Electrophysiological evidence for greater attention to threat when cognitive control resources are depleted

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Abstract

This study investigated the time course of attentional bias for threat-related (angry) facial expressions under conditions of high versus low cognitive (working memory) load. Event-related potential (ERP) and reaction time (RT) data were recorded while participants viewed pairs of faces (angry paired with neutral face) displayed for 500 ms and followed by a probe. Participants were required to respond to the probe while performing a concurrent task of holding in working memory a sequence of digits that were either in the same order (low memory load) or random mixed order (high memory load). ERP results revealed that higher working memory load resulted in enhanced lateralised neural responses to threatening relative to neutral faces, consistent with greater initial orienting of attention to threatening faces (early N2pc: 180-252 ms) and enhanced maintenance of attention towards threat (late N2pc: 252-320 ms; SPCN: 320-500 ms). The ERP indices showed significant positive relationships with each other and also with the behavioural index of attentional bias to threat (reflected by faster RTs to probes replacing angry than neutral faces at 500 ms), although the latter was not significantly influenced by memory load. Overall, the findings indicate that depletion of cognitive control resources, using a working memory manipulation, increases the capacity of task-irrelevant threat cues to capture and hold attention.

Keywords: ERP; attentional bias; threat; N2pc; SPCN.

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Several studies indicate that threat stimuli preferentially attract attention (e.g., Calvo et al., 2007; Holmes et al., 2009; Nummenmaa et al., 2009; Mogg & Bradley, 1999; Öhman et al., 2001). Evolutionary perspectives suggest that a propensity to orient attention rapidly towards a possible cue for threat will prepare an individual to deal with potential sources of danger in the environment (e.g., Davis & Whalen, 2001; Gray, 1982; LeDoux, 1996; McNaughton & Gray, 2000; Öhman et al., 2000). Recent theoretical views propose that threat-related attentional capture is mediated by specialised emotion processing systems, supported by neural circuitry centred on the amygdala, which prioritise the attentional selection of stimuli with high motivational significance (e.g., Öhman & Mineka, 2003; Vuilleumier & Huang, 2009). A ‘biased competition’ account argues that the amygdala biases the representation of threat in a bottom-up manner over competing neutral stimuli by means of amygdala feedback to sensory processing areas of the brain (Pessoa, 2009; Pessoa & Adolphs, 2010; Pourtois, Schettino, & Vuilleumier, 2012; Vuilleumier, 2005).

Biased competition models of selective attention discuss not only mechanisms of bottom-up biasing, but also mechanisms of top-down frontal control that are engaged to enhance processing of task-relevant stimuli and minimize interference from task-irrelevant distractor stimuli (e.g, Desimone & Duncan, 1995; Corbetta et al., 2008). One role of executive control processes is to maintain templates in working memory (WM) that provide top-down biasing signals to support task-relevant processes and suppress task-irrelevant processing (i.e., a goal-directed “attentional set”; De Fockert et al., 2001; Lavie & De Fockert, 2005). The demands on frontal control processes for the inhibition of task-irrelevant distractors are likely to be particularly pronounced when the distractors are of a *threatening* nature, because of the presumed ‘bottom-up’ enhancement of their signal from emotion processing systems.

Following these views, the extent to which attention is allocated to task-irrelevant threat information depends on competition between biasing effects of bottom-up processes (supporting threat-related attentional capture) and executive attention control processes (supporting task-relevant processes). If executive control processes are efficient, attention is more likely to remain task-focused and less likely to be grabbed by task-irrelevant information. However, if executive control resources are weak or depleted, task-irrelevant information is less likely to be effectively inhibited; i.e., under high concurrent cognitive load, threat-related (compared to neutral) distractors would be more likely to intrude into the focus of attention due to insufficient executive attention resources to suppress their processing. The primary aim of the present study is to investigate this directly, by assessing the effect of concurrent WM load on neural and behavioural measures of the allocation of spatial attention to task-irrelevant threat information.

