ATTENTION CAPTURE BY ANGRY FACES DEPENDS ON THE DISTRIBUTION OF ATTENTION

BY

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Abstract

The threat-capture hypothesis posits a threat-detection system that automatically directs visual attention to threat-related stimuli (e.g., angry facial expressions) in the environment. Importantly, this system is theorised to operate preattentively, processing all input across the visual field in parallel, prior to the operation of selective attention. The threat-capture hypothesis generates two predictions. First, because the threat-detection system directs attention to threat automatically, threat stimuli should capture attention when they are task-irrelevant and the observer has no intention to attend to them. Second, because the threat-detection system operates preattentively, threat stimuli should capture attention even when it is engaged elsewhere. This thesis tested these predictions using behavioural measures of attention capture in conjunction with the N2pc, an event-related potential (ERP) index of attention selection. Experiment 1 tested the first prediction of the threat-capture hypothesis – that threat stimuli capture attention when they are task-irrelevant. Participants performed a dot-probe task in which pairs of face cues – one angry and one neutral – preceded a lateral target. On some trials, the faces were Fourier phase-scrambled to control for low-level visual properties. Consistent with the threat-capture hypothesis, an N2pc was observed for angry faces, suggesting they captured attention despite being completely task-irrelevant. Interestingly, this effect remained when faces were Fourier phase-scrambled, suggesting it is low-level visual properties that drive attention capture by angry faces. Experiments 2A and 2B tested the second prediction of the threat capture hypothesis – that threat stimuli capture attention when it is engaged elsewhere. Participants performed a primary task in which they searched a column of letters at fixation for a target letter. The perceptual load of this task was manipulated to ensure that attentional resources were consumed by this task. Thus there were high and low perceptual load conditions in these experiments. Task-irrelevant angry faces interfered with task performance when the perceptual load of the task was high but not when it was low (Experiment 2A). Similarly, angry faces elicited an N2pc, indicating that they captured attention, but only when perceptual load was high and when faces were phase-scrambled (Experiment 2B). These experiments further suggest that low-level visual factors are important in attention capture by angry faces. These results appear to be inconsistent with the threat-capture hypothesis, and suggest that angry faces do not necessarily capture attention when it is engaged elsewhere.

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As we navigate our environment, we are confronted with far more visual information than we can fully process at any given moment. Consequently, the visual system is necessarily selective. That is, we must attend to a subset of the incoming visual information, processing these attended inputs at the expense of unattended inputs. There is considerable evidence from a range of paradigms suggesting that threat-related stimuli (e.g., angry and fearful faces) preferentially attract attention (e.g., Anderson & Phelps, 2001; Holmes, Bradley, Kragh Nielsen, & Mogg, 2009; Vuilleumier & Schwartz, 2001). Indeed, from an evolutionary perspective, the ability to rapidly deploy attention to threat stimuli would be greatly advantageous, enabling quick and appropriate responses to danger, and therefore improving one’s chances of survival (LeDoux, 1996). According to the standard model of early emotional processing, threat-related stimuli are processed *preattentively* (i.e., in parallel across the entire visual field, prior to the operation of selective attention) by a specialised subcortical threat-detection system (Öhman & Mineka, 2001). In other words, the processing of threat-related stimuli is automatic in the sense that it does not require attention. The attentional facet of this model, the so-called *threat-capture hypothesis*, posits that the preattentive threat-detection system automatically directs attention to the location of threat stimuli to facilitate further processing (Feldmann-Wüstefeld, Schmidt-Daffy, & Schubö, 2011; Fenker et al., 2010; Ikeda, Sugiura, & Hasegawa, 2013). Thus, the threat-capture hypothesis holds that an observer’s attention is “captured” by threat-related stimuli.

The threat-capture hypothesis generates two important predictions. First, because threat-related stimuli should capture attention in a purely bottom-up manner, they should capture attention, even when the observer has no intention to attend to them. Second, threat-related stimuli should capture attention even when it is engaged elsewhere. The threat-capture hypothesis has been highly influential and has generated a vast body of empirical work investigating the influence of emotional stimuli on attention (e.g., Eimer & Kiss, 2007; Fenker et al., 2010; Ikeda et al., 2013; Öhman, Flykt, & Esteves, 2001; Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Yates, Ashwin, & Fox, 2010). In this thesis, I will first review research using behavioural, neuroimaging, and electrophysiological approaches to testing the threat-capture hypothesis. I will then present three experiments that directly test both predictions derived from the threat-capture hypothesis.

