RT_{N+1} - RT_{N-1}$)
Correct	Distractors	0 (15)
Correct	Target	65 (13)
Error	Distractors	65 (40)
Error	Target	-137 (39)

Table 1: Mean post-correct and post-error RT adjustments (in ms) for threatening targets vs. threatening distractors. Standard errors are shown in parenthesis.

By combining the data of the three sets of experiments, we were able to assess error reactivity after controlling for sequence effects. We considered the triplets of consecutive trials with matched $N - 1$ and $N + 1$ trial types, and we compared the post-error adjustments for threatening and nonthreatening targets on trial *N*. We found post-threat speeding after errors also when potential sequence effects were statistically controlled (Section S1.4 in Supplement 1).

Post-error speeding might be observed because of the way in which post-error adjustments are computed. It is possible that longer RTs are associated to a reduced alertness leading to an error in the following trial. Post-error speeding, then, might be related to the fact that a reduced alertness in trial $N - 1$ may be the cause of the observed error. To test this hypothesis, the data of the combined experiments were divided into four data sets identified by the quartiles of the distribution of the RTs on the $N - 1$ trials. The quartile split was performed separately for each participant. Within these four sets of trials, we considered the relation between the (post-error and post-correct) RT adjustments and Condition in trial N (nonthreatening target, threatening target, target-absent trials). The effect of the quartile split, as shown in Figure 6, simply indicates that, if we select the faster responses on the $N - 1$ trials (Figure 6, first quartile) then, on average, the $N+1$ trials will be slower. Therefore, the difference between $RT_{N+1} - RT_{N-1}$ will tend to be positive. The opposite happens if we select the slower $N - 1$ trials (Figure 6, fourth quartile). What is interesting is that, within each panel of Figure 6, we found an RT advantage on the $N + 1$ trials when, on the previous trials, participants failed to detect a threatening target. No statistically significant post-correct adjustments were found in any of the four data sets shown in Figure 6. The results of this analysis thus indicate that post-error speeding cannot be attributed to a reduced alertness leading to an error in the following trial (Section S1.5 in Supplement 1).

We also examined the effect of repetition priming between trials N and $N + 1$ (Table 2; Section S1.6 in Supplement 1), and between trials $N-1$ and N (Table 3; Section S1.7 in Supplement 1). In the stop-signal paradigm, for example, Verbruggen, Logan, Liefooghe and Vandierendonck (2008) have shown that stimulus repetitions affect post-error adjustments. In the present case"stimulus repetition" does not correspond to an exact perceptual replica (because the spatial arrangements of target and distractors was randomly determined on a trial-by-trial basis and because the selected facial identities could also vary from trial to trial), but only to the repetition of the experimental condition in successive trials. In our data, repetition priming effects were present, but they did not interact with the effect of target valence on the post-error adjustments[4].

[4]The question remains, however, of whether the null effect of congruency on the post-error RT adjustments may be due to a lack of statistical power.

Trials N and $N+1$	Threat	Error Responses on Trial N	Correct Responses on Trial N
Incongruent	Distractors	188 (33)	-2 (13)
Incongruent	Target	-87 (42)	181 (14)
Congruent	Distractors	16 (90)	-360 (28)
Congruent	Target	-366 (87)	-377 (26)

Table 2: Mean($RT_{N+1} - RT_{N-1}$) for threatening and nonthreatening targets (in ms) as a function of the congruency between trials N and $N+1$, of target type in trial N, and of whether trial N was an error or a correctly performed trial. Standard errors are shown in parenthesis.

$N-1$ and N Trials	Threat	Error Trials	Correct Trials
Incongruent	Distractors	140 (34)	-119 (13)
Incongruent	Target	-206 (41)	-46 (14)
Congruent	Distractors	369 (91)	243 (30)
Congruent	Target	183 (108)	479 (29)

Table 3: Mean($RT_{N+1} - RT_{N-1}$) for threatening and nonthreatening targets (in ms) as a function of the congruency between trials $N-1$ and N, of target type in trial N, and of whether trial N was an error or a correctly performed trial. Standard errors are shown in parenthesis.

Finally, we considered the relation between the post-error RT adjustments and the response latencies on error trials. For nonthreatening targets, slower responses on trial N induced stronger post-error slowing. For threatening targets, instead, the amount of post-error speeding was unrelated to the response latencies on previous trials. This provides further evidence that errors associated to threatening and nonthreatening targets induce different post-error adjustments (Section S1.8 in Supplement 1).

7. General discussion

The present study provides evidence that post-error control adjustments in a visual search task can adapt to the opposite demands deriving from the failure to detect a threatening or a nonthreatening target. We hypothesized that the failure to detect a nonthreatening face would lead to post-error slowing, whereas the failure to detect a threatening face would reduce post-error slowing, or it would produce post-error speeding. These predictions were confirmed.

In our study, we used dynamic faces because they provide a more ecologically valid representation of threat (Arsalidou et al., 2011). Moreover, we carefully controlled several bottom-up confounds that have been described in the literature as alternative explanations of the ASE (Becker et al., 2011), and we also equated the amount of motion across experimental conditions (Horstmann & Ansorge, 2009). Such stimuli proved to be adequate for producing an ASE (Figure 4).

Having found the stimulus conditions that elicit an ASE, we examined error reactivity. Participants showed post-error slowing when they failed to detect a nonthreatening face. To our knowledge, this is the first evidence of post-error adjustments in a visual-search task, where response latencies are much longer than what is typically found in studies using choice reaction time tasks (Laming, 1979; Rabbitt, 1966), Simon tasks (Rigoni, Wilquin, Brass, & Burle, 2013), or Stroop tasks (Suárez-Pellicioni, Núñez-Peña, & Colomé, 2013). This result supports the hypothesis that sequential control adjustments impact performance for a prolonged time period (Cheyne, Carriere, Solman, & Smilek, 2011).

The failure to detect a threatening face is an event that has important survival implications. The main result of the present study is that participants showed post-error *speeding*, when they failed to detect a discrepant angry face in a crowd of faces. It is known that the perception of threat increases arousal and contributes to focus attention in order to facilitate an adequate coping behaviour (Easterbrook, 1959; Gable & Harmon-Jones, 2010; Van Steenbergen, Band, & Hommel, 2011). The present data provide the first evidence that also *the failure to detect a threat* may trigger cognitive control processes that enable faster and more efficient responses.

In Experiment 1, we found a post-threat advantage in the RTs for both error trials and correctly performed trials. Post-threat speeding was also found in Experiment 2 and in the data of Ceccarini and Caudek (2013), but only for error trials[5]. These results suggest that a defensive reaction, which produces a heightened alertness, is more likely to be observed when participants fail to detect an angry face, rather than when an angry target face is correctly detected. We speculate that the uncertainty deriving from the failure of localizing a threat (when a threat may still be present) may trigger a higher level of vigilance than when the threat has been correctly localized.