This research is also guided by Lavie’s (2005; 2010; Lavie et al., 2004) load theory of attention, which emphasises distinct effects of ‘cognitive control’ load (such as WM load) versus perceptual load, on distractor processing. That is, distractor interference is increased by high cognitive control load, but reduced by high perceptual load (see Lavie, 2010, for a review). Several studies have examined effects of perceptual load on emotion processing (e.g. Bishop et al., 2007; Fenker et al., 2010; Okon-Singer et al., 2007; Richards et al., 2011), but this work is outside the scope of the present study, which is concerned instead with the effect of executive control (‘cognitive’) load on attention to task-irrelevant threat (as discussed earlier). Studies examining the effect of cognitive control load on emotion processing have produced mixed findings. For example, some found no effect of manipulating concurrent WM load on discrimination judgements of emotional versus neutral stimuli (e.g., Phillips et al., 2008; Van Dillen & Koole, 2009). Others found that high cognitive load (arithmetic task) reduced amygdala response to aversive stimuli that were passively viewed immediately before the cognitive load (Van Dillen et al., 2009). However, these studies did not directly examine effects of cognitive load on the allocation of attention to task-irrelevant threat. One exception is Pecchinenda and Heil (2007; Experiment 3) who reported that the interference effect of emotional face distractors on valence judgements of emotional word targets (which was used to index attention) was not significantly affected by concurrent WM load. Similarly, a recent study by Berggren, Koster, and Derakshan (2012) has also revealed that the capture of attention by emotional faces in a visual search array was not influenced by a concurrent cognitive load (counting back in multiples of three). Given that previous relevant evidence is very limited, there is a clear need to investigate further the effect of manipulating WM load on the allocation of visuospatial attention to task-irrelevant threat cues.

In the current study we investigated the effect of manipulating top-down executive control resources on selective attention to task-irrelevant threat whilst participants performed a visual probe task. In order to vary the resources available for top-down attentional control we manipulated WM load by requiring participants to remember, across every 2, 3 or 4 visual probe trials, either a fixed order of digits (low load) or a different order of digits (high load). In the visual probe task, on each trial, a threat and neutral stimulus were presented simultaneously (angry and neutral face, side-by-side) and participants required to respond to a target probe that immediately followed the stimulus pair. Thus, the threat and neutral face in each stimulus pair competed with each other for attention, with both stimuli being task-irrelevant. The visual probe task used here provided both neural and behavioural measures of attentional allocation to threat cues. The behavioural measure of attentional bias to threat is obtained from response times (RTs) to the probes, with faster RTs to probes replacing threat, relative to neutral, stimuli indicating that attention is drawn preferentially to threat cues. The neural measures of attentional bias to threat are obtained from lateralised event-related potentials (ERPs) associated with shifts of attention to the threat versus neutral stimuli in each pair (N2pc, SPCN).

An advantage of the ERP technique is that the time course of attentive processing can be characterized at a fine temporal resolution. The N2pc reflects rapid shifts in spatial attention to cue stimuli appearing in the left or right visual field (e.g., Luck & Hillyard, 1994; Woodman & Luck, 1999). It is typically elicited between 180 and 300 ms post-stimulus onset in the hemisphere contralateral to the side of the attended stimulus. Previous research has distinguished between the early and late portions of the N2pc (Eimer & Kiss, 2007; Holmes et al., 2009; Hopf et al., 2000), with evidence of the early N2pc reflecting the initiation of a shift of attention and the late N2pc being involved in the filtering of distractors in order to maintain the focus of attention (Hopf et al., 2000).

A subsequent lateralized ERP component is the SPCN, or sustained posterior contralateral negativity (~300 to 650 ms; Dell’Acqua et al., 2006; Jolicoeur et al., 2006), which is also known as the CDA, or contralateral delay activity (Vogel & Machizawa, 2004). The SPCN is proposed to reflect selection and maintenance of information in visual short-term memory (Dell’Acqua et al., 2006; Jolicoeur et al., 2006). Maintenance of information in visual short-term memory has also been related to holding selected stimuli in the focus of attention, i.e. sustained viusospatial attention (Jonides et al., 2008). Indeed, selective attention and working memory are increasingly conceptualised as overlapping constructs, as there is growing evidence that common neural mechanisms support maintenance of attention on both internal and external stimulus representations (Chun, 2011; Chun et al., 2011; Gazzaley & Nobre, 2012).