Visual Search for Emotional Facial Expressions

Visual search has been used extensively to study the influence of threat-related facial expressions on attention (e.g., Hansen & Hansen, 1988; Horstmann & Bauland, 2006; Williams & Mattingley, 2006; Williams, Moss, Bradshaw, & Mattingley, 2005; for a review, see Frischen, Eastwood, & Smilek, 2008). The visual search paradigm simulates the common scenario of searching a cluttered environment for a desired object. In a typical visual search task, participants search for a target among distractors, and indicate when they have found this stimulus. Early research sought to characterise search tasks as *parallel* or *serial* (e.g., Treisman & Gelade, 1980). Parallel search is unaffected by set size as targets are detected effortlessly and appear to "pop-out" from the display. Parallel search is often taken to indicate that all items in the display are processed simultaneously (i.e., preattentively). In contrast, serial searches are influenced by the number of targets in the display, with search times increasing as more distractors are present. Serial search is thought to involve the focusing of attention on each item in the display in turn (Treisman & Gelade, 1980).

Some studies have found that search for angry faces is unaffected by set size. For example, Williams and Mattingley (2006) had participants search for an emotional face (angry or fearful) among neutral faces. They found that search times did not increase with set size when the target was an angry male face. That is, search was parallel. Interestingly though, this was not the case when the target was an angry female face, which they argued occurred because angry male faces signal a more significant threat in an evolutionary sense. Results like these have been taken to indicate that threatening expressions are detected preattentively and automatically draw attention (e.g., Hansen & Hansen, 1988).

However, search for threat-related facial expressions is not typically parallel; rather search times for negative expressions seem to be less affected by set size than search times for positive expressions (e.g., Eastwood, Smilek, & Merikle, 2001; Gerritsen, Frischen, Blake, Smilek, & Eastwood, 2008; Hahn, Carlson, Singer, & Gronlund, 2006; Hahn & Gronlund, 2007; Williams et al., 2005). That is, search for threatening expressions is more efficient than search for positive or neutral expressions. Based on such findings, it has been concluded that emotional facial expressions *can* be processed preattentively and guide attention to their location (Frischen et al., 2008). The "can" here is important. In visual search studies participants search for a specific emotional expression or for the "odd face out" in terms of emotional expression (e.g., Eastwood et al., 2001; Williams & Mattingley, 2006; Williams et al., 2005). Such visual search studies only tell us that preattentive processes are sensitive to emotional expressions when participants are actively searching for emotion. In other words, top-down search intentions and bottom-up stimulus factors are confounded in the typical visual search study. Thus, it remains to be determined whether threat-related expressions capture attention when they are entirely task-irrelevant as predicted by the threat-capture hypothesis.

Hodsoll, Viding, & Lavie (2011) addressed this issue, having participants search for a gender-singleton target (i.e., the male target face among female distractors). On each trial, participants viewed search displays containing three faces, each slightly tilted to the left or right, and were required to indicate whether the gender singleton was tilted to the left or the right. On some trials all three facial expressions were emotionally neutral. However, on other trials, there was an emotional distractor (i.e., one of the non-target faces was emotional). On other trials still, the target face was emotional. Because participants were searching for a gender singleton, the emotional expressions of the faces were completely irrelevant to the task. Nonetheless, Hodsoll et al. found that an emotional distractor face produced a cost in response times (RTs); participants were slower to indicate the orientation of the target face when an emotional distractor was present than when no such distractor was present, and this was the case when the emotional distractor face was fearful and when it was angry. Hodsoll et al. argued that emotional expressions captured attention in a bottom-up manner such that attention was initially directed to the threat-related distractors and then redirected to the target face, producing longer RTs.

