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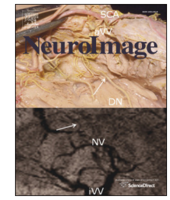

Electrical neuroimaging reveals content-specific effects of threat in primary visual cortex and fronto-parietal attentional networks

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Whereas effects of anticipatory anxiety on attention are usually assumed to remain largely undifferentiated, discrepant findings in the literature suggest that, depending on its content and causes, different modulatory effects on attention control and early sensory processing may arise. Using electrical neuroimaging and psychophysiology in a cross-over design, we tested the hypothesis that different types of anticipatory anxiety (bodily vs. psychological), transiently induced in healthy participants, had dissociable effects on brain systems regulating attention control. Attention control corresponded to the ability to maintain efficient goal-directed processing (indexed by the P300 ERP component and by activations in the attentional networks), as well as the ability to filter out irrelevant stimuli in early sensory cortex (C1 component, indexing attentional gating in V1). Results showed that while psychosocial threat, very much like perceptual load, primarily led to a stronger gating in V1, bodily threat resulted in impaired goal-directed processing within the fronto-parietal attentional network, as well as decreased filtering in V1. These results suggest that anticipatory anxiety is multifaceted, exerting different effects on attention control and early visual processing depending on its sub-type.

Introduction

Attention can bias sensory processing early on following stimulus onset. In monkeys, as well as in humans, top-down attentional gating effects have been shown as early as in the thalamic nuclei (Fischer and Whitney, 2012; McAlonan et al., 2008; O'Connor et al., 2002) and V1 (Schwartz et al., 2005). Yet, affective states provide powerful motivational drives that can influence attentional deployment, sometimes conflicting with top-down goal setting. Sustained anxious anticipation (Davis et al., 2010) of unpredictable and uncontrollable bodily harm (uncued delivery of electric shocks, for example) has consistently been implicated in humans and animals in hypervigilant threat monitoring (Alvarez et al., 2011; Davis and Whalen, 2001; Somerville et al., 2010), which is related to augmented sensory vigilance in order to facilitate threat detection. Critically, although anxious hypervigilance can foster an effective monitoring of the environment, it comes at a price. Stress and anxiety have been shown to induce neural plasticity in key regions such as the hippocampus, the amygdala and the prefrontal cortex (Leuner and Shors, 2013; McEwen et al., 2012), altering cognitive functions, such as emotion regulation, attentional control (Arnsten, 2009; Bishop, 2007; Eysenck et al., 2007; Plessow et al., 2011) and goal-directed stimulus processing (Moser et al., 2005; Shackman et al., 2011).

However, outside the laboratory, threatening events are not restricted to the imminence of potential bodily harm: uncertainty, social stressors, or upsetting visual scenes are also able to trigger anxious responses, implicating activations in the extended amygdala, similarly to physical threats (Grupe et al., 2012; Yassa et al., 2012). Unlike bodily harm, these psychosocial strains have been suggested to *narrow* the attentional scope, resulting in decreased early visual responses to irrelevant sensory information (Easterbrook, 1959; Rossi and Pourtois, 2012a; Schmitz et al., 2009), without systematically affecting goal-directed behavior. By comparison, sustained anxiety related to the anticipation of uncontrollable physical harm seems mainly to impair attentional control functions, in favor of a bottom-up (ventral) attentional system, which might mediate hypervigilance (thus, *enhanced* responses to task-irrelevant, but potentially threatening information, see also Bishop et al., 2004; Choi et al., 2012; Cornwell et al., 2011; Pourtois et al., 2013).

Furthermore, negative affect can be elicited by increasing task difficulty alone, in the absence of a direct mood induction (Nummenmaa and Niemi, 2004). Hence, the typical narrowing of the attentional focus associated with high load tasks (Lavie, 2005; Rauss et al., 2009; Schwartz et al., 2005) might actually be conflated by an uncontrolled increase of negative affect, given that this state has also been related to narrowed attention (Easterbrook, 1959).

Thus, although different forms of anticipatory anxiety and distress seem to impinge on stimulus processing in dissociable ways, no study to date has directly compared their differential effects on specific attention control processes. This may be explained by the challenges posed by bringing up these different affective states in the laboratory and

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comparing them in a systematic way. For example, matching negative affect intensity between different types of strain (physical vs. psychosocial) appears especially challenging in between-subjects experimental designs. On the other hand, having the same participants experience these different strains in a within-subjects design may lead to uncontrolled carryover, with the residual effects of one specific state possibly contaminating the subsequent one.

To overcome these problems, we used in this study a novel experimental design enabling to compare in the same participants the effects of two different types of anticipatory anxiety (physical vs. psychosocial) on the electrophysiological markers of attention control, while minimizing systematic carryover effects. In this paper, we operationalized anticipatory anxiety, or state anxiety, as a state of sustained tension in the anticipation of the possible encounter with a negative event which is not imminent, but looming (Davis et al., 2010). We continuously measured the skin conductance levels (SCLs) to monitor peripheral arousal during the experience of state anxiety, in order to be able to model the physiological response corresponding to the stressor anticipation against the normal habituation curves (measured in a condition in which no stressors were expected). Two types of anticipatory anxiety inductions (physical vs. psychosocial) were chosen given their similarity to published procedures in the literature. For each of them, we could then formulate a clear prediction regarding the specificity of its effects on attentional processes: while the threat of bodily harm would primarily impair goal-directed processing (see for example Shackman et al., 2011), by contrast, an "internal" psychological stressor should be accompanied by a narrowing of the attention focus (e.g., Rossi and Pourtois, 2012a; Schmitz et al., 2009). In agreement with previous reports, we formally operationalized attention control as the ability to maintain efficient goal-directed processing (indexed by the P300 ERP component, see Shackman et al., 2011), as well as the ability to filter out irrelevant stimuli in early sensory cortex (C1 component, indexing attentional gating in V1, see Rauss et al., 2011). We compared effects of anticipatory anxiety driven by physical vs. psychosocial threat on attention control brain processes to a third condition, consisting of enhanced perceptual load, given its well-known effects on both goal-directed processing within the fronto-parietal network (e.g., Lavie, 2005; Schwartz et al., 2005) and early attentional filtering in the primary visual cortex (see Rauss et al., 2009, 2011). Importantly, by measuring self-report distress and autonomic arousal responses, we could also assess whether a possible increase in negative affect would arise in this condition (albeit of lower magnitude compared to the two state anxiety conditions), an element which has typically been overlooked in earlier studies investigating effects of load on attention selection.