Previous research into these neural responses to emotional information has shown rapid initial attentional selection of threat faces, relative to neutral faces, reflected by the early N2pc (~180-250 ms, e.g., Eimer & Kiss, 2007; Holmes et al., 2009), which was maintained across the late N2pc (~250-320 ms) and SPCN (~320-500 ms); consistent with a bias in initial orienting and maintained attention towards threat relative to neutral information over this time-period (Holmes et al., 2009; see also Feldmann-Wüstefeld et al., 2011).

To recap briefly, allocation of attention to task-irrelevant threat cues is assumed to depend on the interplay between bottom-up influences (which automatically direct attention to threat) and top-down influences (which support task-relevant processes and inhibit processing of task-irrelevant information). If executive control resources are depleted by additional cognitive demands (e.g. high WM load), attention to task-irrelevant threat should be less effectively suppressed. Consequently, it is hypothesised that task-irrelevant threat cues will attract greater attention when there is high concurrent WM load, relative to low concurrent WM load. It is predicted that this effect will be found for each measure of attentional bias for threat, i.e. assessed by early N2pc (hypothesis 1), late N2pc (hypothesis 2), SPCN (hypothesis 3), and manual RTs to probes (hypothesis 4). As each measure is assumed to reflect preferential allocation of processing resources to threat relative to neutral cues, it is also hypothesised that these measures will positively correlate with each other (hypothesis 5).

Method

*Participants*

 The participants were 23 healthy volunteers. One participant was excluded because of excessive eye movement artifacts (>80%), so that 22 participants (3 male and 19 female; 18-41 years old; average age: 25.6 years) remained in the sample. All participants had normal or corrected-to-normal vision and all were right-handed. The experiment was performed in compliance with relevant institutional guidelines and was approved by the University ethics committee.

*Stimuli and Apparatus*

In the visual probe task, face stimuli consisted of pairs of grayscale photographs of 32 different individuals (16 male, 16 female) taken from the NimStim Face Stimulus Set (Tottenham et al., 2009). Each pair consisted of two pictures of the same individual, with one photograph portraying an angry expression and the other a neutral expression. An additional set of neutral face pairs using photographs of four individuals (two male, two female) from the NimStim Set was used for practice items. Each face was enclosed within a black rectangular frame measuring 8 cm high x 6.2 cm wide, and the centers of the faces were 5 cm from a white central fixation cross. The faces within each pair were equated for mean luminance and root mean square contrast energy using standard routines in Matlab 7. The probe stimuli were white up- and down-pointing arrows measuring 0.8 cm, and replaced the left or right faces at a position of 3.75 cm from the central fixation cross.

In the memory task, each digit measured 0.3 cm horizontally and 0.5 cm vertically. Each memory set (i.e. string of five digits) subtended 2.8 cm horizontally. All stimuli appeared against a black background. Participants were seated in a dark cabin, and stimuli were presented at a viewing distance of 70 cm on a 17-in ViewSonic G220f computer screen with a refresh rate of 75 Hz, connected to a Dell Precision Pentium IV computer. Stimulus presentation was controlled with E-Prime v2.0 (Psychology Software Tools Inc. <http://www.pstnet.com/prime>). Stimulus parameters were based on those employed by Holmes et al. (2009) and De Fockert et al. (2001).

[\*\* Figure 1 about here \*\*]

*Procedure*

Each WM load trial contained a memory set (digit string) and memory test, interspersed by an unpredictable series of visual probe trials, as described below (Figure 1). After a 500 ms fixation cross, the memory set for that trial was presented for 1500 ms. Under low WM load, the digit string was always: ‘01234’. Under high WM load, the last four digits were in a new random order for each trial, e.g. ‘04312’ (‘01234’ and ‘04321’ were excluded from the high WM load condition). Participants were instructed to remember the order of these digits for the memory test at the end of the trial. After each memory set, a fixation display was presented for 850 ms, followed by 2, 3, or 4 visual probe trials. The number of visual probe trials within each memory task trial was varied to make the onset of the memory probe unpredictable, thus ensuring that the memory set was actively rehearsed throughout each visual probe trial. After the short series of visual probe trials, the memory test was presented, which started with a 500 ms fixation cross followed by a memory probe for 3000 ms. Participants were requested to report the digit that followed this probe in the memory set by pressing the appropriate key (labelled 1, 2, 3 or 4) on the numeric keypad on the computer keyboard using their left hand. In order to ensure that all four responses (including ‘1’ in low WM load trials) were used, a ‘0’ was always the first digit in each memory set. On each trial, the probe digit was randomly selected, ensuring that it was not the same as the last digit in the memory set. Immediately following a response, a new WM load trial was presented. The WM load trial sequence was adapted from De Fockert et al. (2001).

