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Unpleasant stimuli differentially modulate inhibitory processes in an emotional Go/NoGo task: an event-related potential study

Giulia Buodo[a,b], Michela Sarlo[a,b] ⓘ, Giovanni Mento[a], Simone Messerotti Benvenuti[a] and Daniela Palomba[a,b]

[a]Department of General Psychology, University of Padova, Padova, Italy; [b]Center for Cognitive Neuroscience, University of Padova, Padova, Italy

ABSTRACT

Threat stimuli typically elicit a psychophysiological response pattern supporting the organism's preparation for active defence. Differently, blood stimuli prompt a distinctive autonomic response pattern and sustained processing, which do not call for clear-cut mobilisation for action. However, the contribution of motor disposition in these response patterns remains unclear. One way to address this issue is to investigate whether threat and blood stimuli differentially affect the active suppression of an ongoing motor activity. Thirty-two undergraduates were presented with threat, mutilation, pleasant, and neutral pictures in an emotional Go/NoGo task. The amplitudes of the NoGo-N2 and NoGo-P3 components of the event-related potentials were analysed as indices of conflict monitoring and inhibition of motor response, respectively. Reaction times to Go trials were significantly faster for threat than for mutilations. The NoGo-N2 was significantly larger to threat than to mutilations, whereas the NoGo-P3amplitude did not differ between the two conditions. These findings suggest that threat stimuli facilitated the execution of a prepotent response and enhanced conflict monitoring when action must be withheld. In contrast, blood stimuli did not either promote action in the Go trials or increase conflict in the NoGo condition, suggesting a response pattern compatible with defensive immobility.

Introduction

Emotions have been viewed as action dispositions, or motivationally tuned states of readiness (see Frijda, Kuipers, & Ter Schure, 1989; Lang, 1995) that prepare the organism to respond adaptively to environmental stimuli, irrespective of whether or not the acts themselves actually occur. When affective percepts (e.g., pictures or film clips) are employed as experimental stimuli for the investigation of emotional responses, overt actions are usually not included in the emotional output programmes. However, emotional perceptual stimuli can match the "real" object or event to such an extent as to activate a disposition towards action, reflected in a pattern of somatic, autonomic, and cortical changes similar to that prompted by the "real" stimuli (Bradley & Lang, 2000; Lang, Greenwald, Bradley, & Hamm, 1993).

The motivational perspective on emotion assumes that hedonic valence and arousal are the fundamental dimensions of emotions, reflecting the direction (approach–withdrawal) and intensity of the behavioural dispositions supported by the motivational systems (e.g., Bradley & Lang, 2000; see also Russell, 2003). According to this perspective, physiological and behavioural responses to emotional stimuli also reflect these dimensions, covarying primarily with self-reports of affective valence or arousal (Bradley & Lang, 2000). However, unpleasant visual stimuli depicting threatening (e.g., pictures of attacking humans or animals, aimed weapons) vs. blood-related stimuli (e.g., pictures of injuries and mutilated

bodies) have been shown to elicit different psycho-physiological response patterns in healthy individuals. Specifically, a robust and reliable potentiation of the startle eyeblink is elicited when viewing pictures of attacking humans/animals (see Bradley, Codispoti, Cuthbert, & Lang, 2001; Sarlo, Buodo, & Palomba, 2010; Schupp et al., 2004; Stanley & Knight, 2004), indicating priming of the motor system for defensive action. Also, reaction times (RTs) to tone probes are faster during the viewing of threat relative to other highly arousing unpleasant or pleasant pictures (Buodo, Sarlo, & Palomba, 2002), indicating that threat stimuli require fewer attentional resources, with the possible function of facilitating rapid adjustments to environmental demands. When using dynamic emotional stimuli, such as film clips depicting threat of violence, a coherent sympathetic activation has been reported, as indicated by increased skin conductance, heart rate acceleration and decrease of T-wave amplitude (indicating higher sympathetic cardiac control; Palomba, Sarlo, Angrilli, Mini, & Stegagno, 2000), along with startle reflex potentiation (Kaviani, Gray, Checkley, Kumari, & Wilson, 1999). Overall, the response pattern to threat stimuli is strongly suggestive of the organism's mobilisation for active (i.e., fight/flight) defence.

In contrast, the response pattern to blood-related stimuli does not appear to be coherently organised to support defensive action. Notably, during the viewing of pictures of mutilated bodies and injuries, healthy individuals do not show the startle blink potentiation expected for high-arousal unpleasant stimuli (Bradley et al., 2001; Sarlo et al., 2010; Schupp et al., 2004; Stanley & Knight, 2004). In addition, the viewing of a surgery film clip elicits heart rate reduction and T-wave increase (indicating lower sympathetic cardiac control; Palomba et al., 2000), along with inhibition of the startle reflex (Kaviani et al., 1999). Also, pictures of mutilations/injuries have been found to elicit larger positivity of the event-related potentials (ERPs; Buodo, Sarlo, Codispoti, & Palomba, 2006; Schäfer, Scharmüller, Leutgeb, Köchel, & Schienle, 2010; Schupp et al., 2004), greater cortical activation (Sarlo, Buodo, Poli, & Palomba, 2005), and slower RTs to tone probes presented during viewing (Buodo et al., 2002) as compared with threat pictures, consistently suggesting increased and prolonged attentional engagement. In sum, blood-related stimuli appear to command heightened attentional allocation in the absence of robust and clear-cut defensive mobilisation. It might be

speculated that this pattern is a human analogue of defensive freezing behaviour (Azevedo et al., 2005; Facchinetti, Imbiriba, Azevedo, Vargas, & Volchan, 2006; Hagenaars, Stins, & Roelofs, 2012; Stins & Beek, 2007), originally aimed at avoiding detection by predators through "attentive" immobility.