Flanker Tasks and the Role of Perceptual Load

Hodsoll et al.'s (2011) findings suggest that threat-related expressions captured attention, even when they were irrelevant to the visual search task, as predicted by the threat-capture hypothesis. However, it is not clear that attention capture was driven by preattentive processes. While the emotional expressions were irrelevant to Hodsoll et al.'s (2011) gender-search task, the faces themselves were task-relevant because they were often the targets. Thus, it is likely that participants adopted a "broad attentional window" (Belopolski, Zwaan, Theeuwes, & Kramer, 2007), distributing attention across all of the faces. The distribution of attention appears to be important in determining whether or not salient stimuli capture attention. For example, in one recent study perceptually salient (non-emotional) stimuli captured attention and interfered with task performance only when attention was broadly distributed (due to task demands). However, when attention was narrowly focused, the same distractors did not interfere with task performance (Belopolski & Theeuwes, 2010). Thus, it may be that emotional distractors, like perceptually salient distractors, capture attention only when presented inside the attentional window. The study of Hodsoll et al. does not therefore test the prediction that threat-related expressions capture attention when it is engaged elsewhere. One way to overcome this problem is to present threat stimuli at locations that are completely irrelevant to the task, as in a flanker paradigm. In a flanker task, participants identify a task-relevant stimulus that is consistently presented at the same location (often at fixation) and is flanked by task-irrelevant distractors (e.g., Eriksen & Eriksen, 1974).

However, a flanker paradigm alone does not ensure that flankers are unattended (i.e., that attention is successfully focused on the target stimulus alone). The task-irrelevant flankers are often chosen so that they will interfere with task performance (at least on some trials; e.g., Eriksen & Eriksen, 1974; Lavie & Cox, 1997), thus it is in the participant’s best interest to ignore them. Nonetheless, non-emotional flankers often interfere with task performance (e.g., Eriksen & Eriksen, 1974; Lavie, 1995; Lavie & Cox, 1997). So how does one ensure that flankers are strictly unattended? Lavie’s (1995, 2005) load theory of attention provides an answer to this question. Load theory holds that task-irrelevant stimuli are only truly unattended when the processing of task-relevant stimuli exhausts the observer’s capacity for perception. More specifically, load theory posits that perception depends on limited attentional resources that are involuntarily allocated to stimulus processing until they are exhausted. Therefore, load theory predicts that the processing of task-irrelevant stimuli depends on the *perceptual load* imposed on the visual system. When the perceptual load of a task is high, attentional resources are exhausted by task-relevant stimuli meaning that task-irrelevant stimuli are not perceived. Conversely, when the perceptual load of a task is low, processing of task-relevant stimuli does not exhaust attentional resources and “spare” attentional resources are involuntarily devoted to processing task-irrelevant stimuli. These predictions of load theory have received a great deal of empirical support with non-emotional stimuli; high perceptual load reduces behavioural interference caused by task-irrelevant distractors (Beck & Lavie, 2005; Lavie, 1995; Lavie & Cox, 1997), neural activity associated with the processing of distractors (Pinsk, Doniger, & Kastner, 2004; Rees, Frith, & Lavie, 1997; Schwartz et al., 2005; Yi, Woodman, Widders, Marois, & Chun, 2004), and awareness of distractors (Carmel, Saker, Rees, & Lavie, 2007; Carmel, Thorne, Rees, & Lavie, 2011).

Importantly, the threat-capture hypothesis holds that threat stimuli capture attention because a preattentive threat-detection system automatically guides attention to their location. Because this threat-detection system is theorised to operate preattentively, it should not depend on the availability of attentional resources. Consequently, the threat-capture hypothesis predicts that threat stimuli should capture attention when they are presented in task-irrelevant locations, even when observers are performing a task that imposes a high perceptual load. Yates et al. (2010) used a flanker task to test this prediction. In two experiments, participants performed a letter identification task. On each trial, a row of six letters was briefly presented at fixation, and participants were required to identify the target letter contained within this display (an ‘x’ or a ‘z’) with a speeded key-press. On low perceptual load trials, the target letter appeared among homogeneous distractors (e.g., oooxoo), while on high perceptual load trials, the target appeared among heterogeneous distractor letters (e.g., snmxkv). Furthermore, on each trial, a distractor face appeared above or below the letter stimuli. This distractor was either a neutral face, an angry face, or an angry face that had previously been aversively conditioned (repeatedly paired with a loud burst of white noise) to increase emotional salience. On low perceptual load trials, Yates et al. found that emotional distractors interfered with performance of the letter-identification task; RTs were slower when the distractor was an angry face than when it was a neutral face, and even slower still when the distractor was an aversively-conditioned angry face. Thus, emotional distractors appeared to capture attention when the letter-identification task imposed a relatively low perceptual load. However, this was not the case on high perceptual load trials in which the nature of the distractor face did not affect RTs. These findings suggest that threat-related stimuli successfully compete for attention only when sufficient attentional resources are available for their processing. These results are inconsistent with the threat-capture hypothesis, which predicts that threat-related stimuli will capture attention when it is engaged elsewhere.