At the behavioral level, we expected high load to slow down reaction times and decrease accuracy for target detection, compared to low load. Since psychosocial threat does not seem to systematically affect overt behavior (no effects on target detection or discrimination were reported in studies investigating the narrowing of attention during negative affect induced by feedbacks or upsetting picture presentation; see Moriya and Nittono, 2011; Rossi and Pourtois, 2012a, 2013; Schmitz and De Rosa, 2011), we therefore surmised that task performance would not be influenced by this form of anticipatory anxiety. Concerning the effects of bodily threat, a recent review by Robinson et al. (2013) highlighted the lack of consistency in behavioral costs during the anticipation of unpredictable noxious stimuli (threat of mild electric shocks). Nevertheless, two recent electrophysiological studies using the threat of bodily harm (Moser et al., 2005; Shackman et al., 2011) did not report differential effects at the behavioral level between the safe vs. threat condition. Accordingly, we reckoned that bodily threat would not lead to an impaired behavioral performance in this experiment.

However, based on existing dissociations in the literature (e.g., peripheral distractor processing seems to be either decreased or increased under stress depending on situational factors, see Choi et al., 2012 and Schmitz et al., 2009), we predicted that the two types of strains (physical vs. psychosocial) would have dissociable effects on attention control at the electrophysiological level. Hypervigilance and reduced goal-directed processing were hypothesized to be related to the threat of bodily harm, selectively (Choi et al., 2012; Moser et al., 2005; Shackman et al., 2011). Sensory hypervigilance would primarily be translated in maintained or increased early responses to irrelevant information in V1 (C1 component, Weymar et al., 2013) accompanied by an attenuation of goal-directed processing as measured in amplitude of the target-locked P300 (Moser et al., 2005; Shackman et al., 2011). By comparison, we surmised psychosocial threat to narrow the attentional focus around fixation, and therefore selectively increase filtering of peripheral (irrelevant) information in V1 (C1 component). At the same time, goal-directed processing should remain relatively unaffected, as previously reported (Moriya and Nittono, 2011; Rossi and Pourtois, 2012a; Schmitz et al., 2009).

To corroborate the assumption of systematic changes in the fronto-parietal network during goal directed processing (P300 effect) as well as in V1 during the early filtering of irrelevant information (C1 effect) as a function of these two strains, we estimated the intra-cerebral sources of these two ERP components using a distributed inverse solution (standardized Low Resolution Electrical Tomography, sLORETA).

Materials and methods

Participants

Twenty-six right handed undergraduates participated in the study (mean age = 20.4 years, SD = 2.2 years, 7 males). Participants had normal or corrected-to-normal vision, were unaware of the purpose of the study and declared no history of psychiatric or neurological disorders, nor the use of psychoactive medication. The study protocol was conducted in accordance with the Declaration of Helsinki and approved by the local ethics committee.

Stimuli and task

The paradigm was adapted from Rossi and Pourtois (2012a). Participants monitored at fixation a rapid serial visual presentation (RSVP) of tilted gray line segments presented on a black background. Randomly intermixed with standard lines (tilted 35°), target lines with a slightly different in-plane orientation (either 25° or 45°) were presented, with a standard/target ratio of 4/1. Participants were instructed to detect targets in the RSVP and respond with a key press. Target and standard lines were presented for 250 ms, with an average ISI of 1325 ms (range 1150–1500 ms). Peripheral, nonpredictive visual textures composed of horizontal line segments (8.8° × 34° of visual angle) were flashed for 250 ms in the upper visual field during the ISI, in 50% of the trials (see Fig. 1A). These unpredictable and uninformative peripheral stimuli were previously associated with the generation of a reliable C1 component, with its main generators source-localized in V1 (Pourtois et al., 2008; Rauss et al., 2009). In the other 50% of the trials, no peripheral stimulus was shown in periphery during the ISI, but in order to maintain the exact same temporal structure for all trials a black dummy was presented for the same duration (invisible to the participants).

The experimental session comprised a practice block (24 central stimuli, 12 followed by a peripheral irrelevant stimulus and 12 followed by the dummy) and 8 task blocks (each block comprised 100 central stimuli, 50 followed by a peripheral irrelevant stimulus). Unknown to participants, the eight blocks were equally divided into four conditions (see Fig. 1B). Each condition (Control, Load, Bodily Threat — BT, and Psychosocial Threat — PST) was composed of 2 consecutive blocks: a Baseline and a Test block. The critical manipulations were always applied during (or prior to) the Test blocks, with the Baseline blocks being identical across all four conditions.

In the Control condition, Baseline and Test blocks were identical (the Test block was simply the repetition of a new Baseline block),

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