Each visual probe trial started with a central fixation cross (Figure 1). After 500 ms an angry-neutral face pair was also displayed for a further 500 ms. Immediately after the offset of the face cues and fixation cross, a probe was presented until a response was made or until 6 s had elapsed. Participants were instructed to press one of two buttons on a purpose-built response box, using the index finger (upper button) and thumb (lower button) of their right hand, to indicate as quickly and as accurately as possible the type of probe (i.e., up-pointing arrow [upper key] or down-pointing arrow [lower key]). Participants were also asked to keep their gaze focused on the central fixation location throughout the task. There was a variable inter-trial interval (ITI) ranging from 750 to 1250 ms. This trial sequence was used as previous behavioural and electrophysiological investigations have shown it to be sensitive to threat-related attentional bias (e.g., Holmes et al., 2009; Mogg & Bradley, 1998). All visual probe trial types (varying as a function of position of angry face, probe position, and probe type) were equiprobable across the experimental trials, and were presented in a new mixed random order for each participant within each block.

Participants were given two short practice blocks of trials (one high and one low WM load block); each consisting of 5 memory task trials and 16 visual probe trials. This was followed by 8 experimental blocks (4 high WM load alternating with 4 low WM load). Each experimental block consisted of 10 memory task trials and 32 visual probe trials.

*EEG data acquisition*

EEG was recorded using a Neuroscan 64 channel device (Synamps). Horizontal and vertical electrooculographs (EOGs) were recorded using four facial bipolar electrodes placed on the outer canthi of the eyes and in the inferior and superior areas of the left orbit. Scalp EEG was recorded from 62 Ag/AgCl electrodes mounted in a quickcap (extended 10-20 system). All electrodes were referenced online to one electrode (vertex) and bandpass filtered at 0.01-100 Hz. The impedance for electrodes was generally kept below 5 kΩ, and EEG and EOG were sampled online with a digitization rate of 1000 Hz. Following EEG recording, data were down-sampled to 250 Hz to save later computation time, digitally filtered with a low-pass filter at 40 Hz, and all channels were re-referenced using the average of the mastoids (M1 and M2). EEG and horizontal EOGs (HEOGs) were epoched offline relative to a 100 ms pre-stimulus baseline, and extending for 500 ms after stimulus presentation. Trials with lateral eye movements (HEOG exceeding ± 30 μV), as well as trials with vertical eye movements, eye blinks, or other artifacts (a voltage exceeding ±60 μV at any electrode) measured after target onset were excluded from analysis. This resulted in the rejection of 36% of trials.

Separate averages were computed for all combinations of WM load (high vs. low), angry face location (left vs. right), contralaterality (electrodes ipsilateral vs. contralateral to the location of the emotional face), and component (early N2pc vs. late N2pc vs. SPCN). The ipsilateral waveform was computed as the average of the left-sided electrodes to the left-sided angry face and the right-sided electrodes to the right-sided angry face, and the contralateral waveform was computed as the average of the left-sided electrodes to the right-sided angry face and the right-sided electrodes to the left-sided angry face. Regional activity was analyzed at lateral posterior electrodes P7, PO7 (left hemisphere), P8, PO8 (right hemisphere), within post-stimulus time windows of 180-252 ms (early N2pc), 252-320 ms (late N2pc), and 320-500 ms (SPCN). These electrode sites and time windows were determined on the basis of inspection of individual subject waveforms and prior research (e.g., Eimer & Kiss, 2007; Holmes et al., 2009).