However, it would be difficult to claim that the above-described response patterns unequivocally reflect the level of action readiness prompted by affective stimuli depicting threat and mutilations. That is, changes in startle reflex amplitude, heart rate, and electrodermal activity during picture or film viewing all reflect, more or less directly, corresponding changes in orienting, information gathering, and attentional engagement (see Bradley et al., 2001; Lang et al., 1993). In particular, the lack of startle blink potentiation during the viewing of blood-related pictures might result from both increased attentional engagement and reduced mobilisation for active defence, thus making it difficult to discern the unique contribution of action readiness in the observed response (see Sarlo et al., 2010). Similarly, heart rate deceleration can index both sensory intake (Lacey & Lacey, 1974) and reduced metabolic demand of ongoing somatic activity (Obrist, 1981). Thus, the available data do not provide specific and direct indications as to the organism's condition of action readiness upon confrontation with threat and mutilation stimuli.

Few studies have demonstrated the involvement of the motor control system in determining the response pattern elicited by blood stimuli. By exploring the dynamics of postural control during passive viewing, reduced body sway (Azevedo et al., 2005; Facchinetti et al., 2006) and increased rigidity (Facchinetti et al., 2006) were found during the viewing of mutilation as compared with neutral or pleasant pictures. However, when directly comparing mutilation with threat pictures, only modest effects of mutilations on postural changes were found, with a shorter sway path only when balance was challenged (i.e., with a unipedal stance) (Stins & Beek, 2007). On a different but related front, threat pictures were found to speed up the initiation of withdrawal movements to a greater extent than mutilation, pleasant, and neutral pictures (Coombes, Cauraugh, & Janelle, 2007). Taken together, these results suggest a differential modulation of motor disposition by threat and blood-related cues. However, little is known about whether and how these unpleasant conditions differentially affect the active suppression of an ongoing

motor activity. As a core component of executive control, the ability to actively inhibit prepotent or inappropriate responses to achieve a goal (i.e., "response inhibition", or "inhibition of action"; Kok, Ramautar, De Ruiter, Band, & Ridderinkhof, 2004) is indeed critical for successful adaptation to complex social environments. Interestingly, the neural activity related to emotion and that associated with response inhibition have been found to be closely interrelated (Elliott, Rubinsztein, Sahakian, & Dolan, 2000; Goldstein et al., 2007; Shafritz, Collins, & Blumberg, 2006). Therefore, measuring how emotion facilitates or hinders motor inhibition provides a complementary way to test the contribution of action readiness in the response to threat- and blood-related stimuli.

In this context, a useful tool is the emotional Go/NoGo paradigm. In the classic Go/NoGo task (see Falkenstein, Hoormann, & Hohnsbein, 1999), a continuous series of stimuli is presented, including Go cues, to which subjects are required to respond as quickly as possible, and NoGo stimuli, to which subjects have to withhold responding. The high frequency of Go cues (≥70%) determines a prepotent tendency to respond, that must be inhibited upon occurrence of infrequent NoGo stimuli. The recording of the ERPs in response to Go and NoGo stimuli has revealed two inhibition-related components, that is, the NoGo-N2 and the NoGo-P3 (Eimer, 1993; Kiefer, Marzinzik, Weisbrod, Scherg, & Spitzer, 1998). These components have a fronto-central scalp distribution and are reliably larger after NoGo than after Go stimuli. The NoGo-N2 and the NoGo-P3 are thought to reflect different aspects of response inhibition, with NoGo-N2 reflecting the detection of conflict between response execution and inhibition (see Nieuwenhuis, Yeung, van den, Wildenberg, & Ridderinkhof, 2003), and NoGo-P3 more specifically indexing successful motor response suppression and/or the evaluation of the outcome of inhibition (see Bruin, Wijers, & van Staveren, 2001).