Becker (2009) examined the efficiency of visual search for a non-threatening target after the presentation of a spatially non-informative emotional face. He hypothesized that "the detection of threat would also produce a more generalized increase in processing efficiency, thereby allowing one to rapidly identify

[5]Although it is not clear why these methodological differences produce different post-correct adjustments across the three sets of experiments, it is necessary to point out that, differently from the other experiments, in Experiment 1 (1) the facial emotions were not displayed in an ecologically valid manner (*i.e.*, motion was generated by a rigid 3D rotation, rather than by a deformation of the face), (2) there were nine different conditions, versus the three conditions of Experiment 2 and the four conditions of the experiments of Ceccarini and Caudek (2013), and (3) targets were present in 66% of trials versus the 50% of the other experiments; in these conditions, participants may have adopted a low "present" criterion.

objects that would be beneficial to fleeing or fighting the threat, objects that themselves may not be threatening" (p. 435). The results of his experiment indicate that this is indeed the case. Becker (2009) interpreted his findings as indicating that threat processing increases the arousal level which, in turn, leads to a generalized increase in alertness and to an increased search efficiency (Phelps & LeDoux, 2005)[6]. Our results confirm and extend the findings of Becker (2009) and suggest that the failure to detect a threatening face can induce a state of phasic alertness and readiness to respond (see also Matthias et al., 2010; Kusnir, Chica, Mitsumasu, & Bartolomeo, 2011; Weinbach & Henik, 2011).

In the study of Becker (2009), threat was evoked by a fearful face. Olatunji, Ciesielski, Armstrong, and Zald (2011) replicated his findings by measuring the efficiency of visual search after the presentation of a face expressing anger, disgust, fear, happiness, or a neutral emotional state. Faster target detection was found for the exposure to a fearful expression prior to visual search, compared to exposure to other facial expressions. More specifically, Olatunji et al. found that visual search efficiency improved after the presentation of a fearful face, but not after the presentation of an angry face. These results are in apparent contrast with those of the present study, in which we found an effect of angry faces.

Olatunji et al. (2011) point out that fearful faces trigger a defensive reaction more strongly than angry faces. Similarly, in our experiments, the presence of an angry face per se was not sufficient to increase arousal and vigilance. In the case of correct trials, in fact, participants showed a post-threat advantage only in the stimulus conditions of Experiment 1. Instead, an improved response efficiency

[6]There are many lines of (neuroimaging, neuropsychological, and psychophysiological) evidence that indicate that phasic alertness can improve processing speed. For a recent discussion, see Matthias et al. (2010).

was found in all experiments after the failure to detect an angry face. A detection failure can be interpreted as an internal signal of danger, which indicates that the current state of alertness is insufficient and this makes the participant vulnerable. In our experiments, it is this internal signal of danger that seems to trigger an increased state of alertness, not the mere presence of an angry face.

An important question is whether awareness is necessary to elicit post-error behavioral adjustments (Navarro-Cebrian, Knight, and Kayser, 2013). The literature on this issue comprises several contributions, especially from the field of the neurosciences (Wessel, 2012). There are, however, conflicting results: Some studies find similar neural correlated for reported and non-reported errors (Nieuwenhuis et al., 2001; Endrass et al., 2007, 2012; O'Connell et al., 2007; Shalgi et al., 2009; Hester et al., 2005, 2009; Klein et al., 2007), whereas other studies find different neural correlates for aware and unaware errors (Steinhauser and Yeung, 2010; Wessel et al., 2011; Shalgi and Deouell, 2012). It must be considered, however, that most of these studies are limited to the cortical electrophysiology of error reactivity – behavioral adjustments have not been considered. Although we did not set out to study error awareness, spontaneous reports provided in post-experimental interviews indicate that at least some of our participants were aware of committing errors. This awareness may be due to the fact that, having to perform the task under time pressure, response movements are programmed in a ballistic fashion (*i.e.*, once initiated, they cannot be interrupted). While the motor response is executed, however, the visual scanning of the stimulus array continues, and this could make the participants aware of having responded too early (*i.e.*, of having missed a target).

Post-error adjustments have been interpreted as reflecting an attentional shift toward task-relevant stimulus features and away from task-irrelevant features (*e.g.*, Danielmeier, Eichele, Forstmann, Tittgemeyer, & Ullsperger, 2011). This hypothesis predicts stronger post-error adjustments for congruent *N* and *N*+1 trials: If an error is triggered by the failure to detect a threatening face then, in the successive trial, attention should focus on anger-specific facial features. Therefore, stronger post-error adjustments are expected when the target in the *N*+1 trial is an angry face, rather than a happy or neutral face. In the present data, however, such sequential effects were not found. This supports the idea that failing to detect a threatening face impacts generic (*i.e.*, a-specific) alertness, and this has a dramatic impact on how participants subsequently complete the task, rather than enhancing selective attention to threatening-inducing features.

In our data, the amount of post-error slowing for nonthreatening targets was affected by the response latency on error trials; for threatening targets, instead, post-error speeding was unrelated to the *RTs* on error trials. These different qualitative patterns of post-error adjustments suggest that post-error slowing depends on an evaluation of the participants' performance, whereas post-error speeding does not. In turn, this supports the idea that post-error slowing and post-error speeding may be mediated by different underlying mechanisms.

Post-error speeding is inconsistent with the idea that error reactivity necessarily leads to a more conservative response strategy (Laming, 1979), or with the idea that error reactivity only depends on an interference of error-monitoring on post-error processing (*e.g.*, Jentzsch & Dudschig, 2009). Instead, the evidence of post-error speeding provided by the present study, together with other findings – such as the "affective privilege" of Reeck and Egner (2011) (*i.e.*, the finding that task-irrelevant valent distractors interfere with task processing whereas task-irrelevant nonvalent distractors do not) – suggest that, in the presence of valent information, error reactivity is better characterized as a domain-specific process rather than as a domain-general effect.

However, it is important to point out that there are significant methodological differences between the present experiments and the previous investigations on PES. Our average response latencies were longer than two seconds and cannot be directly compared to sub-second responses, which are typically examined in the studies on PES. We used response-stimulus intervals of 3000 ms and Danielmeier and Ullsperger (2011) found no evidence of PES with RSIs greater than 1500 ms[7]. We used valent stimuli, whereas PES is typically investigated with neutral stimuli. For these reasons, our results may describe a different form of cognitive control than the error reactivity that is reflected in PES. We propose that our experiments taps into strategic planning and post-perceptual response selection, whereas the "traditional" studies on PES describe earlier stages of information processing.