Results

*Visual probe task: ERP data*

Figure 2 shows ERPs obtained at electrode sites contralateral to the angry face location (solid lines) and ipsilateral to the angry face location (dashed lines) for high WM load (top panel) and low WM load (bottom panel) conditions. In the high load condition, an enhanced negativity appeared contralateral to angry face cues within the early phase of the N2pc (180-252 ms), and remained present throughout the late phase of the N2pc (252-320 ms) and the SPCN (320-500 ms). By contrast, there was no evidence of an enhanced negative contralaterality effect under conditions of low WM load across any of the component time windows. These observations were confirmed using omnibus analysis of variance (ANOVA) and hypothesis-driven contrasts.

ERP amplitudes were entered into a 2 x 2 x 3 repeated measures ANOVA, with factors of WM load (high vs. low), Contralaterality (electrodes ipsilateral vs. contralateral to location of angry face), and Component (early N2pc vs. late N2pc vs. SPCN). There were significant main effects of Component, *F*(2,42) = 3.91, *p* = .05, *p*η2 = .16, Contralaterality, *F*(1,21) = 1.84, *p* = .002, *p*η2 = .36, and WM load, *F*(1,21) = 5.21, *p* = .03, *p*η2 = .20, and a significant interaction between WM load and Contralaterality, *F*(1,21) = 7.90, *p* = .01, *p*η2 = .27. There were no other significant main effects or interactions. Notably, the WM Load x Contralaterality interaction was not significantly influenced by Component (*F* < 1).

To test specific hypotheses and clarify the significant two-way interaction, contralaterality threat-bias scores (which reflect attentional bias to angry relative to neutral faces) were calculated by taking the mean amplitude contralateral to angry faces minus the mean amplitude ipsilateral to angry faces (an angry and neutral face appeared simultaneously in opposite visual fields on each trial). These bias scores were calculated for each WM load condition, ERP component and participant. Mean contralaterality threat-bias scores (in μV; SD in brackets) for the high and low WM load conditions were -0.53 (0.63) and -0.08 (0.53), respectively for early N2pc; -0.60 (0.75) and -0.08 (0.69) for late N2pc; and -0.62 (0.60) and -0.13 (0.65) for SPCN. Hypothesis-driven paired contrasts indicated that attention bias to angry faces was significantly increased for each ERP component in the high load condition, relative to the low load condition (early N2pc: *t*(21) = 3.27, *p* = .004, *d* = .70; late N2pc: *t*(21) = 2.76, *p* = .01, *d* = .59; SPCN: *t*(21) = 2.14, *p* = .04, *d* = .46). These results support Hypotheses 1 - 3.

[\*\*Figure 2 about here\*\*]

*Visual probe task: RT data*

RTs were excluded from trials with incorrect responses (1.0% of trials) and outliers (RTs <200 ms or >1000 ms; 1.7% of trials). RTs were log transformed before analyses to reduce skewness. Analyses were conducted on transformed data; whereas descriptive statistics are given for untransformed data for ease of comprehension. Mean RTs in each condition were entered into a 2 x 2 repeated measure ANOVA, with factors of WM load (high, low) and Congruency (probe replaces angry face, probe replaces neutral face). There was a significant main effect of Congruency, *F*(1,21) = 4.32, *p* = .05, *p*η2 = .17, as responses were faster on trials where the probe and angry face appeared in the same location (congruent trials: *M* = 557 ms, *SD* = 72) rather than opposite location (incongruent trials: *M* = 561 ms, *SD* = 71); which is consistent with an attentional bias towards threat relative to neutral faces. There was no other significant main or interaction effect. As the congruency effect on RT (indicating attentional bias to threat) was not significantly influenced by the WM load manipulation (*F*<1), Hypothesis 4 was not supported.

*Memory test*

Performance on the memory test indicated that the WM load manipulation was effective. Participants gave more correct responses to the memory test questions in the low load (*M* = 96.5%, *SD* = 3.8) than high load condition (*M* = 84.9%, *SD* = 12.2), paired *t*(21) = 5.15, *p* < .001, *d* = 1.54, and their responses were also faster in the low load (*M* = 1152 ms, *SD* = 278) than high load condition (*M* = 1924 ms, *SD* = 339), paired *t*(21) = 13.93, *p* < .001, *d* = 3.04.