In the emotional variant of the Go/NoGo task, affective stimuli (e.g., emotional words, facial expressions, or pictures) are used in place of standard neutral stimuli, thus providing a reliable measure of the emotional modulation of behavioural inhibition (Schulz et al., 2007). Importantly, in some studies, the emotional valence of the stimuli has been used as an explicit cue for motor response (e.g., respond to positive words and withhold responding to negative and neutral ones; see Chiu, Holmes, & Pizzagalli, 2008), while in others the emotional content was incidental with respect to task demands (e.g., respond to a specific colour of picture frames, and withhold responding to a different colour; see Albert, López-Martín, Tapia, Montoya, & Carretié, 2012). According to most of the available results, the amplitude of NoGo-N2 appears not to be modulated by the emotional valence of the stimuli (Albert, López-Martín, & Carretié, 2010; Chiu et al., 2008; Todd, Lewis, Meusel, & Zelazo, 2008; Yu, Yuan, & Luo, 2009; Zhang & Lu, 2012). However, few studies found greater Nogo N2-related activity for arousing negative pictures (Albert et al., 2012) or highly unpleasant stimuli (Yuan et al., 2012) as compared to pleasant and neutral stimuli, suggesting enhanced monitoring of response conflict. On the other hand, the NoGo-P3 has been reported to be larger to pleasant than unpleasant pictures (Albert et al., 2010, 2012), suggesting that the tendency to approach appetitive stimuli might make inhibiting responses more difficult. Differently, Yuan et al. (2012) found that highly unpleasant pictures elicited reduced inhibitory control (in the P3 time range) than mildly unpleasant and neutral stimuli, whereas a similar modulation was not observed for pleasant stimuli. Other studies found the NoGo-P3 to be unaffected by the emotional content of the stimuli (Chiu et al., 2008), or to be larger to both positive and negative facial expressions as compared with neutral (Zhang & Lu, 2012), suggesting that the more attentional resources are allocated to emotion-laden stimuli, the more effectively the response must be inhibited. Thus, it is still unclear how affective stimuli modulate inhibitory processes, and no study to our knowledge has yet investigated whether inhibition processes are differentially recruited when withholding an action in response to specific unpleasant contents.

The aim of the present study was to investigate whether the different response patterns that have been described in healthy individuals for threat- and blood-related stimuli are related to different dispositions to action, which would be reflected, in turn, in greater or lesser difficulty withholding a prepotent motor response. We employed an implicit emotional Go/NoGo task, where Go and NoGo cues were unrelated to the emotional content of stimuli. By using such indirect task, it is possible to avoid explicit stimulus categorisation interfering with implicit emotional processing, and to let the emotional modulation of action readiness spontaneously emerge (see also Albert et al., 2010, 2012). We hypothesised that activating inhibitory control mechanisms for inhibiting a

prepotent response tendency would be more difficult for threat than for blood stimuli. This would be reflected, at neural level, in larger amplitudes of the NoGo-N2 and the NoGo-P3, and, at behavioural level, in faster RTs to Go trials and more commission errors in NoGo trials.

As a secondary goal, we included equally arousing pleasant stimuli to investigate independent effects of appetitive motivation supporting an action tendency (i.e., approach) opposite to that elicited by threat-related stimuli. This allowed clarifying inconsistencies found in previous research. In addition, recording the neural and behavioural responses to Go and NoGo pleasant stimuli could provide useful information to better characterise the influence of different emotional contents on inhibitory processes. Indeed, action dispositions associated with different emotional stimuli should be reflected in the degree of difficulty inhibiting prepotent responses. However, based on the limited evidence available (Albert et al., 2012), it is possible that pleasant and threat-related stimuli differentially affect conflict- and inhibition-related components of inhibitory control. Neutral stimuli were included as a non-emotional condition that, as such, would not pose any action-related effect on inhibitory control.

Methods

Participants

Thirty-two healthy undergraduates (15 males; mean age 23.2 ± 1.7 years) from the University of Padova volunteered for the study. All participants were right-handed and had normal or corrected-to-normal vision. The study was approved by the local ethics committee and all volunteers gave written consent prior to participation.

Stimuli and procedure

The experimental stimuli consisted of 120 digitised colour pictures (650×850 pixel) selected from the International Affective Picture System (Lang, Bradley, & Cuthbert, 2008) and divided into four categories, that is, Threat (attacking humans and animals), Mutilations (mutilated bodies and injuries), Pleasant (erotic couples and sport/adventure), and Neutral (household objects, urban landscapes and neutral people). Thirty pictures were presented for each emotional category. Threat and Mutilation stimuli were balanced for mean

normative valence ratings (Threat = 2.99; Mutilations = 2.18). Emotional categories were matched for mean normative arousal ratings (Threat = 6.43; Mutilations = 6.28; Pleasant = 6.56; Neutral = 2.95). As confirmed by an univariate analysis of variance (ANOVA; $F(3, 118) = 285.24$, $p < .0001$), normative arousal ratings for emotional pictures were significantly higher than for neutral pictures (all $ps < .0002$) and did not differ as a function of emotional categories (all $ps > .39$).

Each picture was surrounded by a coloured frame (pink or blue), that cued the participant to either press a key (Go trials) or withhold the key press response (NoGo trials). Frame colours indicating Go and NoGo trials were counterbalanced across participants. For each emotional category, the Go/NoGo trial ratio was 70:30. The presentation order was semi-randomised, with the constraint of no consecutive NoGo trials. Each picture was presented five times during two consecutive blocks of 300 trials each, so that for each category, there were 105 Go and 45 NoGo trials.