A final comment concerns the fact that our results do not show that angry faces are in any way special in how they impact subsequent performance, except that they indicate a threat and this is strategically interpreted and impacts cognitive control. Other threatening stimuli could presumably have much the same effect.

[7] van den Brink, Wynn, and Nieuwenhuis (2014) acknowledge that there are several studies in which PES has been found with inter-trial intervals of several seconds (Hajcak et al., 2003; Marco-Pallarés et al., 2008; King et al., 2010; Danielmeier et al., 2011). However, they also point out that all those studies have measured either $PES_{traditional}$ (which is confounded by variations in motivation and task performance in the course of the experiment – Dutilh et al., 2012), or they did not control for differences in pre-error and post-error trial type (another possible confound of PES – Steinhauser & Yeung, 2012). These considerations led van den Brink et al. (2014) to question the idea that PES truly occurs with long RSIs.

7.1. Conclusions

Executive control in a visual-search task was measured by post-error adjustments (RTs on N+1 trials minus RTs on $N-1$ trials). After failing to detect a threatening target, participants showed post-error speeding. These adjustments represent a gain in RTs and may be attributed to increased arousal leading to a generalized increase in vigilance. Instead, after failing to detect a nonthreatening target, participants showed post-error slowing. These adjustments represent a cost in RTs and may be attributed to the adoption of a more conservative response criterion. The present results indicate that the error monitoring system is very flexible and can adapt to the opposite demands of a task on a trial-by-trial basis.

8. References

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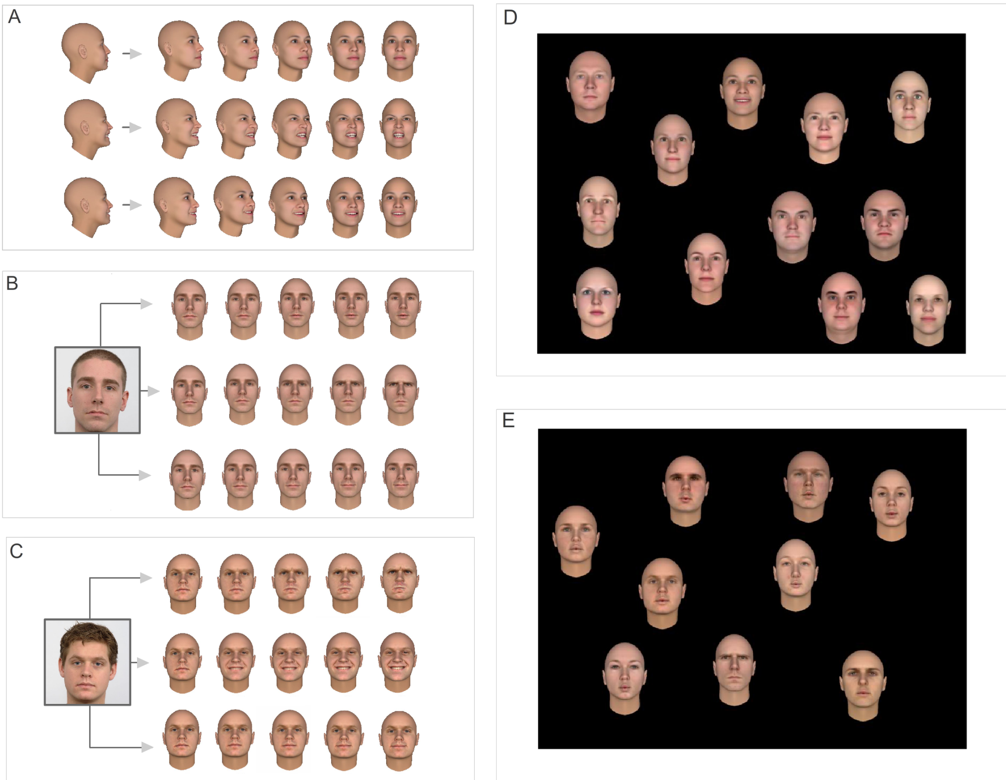
A
B
C
D
E

Figure 1 ***(previous page)*****:** Illustration of the stimulus-generation process. **Panel A:** *Experiment 1.* A female caucasian face with neutral (top), angry (center), and happy (bottom) expressions generated using the Facegen software (`www.facegen.com`). The figure shows some representative frames of the rotation about the vertical axis from the view of the individual's profile to the full frontal view of the face. **Panel B:** *Experiment 2.* The face enclosed in the rectangular frames was selected from the Radboud Faces Database with three emotional expressions: neutral, angry, and happy. These images were transformed to remove hair and then morphed to obtain a smooth transition between the neutral expression and the full-emotion expression. The images of the happy faces were also transformed so as to express happiness with a closed mouth. The figure shows some representative frames of the morph continua in the case of a transition between a neutral expression and the production of the spoken phoneme /W/ (top), a neutral expression and an emotional expression of anger (center), and a neutral expression and an emotional expression of happiness (bottom). **Panel C:** *Stimuli used by Ceccarini and Caudek (2013).* The figure shows an example of the face transitions between the neutral expression and anger (top), and between the neutral expression and happiness, with an open mouth (center) or with a closed mouth (bottom). **Panel D:** *Experiment 1.* Example of a target-present stimulus display at the end of the video sequence (a happy face in a neutral crowd). **Panel E:** *Experiment 2.* Example of a target-present stimulus display at the end of the video sequence (an angry face in a neutral crowd).