Neuroimaging Studies on the Automaticity of Emotion Processing

It often argued that the preattentive threat-detection system posited by the standard model of early emotion processing is centred on the amygdala (e.g., Dolan & Vuilleumier, 2003; Le Doux, 1996; Vuilleumier, 2005). This view was supported by early neuroimaging studies that demonstrated that the amygdala responds to emotional facial expressions (Morris et al., 1996), even when they are backwards masked and fail to reach conscious awareness (Whalen et al., 1998). More recent research suggests that the amygdala may modulate visual processing directly through feedback connections to visual cortex (Amaral, Behniea, & Kelly, 2003; Vuilleumier, 2005) or indirectly via the dorsal fronto-parietal attention network (Vuilleumier & Driver, 2007). Indeed, evidence for modulation of visual processing by the amygdala has come from neuroimaging studies, which have revealed a correlation between activation of the amygdala and visual cortex in response to fearful faces (Morris et al., 1998), and that this relationship is disturbed by amygdala damage (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004).

The possibility that the amygdala may be involved in preattentive processing of threat-related facial expressions has generated considerable empirical inquiry, with a number of researchers investigating the role of attention in the amygdala response to these stimuli (e.g., Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Pessoa, McKenna, Guiterrez, & Ungerleider, 2002; Vuilleumier, Armony, Driver, & Dolan, 2001). These studies have all adopted variations on the basic flanker paradigm. For example, in one study (Vuilleumier et al., 2001) participants were briefly presented with displays comprising two faces and two houses arranged in horizontal and vertical pairs around a central fixation point. On each trial, a cue indicated which pair of stimuli (faces or houses) was task-relevant, and participants indicated whether the task-relevant pair of stimuli were the same or different. Thus, on some trials the faces were the task-relevant targets, and on other trials they were the task-irrelevant flankers. Vuilleumier et al. also manipulated the expressions of the faces, which were either fearful or neutral. The authors reported greater activation of the amygdala and visual cortex in response to fearful than to neutral facial expressions, and these differential responses were observed regardless of whether the faces were task-relevant or task-irrelevant. This finding suggests that the emotional significance of facial expressions is processed by the amygdala, even when attention is engaged elsewhere (i.e., preattentively). However, Vuilleumier et al. did not manipulate the perceptual load of the house-matching task. Therefore, their study left open the possibility that when the house stimuli were task-relevant, the perceptual load of the house-matching task was not sufficiently high to ensure that the face stimuli were truly unattended (Pessoa et al., 2002).

Drawing on load theory, a number of researchers have investigated the role of perceptual load in amygdala response to emotional facial expressions (e.g., Lim, Padmala, & Pessoa, 2008; Pessoa et al., 2002; Pessoa, Padmala, & Morland, 2005; Silvert et al., 2007). Consistent with load theory, high perceptual load has been found to eliminate enhanced activation of the amygdala to fearful facial expressions (Pessoa et al., 2002; Pessoa et al. 2005; Silvert et al., 2007). For example, Pessoa et al. (2005) had participants view briefly presented displays comprising a face at fixation flanked by two bars. In some blocks of trials, participants attended to the face, indicating whether it was male or female. In other blocks, participants attended to the bars, indicating whether or not the orientations of the bars either side of the face were identical. Thus, the face was task-irrelevant in these blocks. Furthermore, the authors parametrically varied the perceptual load of the bar-orientation task by adjusting the angular difference between the bars on non-matching trials, generating three levels of perceptual load (low, medium, and high). Pessoa et al. observed a greater amygdala response to fearful faces than to neutral faces when participants performed the sex-discrimination task, and this valence effect was present when participants performed the low-load version of the bar-orientation task. However, when participants performed the medium- or high-load versions of the task, no such effect was observed. Furthermore, high perceptual load has been found to abolish differential amygdala activation to fearful faces even when they have been aversively conditioned (Lim et al., 2008). Therefore, consistent with behavioural flanker experiments (e.g., Yates et al., 2010), it appears that attentional resources must be available for the processing of threat-related facial expressions, even in the amygdala, a structure thought to play a key role in a preattentive threat-detection system.