Each trial began with a 500-ms white central fixation cross on a black background, followed by the presentation of a framed picture. NoGo stimuli were displayed for a fixed duration of 600 ms, whereas Go stimuli were terminated by key press responses (up to 1000 ms). The reasons for having Go stimuli disappear upon key press were to potentiate the behavioural expression of readiness to disengage from interaction (i.e., avoidance) with unpleasant stimuli. The inter-trial interval varied between 500 and 800 ms.

Participants were seated 100 cm away from a computer monitor, in a dimly lit, sound-attenuated room, and an elastic cap embedded with 19 electrodes was applied for electroencephalographic (EEG) recording. After a 10-min adaptation period, instructions for the task were given. Participants were required to press a key with the right index finger as rapidly and accurately as possible whenever a picture surrounded by the Go colour frame was presented, and to withhold pressing the key when the picture had a NoGo colour frame. Picture content was incidental to the task, and therefore it was unrelated to Go/NoGo instructions. Also, participants were asked to maintain fixation and avoid blinking during picture presentation. Ten practice trials with neutral pictures (seven Go and three NoGo) were provided before the experimental session. The task was presented by a Pentium IV computer on a 19-inch computer screen, using E-prime 2.0 presentation software (Psychology Software Tools, Pittsburgh, PA, USA).

Behavioural measures

RTs to Go trials and omission and commission error rates (i.e., no responses in Go trials and button presses in NoGo trials, respectively) were calculated for each emotional category. RTs below 150 ms were excluded from analyses.

RTs were analysed with an univariate ANOVA, with Category (Threat, Mutilations, Pleasant, Neutral) as independent variable. The ANOVA on error rates in Go and NoGo trials included Category and Trial Type (Go, NoGo) as independent variables. The Bonferroni correction for post-hoc comparisons was applied.

Electrophysiological recording and data analyses

The EEG was recorded with tin electrodes mounted in an elastic cap from 19 scalp sites (Fp1, Fp2, F3, Fz, F4, F7, F8, C3, Cz, C4, P3, Pz, P4, T3, T4, T5, T6, O1, O2) referenced to linked mastoids, according to the International 10–20 System. For the purpose of artefact scoring, vertical and horizontal electrooculograms (EOGs) were recorded from electrode pairs (bipolar) placed above and below the right eye and at the external canthi of both eyes. All electrode impedances were kept below 5 kΩ. Signals were bandpass filtered (0.05–40 Hz), digitised at 250 Hz (16 bit A/D converter; resolution 0.033 uV/LSB) and stored on to a Pentium IV computer. The EEG and the EOG signals were filtered and amplified by a SynAmps unit amplifier (Neuroscan, Inc., Compumedics, Ltd, El Paso, TX, USA).

Continuous EEG data were refiltered offline with a low-pass filter set at 30 Hz (12 dB/oct, zero phase filter) and corrected for eyeblinks using a regression-based weighting coefficients technique, as implemented in the SCAN 4.1 software (Edit module; Neurosoft, Inc.). The EEG was then segmented offline into 700-ms epochs from 100 ms before to 600 ms after picture onset. The EEG epochs were baseline-corrected against the mean voltage during the 100-ms prestimulus period. All EEG epochs were visually scored for eye movements and other artefacts, and each portion of data containing artefacts greater than ±70 uV in any channel was rejected for all the recorded channels prior to further analysis. Artefact-free trials with correct behavioural responses were separately averaged for each subject and each condition. ERP analyses focused on fronto-central sites, where N2 and P3 amplitudes reach their maximum on response inhibition tasks (e.g., Falkenstein et al.,

1999). On the basis of the inspection of grandaverage ERP waveforms, the N2 was computed as the mean amplitude in the 230–290 ms time window from stimulus onset, and the P3 as the mean amplitude in the 340–440 ms time window from stimulus onset.

A repeated measures ANOVA was conducted on NoGo trials, with Category (Threat, Mutilations, Neutral, Pleasant), Area (frontal, central, parietal), and Laterality (left, midline, right) as within-subject factors. The reasons for focusing on NoGo trials were twofold, (1) only NoGo-N2 and NoGo-P3 amplitude reflect inhibitory processes and are thus directly relevant for the research question addressed in the present study, and (2) NoGo and Go stimuli had different durations, as NoGo stimuli were displayed for 600 ms, whereas Go stimuli were terminated by key press responses. Therefore, a possible overlap with ERP activity related to picture offset in the Go condition would have made N2 and P3 amplitudes to Go and NoGo stimuli not directly comparable. However, preliminary ANOVAs including Trial type (Go, NoGo) were performed to ensure the presence of the Go/NoGo effect (i.e., larger N2 and P3 amplitudes to NoGo than Go trials) for each emotional category. For post-hoc comparisons, the Bonferroni correction was applied.

Pearson's correlations between mean RTs and mean error rates, and between the behavioural and the electrophysiological measures, were performed across emotional categories to further assess the functional meaning of the obtained response patterns.

Results

Behavioural measures

The Category effect ($F(3, 93) = 21.35$, $p < .0001$, $\eta_p^2 = .41$) was significant for RTs to Go stimuli. Specifically, RTs to Threat pictures were significantly faster than to Mutilation and Pleasant pictures ($ps < .002$), and RTs to Mutilations were significantly slower than to Neutral pictures ($p < .0001$). The comparisons between RTs to Threat and Neutral pictures and between RTs to Mutilation and Pleasant pictures were not significantly different (see Table 1).