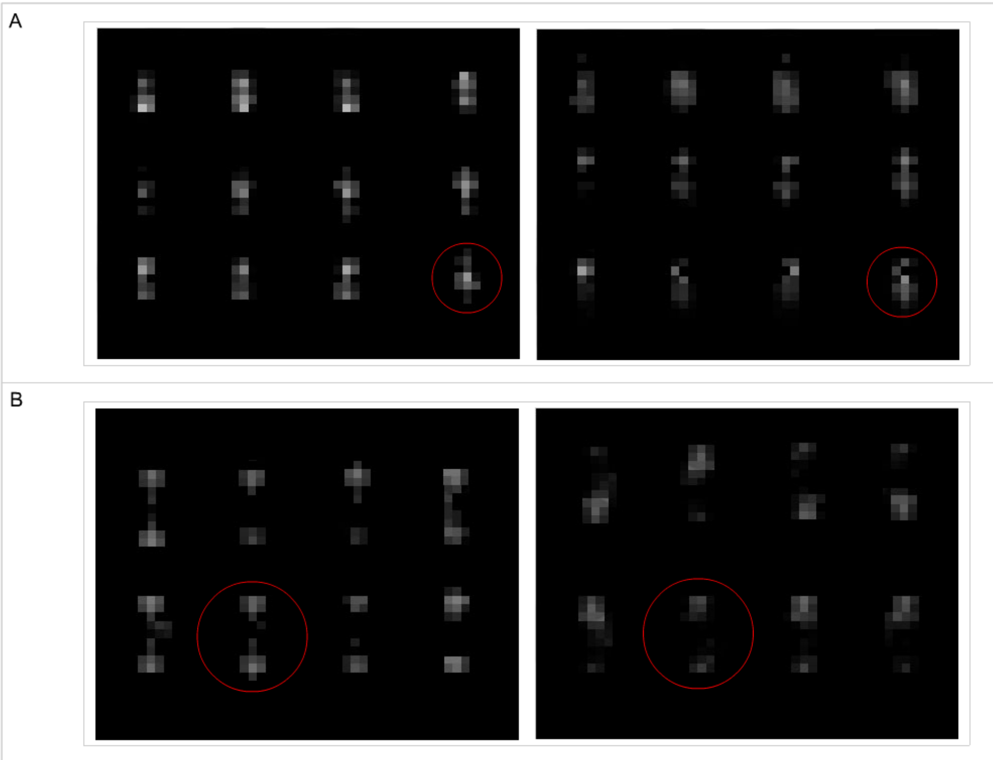

Figure 2: Examples of salience map computed according to the algorithm of Itti and Koch (2000, 2001). **Panel A:** *Experiment 1*. Left: happy target face in an angry crowd; right: angry target face in a happy crowd. **Panel B:** *Experiment 2*. Left: happy target face in a neutral crowd; right: angry target face in a neutral crowd. The red circle indicates the position of the target face. Each panel shows the mean of 12 salience maps. Each salience map was computed by using a different target face identity. The target was always located in the highlighted position among 11 distractors with different face identities. The arrangement of the distractors' face identities was reshuffled on each salience map.

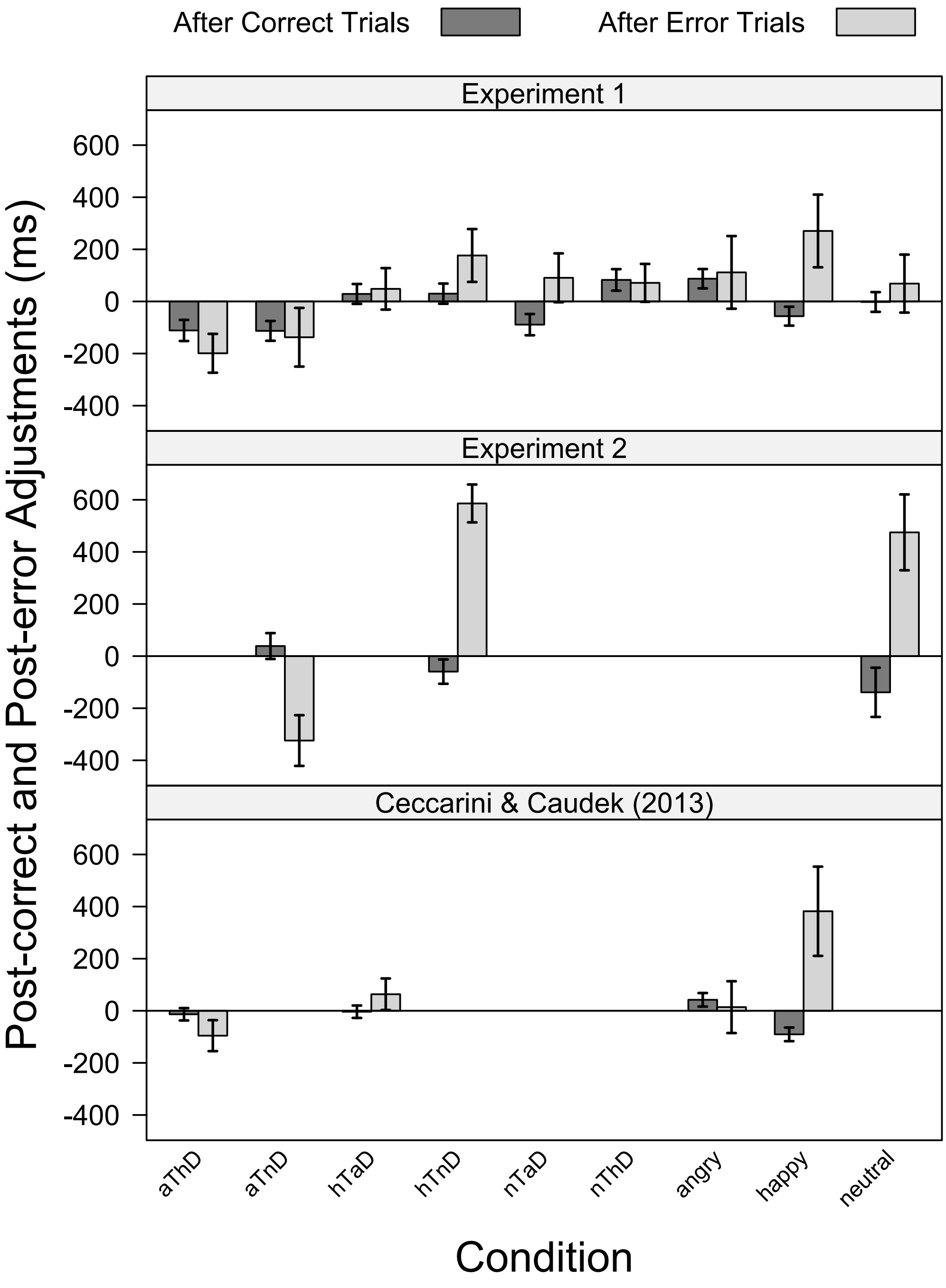
After Correct Trials
After Error Trials
Experiment 1
Experiment 2
Ceccarini & Caudek (2013)
Post-correct and Post-error Adjustments (ms)
600
400
200
0
-200
-400
aThD
aTnD
hTaD
hTnD
nTaD
nThD
angry
happy
neutral
Condition

Figure 3 ***(previous page)*****:** Mean post-correct and post-error adjustments $[RT(N{+}1){-}RT(N{-}1)]$, where N, $N{+}1$, and $N{-}1$ denote a triplet of consecutive trials, with $N{+}1$ and $N{+}1$ being correctly performed trials], as a function of Condition, for each experiment. Positive values indicate post-error slowing. The target-distractors combinations are denoted by the strings "*aTnD*", "*aThD*", "*hTaD*", "*hTnD*", "*nThD*", "*nTaD*", "*neutral*", "*angry*", "*happy*", where the lowercase letters *a*, *h*, and *n* denote "angry", "happy", and "neutral" faces, respectively; the uppercase letters *T* and *D* denote "target" and "distractor", respectively. "*neutral*", "*angry*", and "*happy*" denote target-absent trials with neutral, angry, and happy faces, respectively. Vertical bars indicate standard error of the mean.