Threat-capture: Evidence from Electrophysiology

Evidence from flanker tasks using behavioural and neuroimaging measures to probe the processing of task-irrelevant threat-related facial expressions appears to be largely inconsistent with the threat-capture hypothesis. However, it is important to note that neuroimaging studies of the amygdala do not directly test the hypothesis. It is entirely possible that capture of attention by threat-related stimuli does not rely on the amygdala, as is commonly assumed. Consistent with this possibility, a recent study reported unimpaired rapid detection of fearful faces in a patient with complete bilateral lesions of the amygdala (Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009). Additionally, behavioural measures of attention capture (as used by Yates et al., 2010) may simply not be sensitive to transient shifts of attention to emotional distractors.

Despite the evidence against the threat-capture hypothesis, evidence in favour of the hypothesis has come from electrophysiological studies. These studies have focused on the *N2pc* (N2 posterior contralateral), an event-related potential (ERP) component thought to index processes involved in attentional selection of a lateralised stimulus (for a review, see Luck, 2012). The N2pc is a *lateralised* ERP component. That is, the N2pc manifests as a difference in ERP activity detected at corresponding electrodes on either side of the head. Specifically, when participants view a bilateral stimulus pair and attend to one stimulus in the pair, they produce a more negative wave over the side of the head opposite the attended stimulus (i.e., the *contralateral* side) compared to the side of the head on the same side as the attended stimulus (i.e., the *ipsilateral* side). This difference is the N2pc component (see Figure 1). By comparing the contralateral and ipsilateral waveforms, one can determine which of the two stimuli was attended to. The N2pc is observed over occipito-temporal scalp sites (e.g., at electrodes P7 and P8 according to the modified 10-20 system; American Electroencephalographic Society, 1994), and is typically observed between 200 and 300 ms after stimulus onset (Luck, 2012).

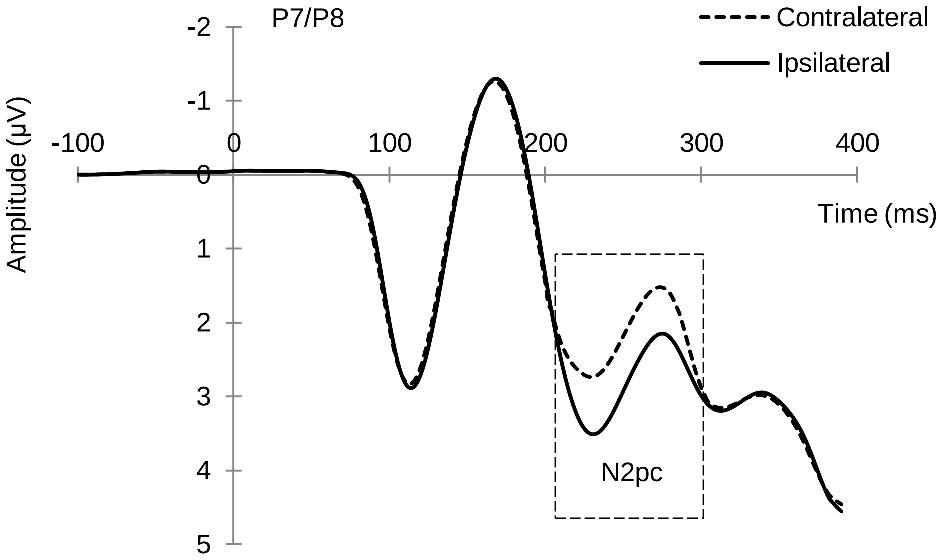

Figure 1. A schematic of a typical N2pc observed when participants attend to a lateralised stimulus. Waveforms from occipito-temporal electrodes are presented separately for electrodes positioned on the contralateral and ipsilateral sides of the head in relation to the position of the attended stimulus. The N2pc manifests as a more negative voltage detected at electrodes located on the contralateral side relative to the ipsilateral side, typically observed between 200 and 300 ms after stimulus onset. Negative is plotted up by convention.