With respect to error rates, the Trial type main effect ($F(1, 31) = 90.04$, $p < .0001$, $\eta_p^2 = .74$) showed that, overall, error rates were higher on NoGo than Go trials (.07 vs. .003, respectively). The Trial type × Category interaction ($F(3, 93) = 3.75$, $p = .014$, $\eta_p^2 = .11$) further specified that in the NoGo condition,

Table 1. Means (and standard deviations) for RTs in Go trials and omission/commission error rates for each emotional category

Category	Go RTs (ms)	Omission error rates	Commission error rates
Threat	354.51 (26.61)[a]	.002 (.005)[a]	.05 (.05)[a]
Mutilations	366.94 (31.23)[b]	.005 (.007)[a]	.08 (.06)[a,b]
Neutral	352.47 (26.84)[a]	.002 (.005)[a]	.07 (.05)[a,b]
Pleasant	363.62 (29.15)[b]	.004 (.01)[a]	.08 (.05)[b]

Notes: Within each dependent variable, letter sets indicate the results of Bonferroni corrected post-hoc comparisons. Categories that share at least one letter do not significantly differ.

commission errors were significantly higher for Pleasant as compared with Threat trials ($p = .001$). All other comparisons failed to reach significance. Error rates in the Go condition did not vary as a function of emotional content.

Event-related potentials

The preliminary ANOVAs conducted on N2 and P3 amplitudes yielded a main effect of Trial type ($F(1, 31) = 71.54$, $p < .0001$, $\eta_p^2 = .70$, $F(1, 31) = 26.46$, $p < .0001$, $\eta_p^2 = .46$, respectively) that confirmed the larger amplitude of both N2 and P3 in NoGo than Go trials (Figure 1). T-test comparisons further indicated a significant Go/NoGo effect for each emotional category (all $ps < .003$).
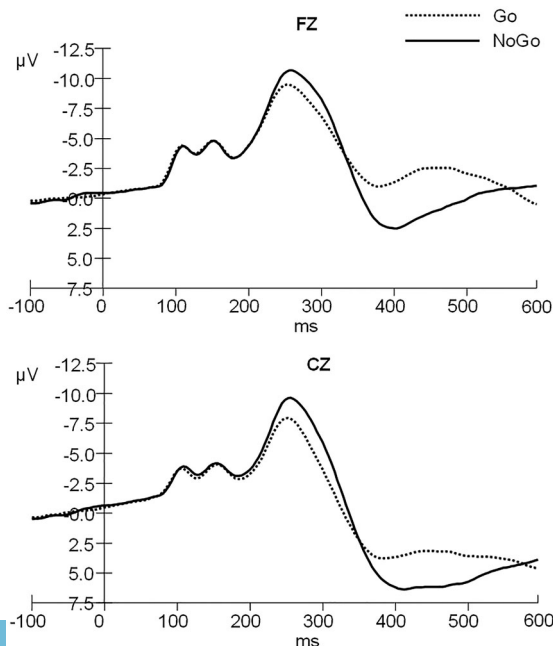

Figure 1. Grand average ERP waveforms recorded at Fz and Cz sites to Go and NoGo trials.

The ANOVA on NoGo trials revealed a main effect of Category ($F(3, 93) = 12.31$, $p < .0001$, $\eta_p^2 = .28$) for the N2. As reported in Table 2, the N2 amplitude was significantly larger to Threat than to Mutilation pictures ($p = .035$); the N2 to Pleasant pictures did not differ significantly from the N2 to Threat and Mutilation pictures; the N2 to Neutral stimuli was significantly larger than to all other picture contents (all $ps < .02$). The NoGo-N2 was larger at frontal than at central sites, and at central than at parietal sites (Area main effect: $F(2, 62) = 68.65$, $p < .0001$, $\eta_p^2 = .69$). A larger amplitude was found along the midline as compared with the right and left sides (Laterality main effect: $F(2, 62) = 81.29$, $p < .0001$, $\eta_p^2 = .72$). As clarified by the significant Area × Laterality interaction ($F(4, 124) = 16.36$, $p < .0001$, $\eta_p^2 = .35$), larger N2 amplitudes were observed at F3 and F4 than at C3 and C4, whereas no significant difference was found between Fz and Cz, at which the maximal amplitude was obtained. A significant Emotion × Area × Laterality interaction was also found ($F(12, 372) = 2.21$, $p = .011$, $\eta_p^2 = .07$). However, the emotion effects did not survive the Bonferroni correction, and no further information was provided.