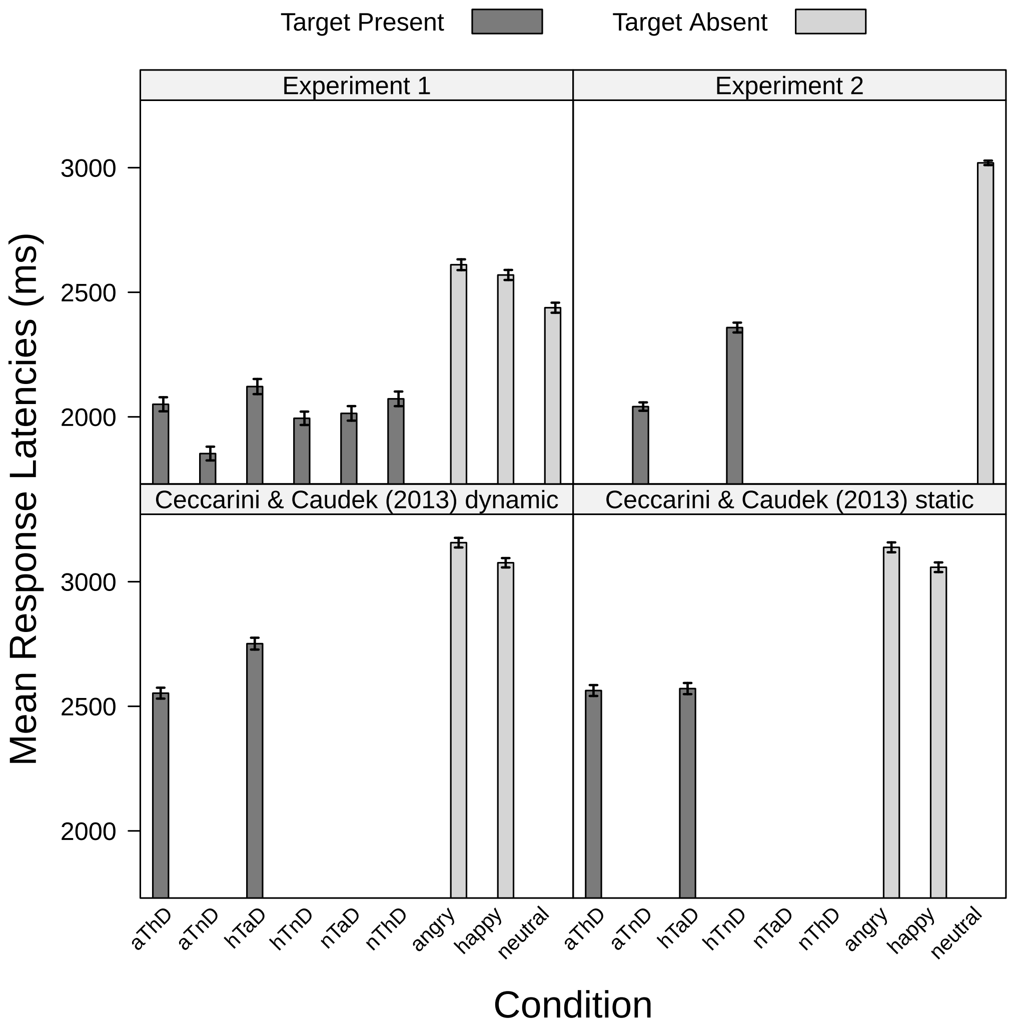

Figure 4: Mean response latencies as a function of Condition (see figure caption 3), for each experiment. Vertical bars indicate standard error of the mean.

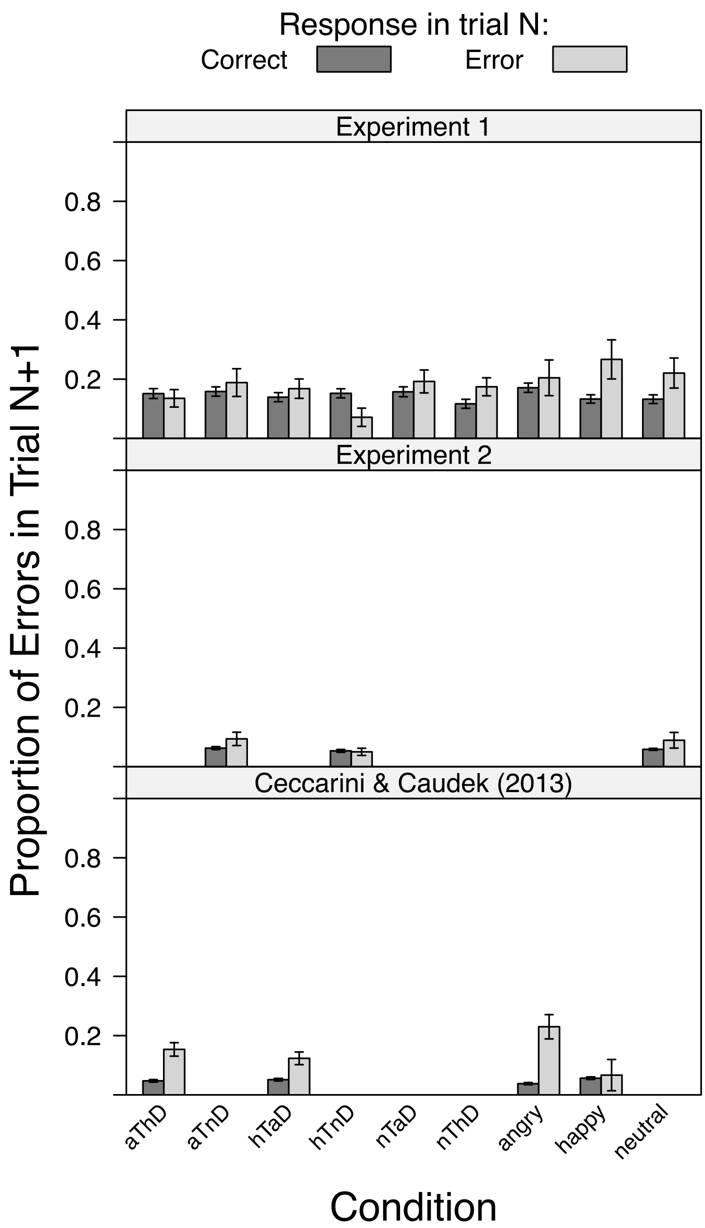

Figure 5: Proportions of errors in trial $N + 1$ as a function of performance accuracy in trial N and Condition (see figure caption 3), for each experiment. Vertical bars indicate standard error of the mean.