Researchers generally agree that the N2pc indexes processes involved in attentional selection of a lateralised stimulus (e.g., Luck, Fan, & Hillyard, 1993; Luck & Hillyard, 1994a, 1994b; Eimer, 1996; Mazza, Turatto, Umiltà, & Eimer, 2007; Mazza, Turatto, & Caramazza, 2009; Woodman & Luck, 1999, 2003), although the precise processes that the N2pc reflects remain unclear (Luck, 2012). For example, there has been considerable debate as to whether the N2pc reflects a filtering process involved in suppressing signals elicited by non-selected stimuli (Luck & Hillyard, 1994b) or a selection process that directly enhances signals elicited by the selected stimulus (Eimer, 1996; Mazza et al., 2009). Although the precise mechanisms indexed by the N2pc are not completely understood, the N2pc itself remains a useful indicator of attentional selection and is commonly used as such (e.g., Eimer & Kiss, 2007; Hickey, McDonald, & Theeuwes, 2006; Woodman & Luck, 1999, 2003).

Because the N2pc provides an electrophysiological index of attentional selection, it is a powerful tool for investigating attention capture by threat-related facial expressions. Indeed, an N2pc is commonly observed for lateralised threat-related expressions when they are relevant to the goals of the individual (Feldmann-Wüstefeld et al., 2011; Weymar, Löw, Öhman, & Hamm, 2011). However, according to the threat-capture hypothesis, threat-related facial expressions should capture attention, and therefore produce an N2pc, even when they are completely task-irrelevant and the observer has no intention to attend to them. Evidence supporting this prediction has come from the dot-probe paradigm (e.g., Grimshaw, Foster, & Corballis, 2013; Holmes et al., 2009). In a typical dot-probe task, a pair of cue stimuli (often faces, one emotional and one neutral) is briefly presented, followed by a target stimulus presented at the location previously occupied by one of the cue stimuli. The participant’s task is to identify the target stimulus as quickly as possible (MacLeod, Mathews, & Tata, 1986). Importantly, the location of the emotional stimulus typically does not predict the location of the target. Therefore, participants have no incentive (at least in terms of task performance) to preferentially attend to the emotional stimulus. Often a behavioural measure of attentional bias is obtained from this paradigm by comparing RTs to targets that are presented at the same location as the emotional cue with RTs to targets that are presented at the same location as the neutral cue. Using this approach, an attentional bias towards emotional stimuli manifests as faster RTs to targets replacing emotional cues than to those replacing neutral cues. When the cue stimuli are presented bilaterally (i.e., one in each visual field), an N2pc reflecting attentional selection of the emotional stimulus can be isolated by comparing ERP waveforms recorded from electrodes contralateral and ipsilateral to the emotional stimulus. In line with the threat-capture hypothesis, an N2pc is observed for threat-related facial expressions in the dot-probe paradigm (Holmes et al., 2009), even when participants are instructed to ignore these stimuli (Grimshaw et al., 2013). These findings suggest that threat-related expressions capture attention in a bottom-up manner. However, because targets can appear in either visual field, participants are likely to broadly distribute attention across the face stimuli. Therefore, these studies do not test the prediction of the threat-capture hypothesis that threat stimuli capture attention when it engaged elsewhere. To achieve this, one needs to control the allocation of attention by having participants perform a central task, and by manipulating the perceptual load of the task.

A very recent study has taken this approach to examine the automaticity of attention capture by threat-related facial expressions, measured using the N2pc component. Ikeda et al. (2013) examined the effect of perceptual load on the N2pc elicited by task-irrelevant fearful faces, and on the late positive potential (LPP), an ERP correlate of emotion processing that likely reflects sustained attention to emotional stimuli (Sabatinelli, Lang, Keil, & Bradley, 2007). The LPP is a central-parietal component emerging around 300 ms after stimulus onset and is observed for emotional stimuli compared with neutral stimuli, including emotional facial expressions (MacNamara, Schmidt, Zelinsky, & Hajcak, 2012; Schupp et al., 2004; for a review, see Eimer & Holmes, 2007). Ikeda et al. had participants search a vertical column of letters to detect or identify a target letter. On high perceptual load trials, participants performed a letter-identification task in which they indicated which of two possible targets letters (M or N) was presented among heterogeneous distractor letters. On low perceptual load trials, participants performed a less demanding task in which they indicated the presence or absence of a target (X) among homogeneous distractors (Os). These task-relevant letters were flanked bilaterally by task-irrelevant faces. In each trial, the bilateral faces comprised two neutral faces (*bilateral neutral trials*), two fearful faces (*bilateral fearful trials*), or one neutral face and one fearful face (*lateralised fearful trials*). As in the dot-probe studies previously discussed, the lateralised fearful trials allowed Ikeda et al. to isolate the N2pc elicited by a fearful face[1]. Ikeda et al.'s design allowed them to examine the LPP elicited by the presence of a fearful face by comparing ERPs for trials on which a fearful face was present (i.e., lateralised fearful and bilateral fearful trials) with trials on which no fearful face was present (i.e., bilateral neutral trials). By examining the N2pc and the LPP within the same experiment, Ikeda et al. were able to shed light on automaticity of attention capture, as indexed by the N2pc, relative to those processes indexed by the LPP.