With regard to the NoGo-P3, the Category main effect was significant ($F(3, 93) = 19.59$, $p < .0001$, $\eta_p^2 = .39$). As reported in Table 2, P3 amplitudes to Threat, Mutilation, and Pleasant pictures were significantly larger than to Neutral pictures (all $ps < .0001$) and did not differ from each other. Overall, the NoGo P3 was larger at parietal than central sites, and at central than frontal sites (Area main effect: $F(2, 62) = 46.80$; $p < .0001$, $\eta_p^2 = .60$). The significant Category × Area interaction ($F(6, 186) = 5.86$; $p < .0001$, $\eta_p^2 = .16$) only specified that the Category effect was significant in all three areas, but largest in the parietal area.

The significant Area × Laterality interaction ($F(4, 124) = 8.05$; $p < .0001$, $\eta_p^2 = .21$) indicated that only in the parietal area the P3 amplitude was larger at lateral sites than at midline ($ps < .004$), whereas no differences in laterality were found in the frontal and central areas.

Figure 2 shows the grand average ERP waveforms for Threat, Mutilation, Pleasant, and Neutral NoGo stimuli.

Correlations

A significant positive correlation was found between mean commission errors and mean omission errors only for Pleasant pictures ($r = .41$, $p = .02$).

Table 2. Means (and standard deviations) for NoGo N2 and P3 amplitudes for each emotional category

Category	NoGo-N2	NoGo-P3
Threat	−5.76 (4.00)[a]	5.16 (5.22)[a]
Mutilations	−4.93 (4.02)[b]	5.09 (4.96)[a]
Neutral	−6.88 (4.12)[c]	2.30 (4.86)[b]
Pleasant	−5.63 (4.14)[a,b]	4.79 (5.12)[a]

Notes: Within each dependent variable, letter sets indicate the results of Bonferroni corrected post-hoc comparisons conducted on the ANOVA *Category* main effects. Categories that share at least one letter do not significantly differ.

Significant positive correlations were found between mean commission errors and mean NoGo-P3 amplitudes at Cz and C3 EEG sites only for Threat pictures ($rs = .36$, $ps < .05$).

Significant negative correlations were found between mean Go-RTs and mean NoGo-P3 amplitudes at F3, F4, C3 and C4 EEG sites for Mutilation pictures, at Fz and F4 EEG sites for Neutral pictures, and at Fz, F4, Cz, C4 EEG sites for Pleasant pictures (rs ranging from −.36 to −.46, ps ranging from .046 to .008).

No significant correlations emerged between performance measures and NoGo-N2 amplitudes for any of the emotional categories.
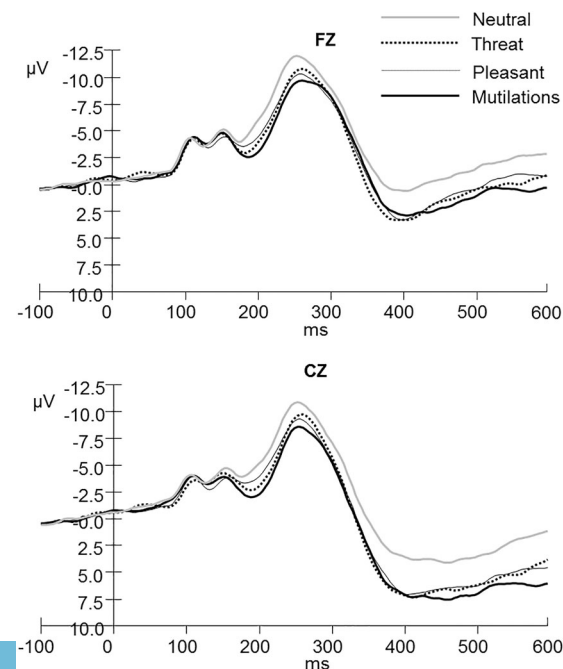

Figure 2. Grand average ERP waveforms recorded at Fz and Cz sites to NoGo trials for Threat, Mutilation, Pleasant, and Neutral pictures.

Discussion

The present study was aimed at investigating the modulation of threat- and blood-related stimuli over action readiness, as reflected in their ability to facilitate or hinder the inhibition of prepotent responses. The ERPs were recorded during an implicit emotional Go/NoGo task, requiring participants to respond or withhold a motor response to frames of different colours surrounding emotional pictures. We hypothesised that threat-related stimuli would elicit larger amplitudes of the NoGo-N2 and NoGo-P3, faster RTs to Go trials, and more commission errors in NoGo trials, reflecting greater difficulty inhibiting a prepotent response tendency as compared with blood-related stimuli.

As expected, employing an emotional Go/NoGo task with a 70:30 Go/NoGo ratio proved to be effective in inducing prepotent response tendencies, as indicated by significantly higher error rates in NoGo (i.e., commission errors) than in Go (i.e., omissions) trials. Crucially, the task was effective in activating the processes involved in response inhibition, as a Go/NoGo effect was reliably obtained for both the N2 and the P3 ERP components (i.e., larger amplitudes to NoGo than Go trials) for each emotional category.

A key finding in the present study was the modulation operated by specific unpleasant contents over inhibitory processes at both behavioural and neural levels. On the behavioural level, the dominant tendency to respond to frequent Go cues was differently affected by the unpleasant picture context, in that RTs were significantly faster to threat than to mutilations. Such finding suggests that action readiness was specifically facilitated when threat pictures were presented. This interpretation is further strengthened by the significant difference found with the pleasant, comparably arousing pictures, which produced slower RTs. Consistently, the N2 ERP amplitude in NoGo trials was found to be larger to threat than to mutilation pictures, suggesting that greater response conflict was generated when NoGo stimuli required to refrain from prepotent responding in the context of threat- than blood-related stimuli.