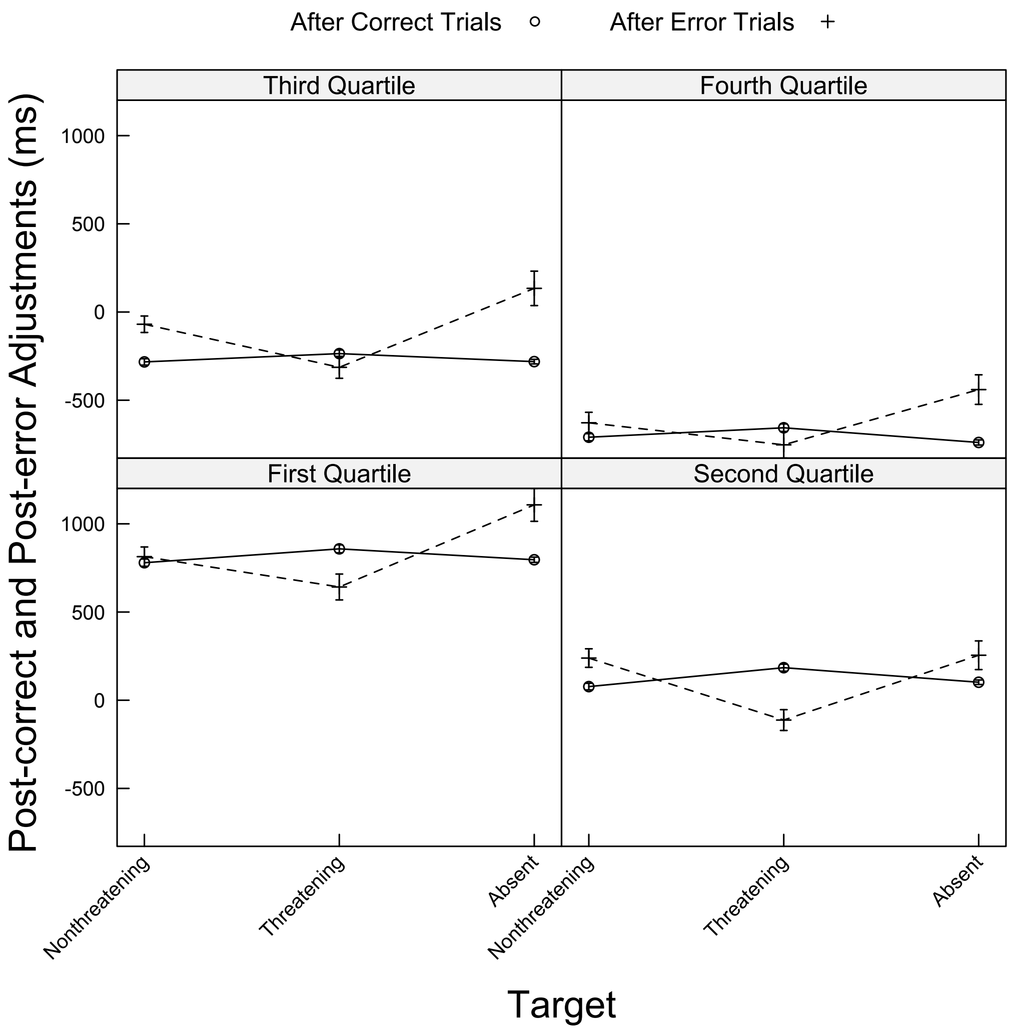

Figure 6: Mean post-correct and post-error adjustments ($RT_{N+1} - RT_{N-1}$, where N, $N + 1$, and $N - 1$ denote a triplet of consecutive trials, with $N - 1$ and $N + 1$ being correctly performed trials) as a function of target type. Each panel describes the subset of trials defined by the quartiles of the distribution of the RTs in the $N - 1$ trials. Data have been combined from the three sets of experiments. Vertical bars indicate standard error of the mean.

Appendix A.

Dutilh et al. (2012) have shown that the traditional way of computing the post-error adjustments, $PES_{traditional} = MRT_{N+1} - MRT_{N-1}$, where MRT is the mean of the RTs, is vulnerable to a confound that occurs when "slow RTs co-occur with low accuracy. In this case, calculation of $PES_{traditional}$ may result in spurious or inflated estimates of PES" (p. 210) – see also Laming (1979). An inflated PES means a spurious or *deflated* estimates of post-error speeding. It is thus interesting to consider whether this confound may occur in the present data. In Figure A.7 are shown, for each Experiment, the mean RTs as a function of the quartiles of binned trials (ordered from 1 to n) for nonthreatening targets, threatening targets, and for distractor-only trials[8]. Figure A.8 shows the proportion of error trials as a function of the quartiles of binned trials (or-

[8]For Experiment 1, an LME autoregressive model with (centered) log Trial number (representing the rank-order of a trial in its experimental sequence) and Condition (nonthreatening target, threatening target, target absent) as fixed-effects, with by-participant random intercepts and random slopes for Trial and Condition, indicated that the Trial × Condition interaction was statistically significant, $\chi^2_2 = 31.46$, $p = .0001$. (log) RTs decreased as a function of Trial for nonthreatening targets, $t_{5486} = -3.56$, $p = .0004$; the effect was the same for threatening targets, $t_{5486} = 0.40$, $p = .6862$; no effect of Trial was instead found for target-absent trials, $t_{5486} = -0.61$, $p = .5427$. The Trial × Condition was statistically significant also for Experiment 2, $\chi^2_2 = 13.13$, $p = .0014$. (log) RTs decreased as a function of Trial for nonthreatening targets, $t_{5021} = -2.07$, $p = .0381$; the effect was the same for threatening targets, $t_{5021} = 0.18$, $p = .8565$; no effect of Trial was instead found for target-absent trials, $t_{5021} = 0.33$, $p = .7387$. The Trial × Condition was statistically significant also for the data of Ceccarini and Caudek (2013), $\chi^2_2 = 26.79$, $p = .0001$. (log) RTs decreased as a function of Trial for nonthreatening targets, $t_{10852} = -2.07$, $p = .0381$; the effect was the same for threatening targets, $t_{10852} = 0.18$, $p = .8565$; the effect of Trial was smaller for target-absent trials, $t_{10852} = 5.17$, $p = .0001$.

dered from 1 to *n*)[9]. It is clear that, in our data, slow RTs tend to co-occur with higher error rates. This consideration strengthens our choice of estimating the post-error and the post-correct RT adjustments as $RT_{N+1} - RT_{N-1}$, as suggested by Dutilh et al. (2012). Figure A.9 shows the mean RTs in the pre-error and post-error trials for nonthreatening targets, threatening targets, and target-absent trials, in the three experiments[10].