*Correlations between attentional bias measures*

Correlations were calculated to test the prediction that the ERP and RT measures of attentional bias would be positively correlated with each other (Hypothesis 5). The ERP measures were the contralaterality threat-bias scores for each of the three ERP components (which reflect enhanced processing of threat relative to neutral faces) described earlier. These scores were highly inter-correlated (i.e., early N2pc bias score correlated .90 with late N2pc bias score, and .82 with SPCN bias score; late N2pc bias score correlated .82 with SPCN bias score; all *p*s < .01).

The probe RT measure of attention bias was calculated as the difference in mean RT between incongruent versus congruent trials (this difference corresponds to the ‘Congruency effect’ in the analysis of RT data described earlier). The RT index of attentional bias correlated positively with each ERP measure of threat-related bias (i.e., RT bias correlated .43, .45 and .48 with early N2pc, late N2pc and SPCN contralaterality bias scores, respectively; all *p*s < .05). The RT bias measure significantly correlated .47, *p* < .05, with the overall ERP bias index (contralaterality bias score for threat relative to neutral faces, averaged across the three ERP components).

Discussion

The aim of the study was to investigate whether threatening faces attract greater attention under high compared with low concurrent cognitive load. The main results can be summarized as follows: The ERP results revealed that threat-related attentional bias was significantly greater under conditions of high than low WM load. This enhanced attentional prioritisation of angry faces was found across three time windows following the onset of the face-pair (corresponding to early N2pc, late N2pc and SPCN), supporting the first three experimental hypotheses. The probe RT results showed evidence for an attentional bias towards angry faces; however, this bias was not modified by WM load, providing no support for our fourth hypothesis. Correlational evidence showed that the behavioural index of threat-related attentional bias was significantly associated with each ERP measure of attentional bias, and that the ERP measures were also significantly inter-correlated, as predicted by our fifth hypothesis.

Only a few studies to date have investigated lateralized ERP correlates of threat-related attentional bias. As noted earlier, the N2pc has a notable advantage of providing an objective neural index of early shifts in visuospatial attention, which has high temporal sensitivity. A consistent finding across previous studies is that attentional shifts towards threatening faces arise rapidly, with the emergence of an N2pc as early as ~180-250 ms post-stimulus onset (e.g., Eimer & Kiss, 2007; Fox et al., 2008; Holmes et al., 2009). Various mechanisms have been proposed to underlie rapid attentional orienting towards sources of threat, including the facilitation of sensory processing by the amygdala (e.g., Pessoa, 2009; Pessoa & Adolphs, 2010; Pourtois, Schettino, & Vuilleumier, 2012) and attentional networks in frontoparietal cortex (e.g., Armony & Dolan, 2002). Crucially, the current findings of early N2pc reveal that this initial stage of visuospatial selection (i.e., 180-252 post-cue onset) is modulated by concurrent demands on processing: when top-down cognitive control processes were depleted by a concurrent WM task, task-irrelevant threat was more likely to capture attention. These findings relate to growing evidence that the attentional processes typically considered to be primarily bottom-up driven (e.g. those involved in initial attention capture), can be influenced by executive control mechanisms (Kiefer, 2012). Thus, bottom-up influences on attention capture by threat also appear to be context-dependent, as suggested by the present findings from the early N2pc.