In the last decade, it has become increasingly clear that the Nogo-N2 does not properly reflect response inhibition, or only to a limited extent (Bruin et al., 2001; Donkers & van Boxtel, 2004; Nieuwenhuis et al., 2003). In the present study, the lack of significant correlations between performance measures and Nogo-N2 amplitudes for any of the employed stimulus

categories seems to support this interpretation. Instead, this ERP component is now more commonly regarded as the electrophysiological correlate of conflict monitoring performed by the anterior cingulate cortex (ACC; Donkers & van Boxtel, 2004), as supported by source localisation analysis (Bekker, Kenemans, & Verbaten, 2005; Nieuwenhuis et al., 2003) and neuroimaging evidence showing that ACC activity is strongly engaged during Go/Nogo tasks (Braver, Barch, Gray, Molfese, & Snyder, 2001; De Zubicaray, Andrew, Zelaya, Williams, & Dumanoir, 2000). As a critical remark, in this context, the conflict is supposed to arise between the generation and the suppression of the overt response (Braver et al., 2001). Therefore, the nature of conflict seems to lie at the level of response (rather than stimulus) stage of processing, where the internal representation of response withholding actively competes with the internal representation of overt response (Botvinick, Cohen, & Carter, 2004; Braver et al., 2001), in line with the evidence of extensive connections between ACC and premotor, supplementary motor, and primary motor areas (e.g., Paus, 2001). Recent studies suggest that dorsal ACC activity, in particular, critically reflects disengagement from an ongoing incorrect action, clearing the way for the correct response (Hochman, Vaidya, & Fellows, 2014), and that adaptive adjustment of behaviour reflected by a variety of control-related ERP components is related to increased frontal midline theta signals generated in the dorsal ACC (Cavanagh & Shackman, 2015). Following the conflict-monitoring hypothesis, we suggest that the representation of the Go response had a greater level of readiness, and participants' response tendency was more strongly biased towards the Go response during the processing of threat than blood-related stimulus. In other words, the conflict arising when the prepotent response tendency established by Go trials must be overridden might be stronger in the case of threat pictures because of the intrinsic ability of threat stimuli to activate mobilisation for rapid response. As the other side of the coin, less conflict occurs when the representation of response withholding must override the activation of the Go response to blood-related pictures because these stimuli would inherently promote defensive immobility.

Interestingly, however, the NoGo-P3 was not modulated by the content of the emotionally arousing pictures. No differences in amplitude were observed between threat, mutilation or pleasant pictures, indicating that specific emotion did not differentially

affect inhibitory processes at the stage of response inhibition proper. Indeed, the dominant position in the relevant literature is that the NoGo-P3 is directly related to the suppression of an overt motor response (Huster, Enriquez-Geppert, Lavallee, Falkenstein, & Herrmann, 2013). In particular, while peaking too late (between 340 and 440 ms in the present study) to reflect a processing stage representing actual response inhibition, this ERP component might rather signal the closure of the inhibition process after the decision (Gajewski & Falkenstein, 2013), the evaluation of the inhibitory performance (Bruin et al., 2001; Roche, Garavan, Foxe, & O'Mara, 2005), or the effectiveness of motor inhibition engaged in or near the motor or premotor cortices (Kok et al., 2004; Ramautar, Kok, & Ridderinkhof, 2004). On these grounds, the results obtained for the NoGo-P3 indicate that the stronger response tendency elicited by threat than blood-related stimuli, reflected in the faster RTs to Go cues and the greater conflict monitoring in the NoGo condition, was not paralleled by less efficient motor inhibition when responses had to be withheld. This conclusion is strongly supported by the lack of difference in commission error rates between threat and mutilation pictures. Therefore, despite the greater conflict between the generation and the inhibition of the overt response, threat stimuli seem to tune inhibitory processes to effective regulation of performance, that is, greater response tendency when action is required, associated with effective inhibition when withholding is more appropriate (cf. Nieuwenhuis et al., 2003), thus implying a lack of speed–accuracy trade-off in the context of Go/NoGo tasks. Such efficiency of inhibitory control would play a key role in providing flexible adaptation to rapidly changing environmental demands in the face of danger. In this framework, the positive correlation between NoGo-P3 amplitude and commission errors, which was observed at central locations for threat pictures only, suggests that the underlying inhibitory process modulated by this emotional condition is mainly related to the evaluation of the inhibitory performance in case of failed stops (cf. Bruin et al., 2001; Roche et al., 2005). In contrast, for all the other conditions (i.e., mutilation, pleasant, and neutral pictures), negative correlations emerged at frontocentral sites between NoGo-P3 amplitude and Go-RTs, indicating that a more prepotent tendency to respond was associated with a greater and/or more effortful inhibitory response. This relationship has been observed with classic, non-emotional Go/

NoGo tasks and is taken to support the idea that the NoGo-P3 reflects an inhibitory mechanism per se (Smith, Johnstone, & Barry, 2008; Vallesi, 2011; see Dimoska, Johnstone, & Barry, 2006, for similar results with a stop-signal task). Thus, our results suggest that the NoGo-P3 may be specifically modulated by threat stimuli in relation to the evaluation of the inhibitory performance (cf. Roche et al., 2005), whereas under the other conditions, its amplitude may mainly reflect a task-related need for greater inhibitory control in relation to faster go-responses.