Consistent with the predictions of the threat-capture hypothesis, Ikeda et al. (2013) found that a lateralised fearful face elicited an N2pc, regardless of the perceptual load of the primary task. Thus fearful faces captured attention and this capture appeared not to rely on the availability of attentional resources for their processing. In other words, Ikeda et al. found that fearful faces captured attention when it was engaged elsewhere, as predicted by the threat-capture hypothesis. In contrast to the N2pc results, it was found that an LPP was observed when participants performed the low-load task but not when they performed the high-load task. This is consistent with previous studies that have found that the LPP to emotional facial expressions is eliminated when attention is focused elsewhere (Eimer, Holmes, & McGlone, 2003; Holmes, Vuilleumier, & Eimer, 2003; Holmes, Kiss, & Eimer, 2006). Based on this finding, the authors argued that the N2pc effect occurs automatically, and independently of later aspects of emotional processing that are indexed by the LPP. Thus, the study of Ikeda et al. provides what might be the strongest empirical support to date for the threat-capture hypothesis.

In a second experiment, Ikeda et al. (2013) sought to rule out the possibility that load-resistant capture of attention by fearful faces was driven by low-level visual properties of these faces. To achieve this, they conducted an experiment in which the faces were inverted on some trials. Inverted faces are commonly used to control for low-level visual properties (e.g., luminance, contrast, and configural properties of the stimulus) because these are preserved while the perception of emotional facial expressions is disrupted when faces are inverted (de Gelder, Teunisse, & Benson, 1997;

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[1] Attentional selection of a stimulus on the vertical meridian is presumed not to contribute to the N2pc because selection of such stimuli involves visual cortex in both the left and right hemispheres (Hickey et al., 2006; Hilimire, Mounts, Parks, & Corballis, 2011; Woodman & Luck, 2003). Thus, the selection of a target letter in Ikeda et al.'s task should not contaminate the N2pc produced by lateralised, task-irrelevant faces.

Eimer & Holmes, 2002; Searcy & Bartlett, 1996). Again, Ikeda et al. found that an N2pc was elicited by a lateralised fearful expression when upright. However, no such effect was observed when faces were inverted. Based on this finding, Ikeda et al. argued that attention capture by fearful faces is driven by perception of the emotional expression rather than by the low-level visual properties that characterise fearful faces. Thus threat capture appears to be driven by the emotional significance of threat-related facial expressions.

The Current Experiments

To summarise, the study of Ikeda et al. (2013) provides the only compelling support for the threat-capture hypothesis. Visual search studies suggesting that emotional expressions capture attention (e.g., Hodsoll et al., 2011) do not adequately test the prediction of the threat-capture hypothesis that these stimuli capture attention when it is engaged elsewhere. Studies that have addressed this issue using a flanker paradigm have found that task-irrelevant angry faces interfere with task performance when the perceptual load of the primary task is low but not when it is high (Yates et al., 2010). Similarly, the amygdala response to task-irrelevant threat-related expressions is abolished when the perceptual load of a primary task is high (e.g., Pessoa et al., 2002, 2005). Therefore, these studies suggest that attention is required for the processing of threat-related facial expressions. That is, these stimuli appear not to be processed preattentively as posited by the threat-capture hypothesis.