High WM load was also associated with subsequent enhanced processing of threat cues, as reflected by the late N2pc and SPCN (i.e., 252-320 ms; and 320-500 ms, respectively). Holmes and colleagues (2009) noted that enhanced processing of angry faces across both N2pc and SPCN is consistent with proposals that threatening stimuli not only rapidly capture attention (e.g. Öhman & Mineka, 2003), but also hold it (at least over the relatively short time intervals assessed here; Fox et al., 2001). From an evolutionary perspective, such holding of attention may allow novel or potentially significant events to be monitored. Holding attention on threat cues may relate to maintenance of such information in visual short-term memory, which contributes to the SPCN (e.g., Dell’Acqua et al., 2006; Jolicoeur et al., 2006; Vogel & Machizawa, 2004). It should be noted, however, that the SPCN was measured whilst face stimuli were still displayed on the screen. It is therefore hard to disentangle the extent to which the SPCN findings reflect maintained processing of threat information in visual short-term memory versus maintained attention focusing on external threat stimuli. However, as noted earlier, working memory and selective attention are increasingly conceptualised as closely related, overlapping constructs, which are supported by common neural mechanisms (Chun et al., 2011; Gazzaley & Nobre, 2012). Thus, the present SPCN results may reflect activation in neural mechanisms associated with maintaining attention on both internal and external stimulus representations of threat.

The primary results from this study indicate that, when executive control resources are depleted by additional cognitive demands (i.e., in this case, high WM load), the capture and holding of attention by task-irrelevant threat cues is enhanced. One explanation for this is that, under conditions of depleted cognitive control, task-irrelevant threat is less efficiently inhibited and therefore more likely to intrude into the focus of attention. The present findings are novel because, to our knowledge, no previous study has demonstrated an effect of cognitive (WM) load on attention allocation to threat. Notably, this effect extends across distinct attentional operations relating to initial orienting and subsequent maintenance of attention.

Additional notable findings are the significant positive relationships between the behavioural and ERP measures, which support the view that they reflect common mechanisms underlying attentional threat-prioritisation. Specifically, greater N2pc and SPCN responses to threat, relative to neutral, cues, predicted faster RTs to probes which subsequently replaced the threat cues, which is a widely used behavioural index of attentional bias to threat. Despite these positive inter-correlations between the RT and ERP measures, only the ERP measures confirmed the hypothesised effect of cognitive load on increasing attention to task-irrelevant threat. A recent MEG study also reported that N2pc and RT data showed different effects of processing demands on attention to threat (Fenker et al., 2010). However, this study examined the effect of varying perceptual load; which, as noted earlier, is argued to have the *opposite* effect on distractor processing than cognitive (WM) load (Lavie, 2010). Results indicated that perceptual load did not significantly influence N2pc which was elicited by task-irrelevant fearful faces; whereas RT data showed an attentional bias for fearful faces only when perceptual load was low. Comparison of results with the present ones is complicated by substantial methodological differences, such as different types of load manipulation (perceptual versus WM load) and attentional tasks (visual search versus visual probe). These findings highlight the need to clarify the effects of cognitive (WM) versus perceptual load manipulations on threat processing, to assess prioritization of threat processing in the context of Lavie’s (2010) load theory of attention. Further work is also required in order to determine the extent to which cognitive (WM) load influences the capture of attention by task-irrelevant cues when these cues are more generally negative or positive in terms of emotional valence, as opposed to being specifically threat-related.

Regarding the lack of effect of WM load on the behavioural RT index of attentional bias in this study, it should be noted that the RT index is less direct than the ERP measures and is obtained after the offset of the threat stimuli (i.e. the RT measure reflects attention allocation to probes that replace threat cues, rather than attention allocation to the cues per se). These results highlight the importance of using temporally sensitive measures such as ERPs, as they can provide a more detailed account of the temporal dynamics of attentive processing than RTs.

In conclusion, to our knowledge, this is the first study to demonstrate a modulatory role of cognitive control resources on neural processes underlying visuospatial attentional bias to task-irrelevant threat. Angry face stimuli attracted greater attention when cognitive control resources were depleted (i.e. under high, relative to low, concurrent WM load). The present findings indicate the importance of executive processes for the resistance of interference from distracting threat cues.

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Figure Legends

 *Figure 1.* Example of the sequence of events within a high working memory (WM) load trial (left panel) and a visual probe trial (right panel). Please note that the stimuli are not to scale.

*Figure 2.* Grand averaged ERPs for regional analyses of posterior electrode sites (P7, P8, PO7, PO8) elicited to stimulus pairs containing a neutral and an angry face under high WM load (top panel) and low WM load (lower panel). ERPs are shown at electrodes contralateral (solid lines) and ipsilateral (dashed lines) to the angry face.