[9]For Experiment 1, a probit generalized estimating equation model with an autoregressive lag one correlation structure (Zorn 2001) showed a statistically significant effect of Condition (nonthreatening target, threatening target, target absent), $\chi^2_2 = 24.69$, $p = .0001$. The proportions of error trials were equal .08, .19, and .17 for target-absent, nonthreatening targets and threatening targets, respectively. There as a statistically significant effect of Trial, $\chi^2_1 = 10.83$, $p = .0010$. For nonthreatening targets, an increase of 100 trials had a multiplicative effect of 0.79 on the odds that Y = 1 (error response) – *i.e.*, *p*(error) decreased as a function of trial number. The Condition × Trial interaction was not statistically significant, $\chi^2_2 = 4.01$, $p = .1349$. A similar result was found for Experiment 2. The effect of Condition was statistically significant, $\chi^2_2 = 50.5$, $p = .0001$. The proportions of error trials were equal .02, .13, and .07 for target-absent, nonthreatening targets and threatening targets, respectively. The effect of Trial was statistically significant, $\chi^2_1 = 11.2$, $p = .0008$. For nonthreatening targets, an increase of 100 trials had a multiplicative effect of 0.77 on the odds that Y = 1 (error response). The Condition × Trial interaction was not statistically significant, $\chi^2_2 = 1.7$, $p = .4261$. Similarly, for the data of Ceccarini and Caudek (2013), the effect of Condition was statistically significant, $\chi^2_2 = 15.47$, $p = .0004$. The proportions of error trials were equal .021, .085, and .093 for target-absent, nonthreatening targets and threatening targets, respectively. The effect of Trial was statistically significant, $\chi^2_1 = 17.18$, $p = .0001$. For nonthreatening targets, an increase of 100 trials had a multiplicative effect of 0.68 on the odds that Y = 1 (error response). The Condition × Trial interaction was not statistically significant, $\chi^2_2 = 2.83$, $p = .24347$.

[10]In Experiment 1, an LME model with random effects for participants and stimulus ID, and with fixed effects for Condition (nonthreatening target, threatening target, target-absent) and Pre-error/Post-error Trial (PPT, which identifies the $N - 1$ and $N + 1$ trials) revealed a statistically

————— Please insert Figures A.7, A.8 and A.9 about here —————

significant effect of Condition, χ^2_2 = 63.8, p = .0001. Neither the variable PPT, nor the Condition × PPT interaction were statistically significant, χ^2_3 = 2.59, p = .4599. In Experiment 2, the same analysis showed that the interaction Condition × PPT was statistically significant, χ^2_2 = 10.68, p = .0048, suggesting that the difference in RTs between the pre-error and the post-error trials is smaller for the threatening target trials than in the other trials. Finally, in Experiment 3, there was a significant effect of Condition, χ^2_2 = 51.19, p = .0001; neither the variable PPT, nor the Condition × PPT interaction were statistically significant, χ^2_3 = 2.14, p = .5443.

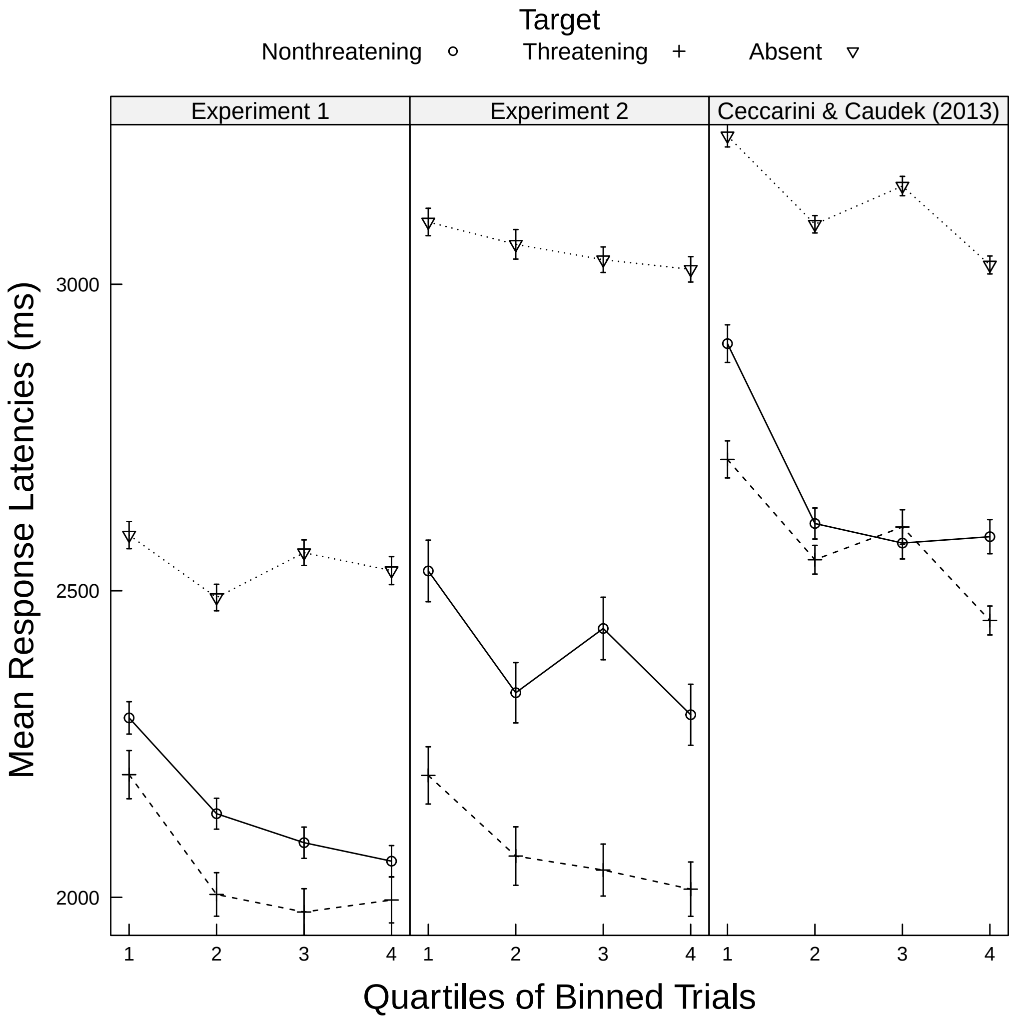

Figure A.7: Mean response latencies as a function of the quartiles of binned trials (ordered from 1 to *n*) and target type, for each experiment. Vertical bars indicate standard error of the mean.