In contrast with what previously reported by Albert et al. (2010, 2012), in the present study, pleasant pictures did not prompt shorter RTs or larger NoGo-P3 amplitudes than unpleasant pictures (either mutilations or threat). Therefore, our data do not support the idea that appetitive stimuli make withholding responses more difficult. The significantly higher number of commission errors in NoGo trials for pleasant as compared with threat pictures can be interpreted as likely reflective of interference due to greater attentional deployment, as supported by the significant positive correlation between omission and commission errors (cf. Silverstein, Weinstein, & Turnbull, 2004). This interpretation is strengthened by the observation of slower RTs for pleasant than neutral and threat pictures, suggesting an interference-mediated lack of speed–accuracy trade-off. Taken together, these results are consistent with the idea that action readiness was specifically facilitated when threat (but not pleasant) pictures were presented.

As a word of caution, it has to be stated that our paradigm was designed to probe response inhibition in the context of unpleasant rather than pleasant stimulation. Specifically, in the Go condition, picture presentation was terminated by key press to reproduce the congruent process in which action readiness in response to aversive stimulation translates into avoidance-related behaviour. As a consequence, our experimental task, as such, might have hindered the emergence of action readiness supporting approach-related behaviour, because of the incongruent association between motivation to approach appetitive stimuli and stimulus disappearance. Future studies should experimentally manipulate the presence/disappearance of emotional pictures following Go responses to clarify how this variable might modulate action readiness as a function of stimulus valence.

Lastly, it has to be noted that the amplitudes of the NoGo-N2 and NoGo-P3 were significantly larger and smaller, respectively, for neutral than for emotional pictures. However, such effects can hardly be interpreted as evidence of the specific operation of response inhibition processes. Indeed, if, on the one hand, the lower P3 amplitude might reflect a less demanding inhibition (see Bruin et al., 2001), on the other hand, it is unlikely and, in fact, inconsistent that the higher N2 amplitude can be viewed in terms of higher response conflict in the context of neutral than emotional stimuli. A more parsimonious account of these findings is that cortical positivity was globally lower throughout the processing of neutral than emotional stimuli (i.e., arousal effect), reflecting less need for attentional deployment. In fact, ERP studies on affective picture processing typically report lower positivity to neutral than to emotional pictures starting in the 200–300 ms time window after onset, and continuing throughout picture presentation (e.g., Amrhein, Mühlberger, Pauli, & Wiedemann, 2004; Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000). A similar interpretation has been provided in the context of an emotional Go/NoGo task by Yu et al. (2009), who reported a larger Nogo-N2 to neutral than to positive and negative sounds.

It might be argued that the behavioural and neural differences found in the present study between the two unpleasant contents are still not unequivocally determined, in that the greater attentional demands associated with the processing of blood-related stimuli might have globally interfered with inhibitory processes due to the competition for attentional resources. This interpretation would account for the prolonged RTs to Go cues and for the relatively greater positivity of the NoGo-N2 found for mutilation than threat pictures. However, two key remarks on our findings allow supporting the differential involvement of processes related to action inhibition proper. First, attentional interference would have led to higher rates of both omission and commission errors (cf. De Houwer & Tibboel, 2010) in the context of mutilations as compared with the other emotional contents. In contrast, mutilation pictures did not yield any difference in performance accuracy either in the Go or in the NoGo condition (see Table 1). Second, a greater allocation of attentional resources would have been maximally reflected in a larger positivity occurring in the P3 (rather than in the N2) time window for mutilation than the other emotional contents (cf. Buodo et al., 2006). In contrast, no differences among emotional categories were found in the NoGo-P3

amplitude, suggesting that inhibition-related processes largely prevailed over attentional deployment occurring in the same time window, with the arousal effect being the only significant difference driven by attentional processing, as discussed above for neutral stimuli.

In conclusion, our results converge in support of the idea that threat and blood-related stimuli differentially affect inhibitory processes based on the different state of motor readiness they induce. However, such modulation seems to operate at the level of conflict monitoring between the generation and the suppression of the overt response, rather than at the later stages of motor inhibition proper. Threatening stimuli were found to facilitate the execution of a pre-potent response and to enhance conflict monitoring when action must be withheld. In contrast, blood-related stimuli did not either promote action in the Go trials or increase conflict in the NoGo condition, suggesting a response pattern compatible with defensive immobility. Importantly, our findings are not simply accounted for by differences in attentional engagement between unpleasant contents.

Acknowledgments

Disclosure statement

ORCID

Michela Sarlo http://orcid.org/0000-0001-6652-7604

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