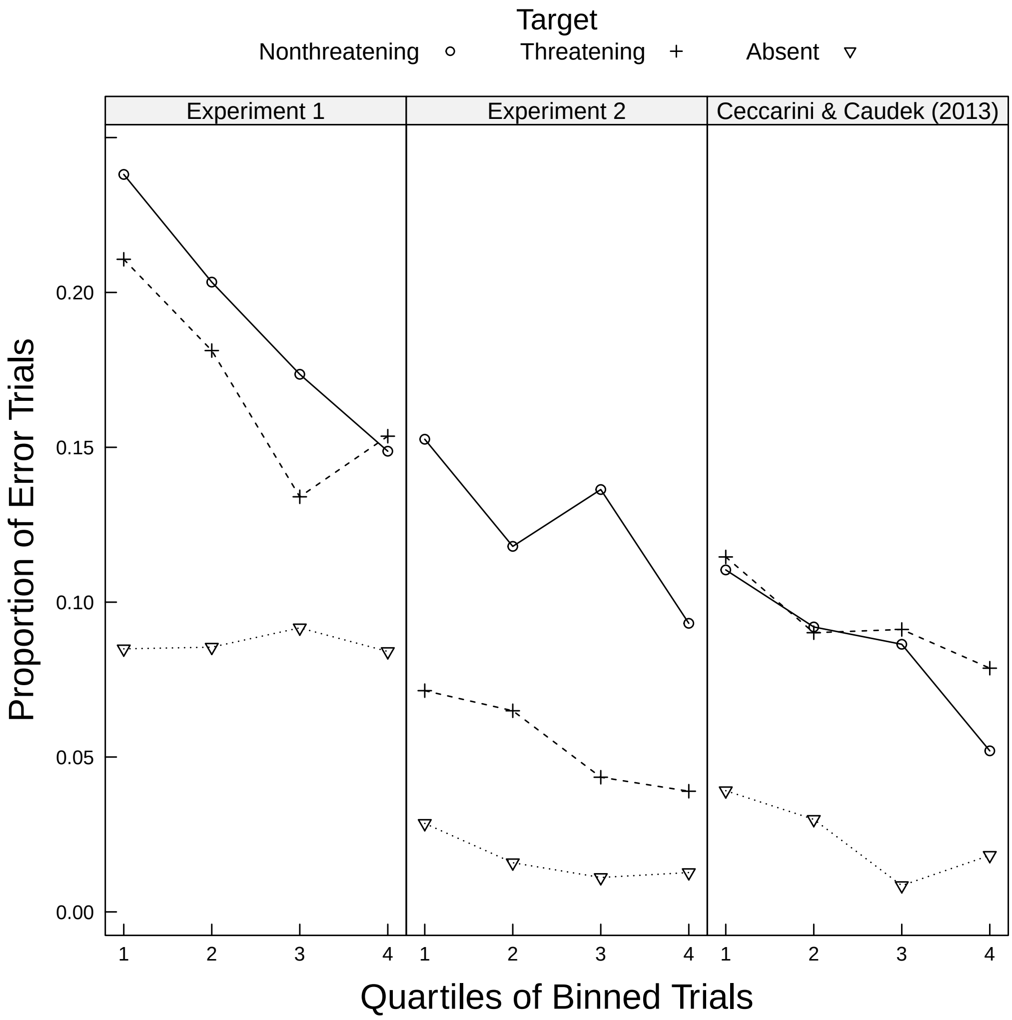

Figure A.8: Proportions of error trials as a function of the quartiles of binned trials (ordered from 1 to *n*) and target type, for each experiment.

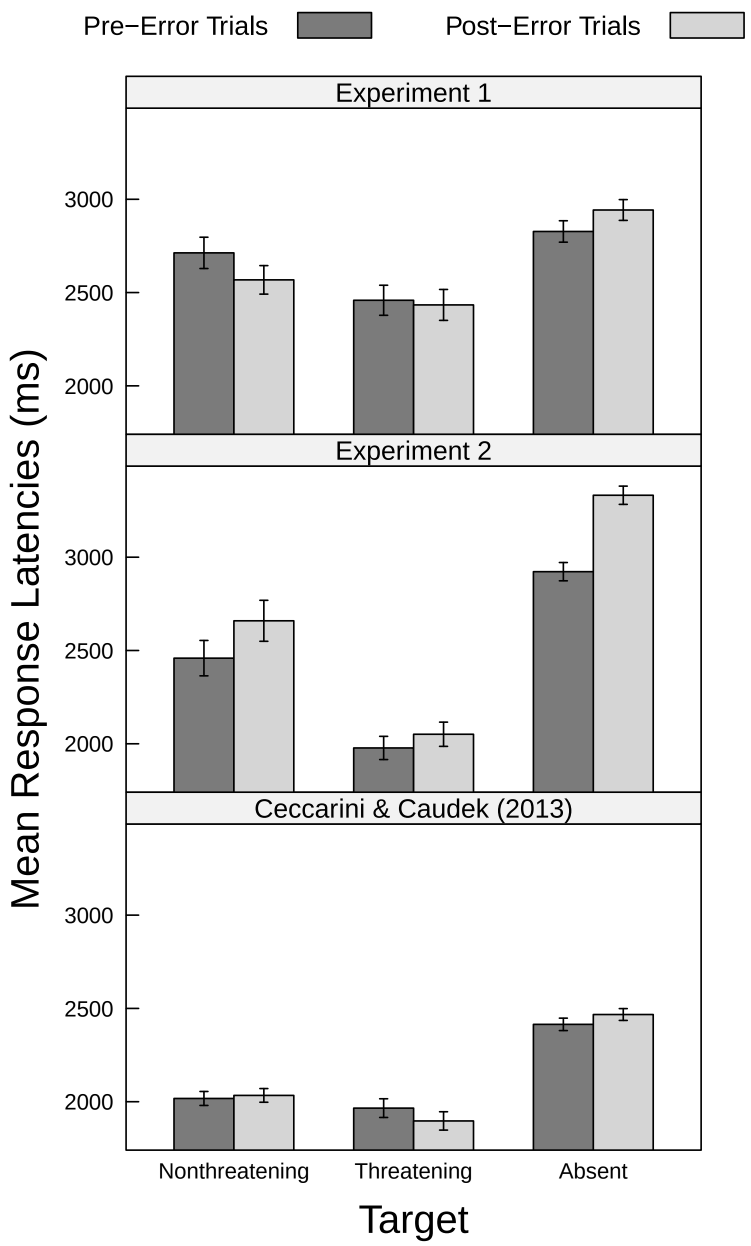

Figure A.9: Mean response latencies for pre-error and post-error trials as a function of target type, for each experiment. Vertical bars indicate standard error of the mean.