The current experiments were intended to further test the key predictions generated by the threat-capture hypothesis. Experiment 1 tested the prediction that threat-related expressions capture attention when they are task-irrelevant. This experiment employed a dot-probe paradigm to examine the N2pc in conjunction with behavioural measures of attention capture. Experiments 2A and 2B tested the prediction that task-irrelevant angry faces should capture attention when it is engaged elsewhere. To ensure that attention was engaged elsewhere, participants performed a letter-identification task at fixation similar to that used by Ikeda et al. (2013), and the perceptual load of this task was varied. Experiments 2A and 2B were complementary experiments that were designed to examine behavioural interference produced by task-irrelevant angry faces (Experiment 2A), and the N2pc elicited by these stimuli (Experiment 2B). This thesis focused on capture of attention by angry faces rather than fearful faces (as used in previous studies; e.g., Ikeda et al., 2013) because they signal not only the presence of a threat but also its location and therefore may have a stronger influence on attention (Eimer & Kiss, 2007; Whalen, 1998). Moreover, this thesis focused specifically on capture of attention by angry male faces because these are thought to have a more potent influence on attention than angry female faces as they signal a more significant threat in an evolutionary sense (Williams & Mattingley, 2006).

The study of Ikeda et al. (2013) suggests that attention capture by emotional facial expressions is driven by perception of the facial expression rather than by low-level visual properties of these stimuli. This study used inverted faces to control for low-level properties. However, face inversion does not completely eliminate the emotional information portrayed by emotional facial expressions (Eimer & Holmes, 2002). For this reason, I used *Fourier phase-scrambled* faces to control for low-level visual properties in the current experiments. All visual stimuli can be decomposed into overlapping spatial frequency components that vary in orientation, power, and phase (i.e., their location within the image). Fourier phase scrambling randomises the *phase* of spatial frequency components but does not alter the global distribution of orientations and spatial frequencies (i.e., the Fourier amplitude spectrum). Phase information is crucially important for perceiving – the experience of seeing – emotional facial expressions because it determines the position of contour information. Consequently, phase scrambling produces images that convey no emotional information while preserving the global low-level properties (e.g., the relative intensities of spatial frequency components across orientations [i.e., the Fourier amplitude spectrum], as well as the average pixel luminance, and root mean square [RMS] contrast) of their intact counterparts (Honey, Kirchner, & VanRullen, 2008; Rossion & Caharel, 2011).

Experiment 1

Experiment 1 tested the first prediction of the threat-capture hypothesis – that angry faces attract attention, even when they are task-irrelevant. Participants performed a go/no-go dot-probe task similar to those used in previous studies examining the effect of emotional facial expressions on attention (e.g., Pourtois et al., 2004; Brosch, Pourtois, Sander, & Vuilleumier, 2011). On each trial, a bilateral pair of faces was briefly presented, consisting of one angry and one neutral face. These displays allowed me to examine the N2pc elicited by an angry face, as in previous dot-probe studies (Grimshaw et al., 2013; Holmes et al., 2009). A lateral probe was then presented, replacing either the angry face or the neutral face. The orientation of this probe indicated whether participants needed to make a speeded key-press or withhold a response. Because the probe could be presented in either visual field, this task encouraged participants to broadly distribute their attention. Furthermore, the face stimuli were completely task-irrelevant and non-predictive of the location of the probe. This task therefore enabled me to examine the influence of an angry face on attention when it was broadly distributed and when participants had no incentive to attend to the angry face. On the basis of the threat-capture hypothesis, and in line with previous dot-probe studies (e.g., Holmes et al., 2009), it was predicted that angry faces would produce an N2pc, despite these stimuli being task-irrelevant. Furthermore, it was expected that capture of attention by angry faces would also influence performance on the go/no-go task. Specifically, it was expected that responses would be faster and/or sensitivity to the go/no-go signal would be greater when the lateral probe replaced the angry face cue than when it replaced the neutral face cue.

A second aim of this experiment was to verify that the face stimuli used in the present set of experiments (presented at certain size, eccentricity, and timing parameters) were effective in eliciting an N2pc for task-irrelevant angry faces. These same stimuli and parameters were used in Experiments 2A and 2B while participants performed a primary task to engage attention. Should these stimuli not capture attention in Experiments 2A and 2B, it is important to establish that any null results are not due to the stimuli being ineffective at eliciting threat capture entirely.

To ensure that capture of attention by angry faces depends on the emotional expression itself, and not low-level visual properties of these stimuli, control trials were included in which the face stimuli were phase-scrambled. If the N2pc for angry faces depends on perception of an angry facial expression itself, then the N2pc should be observed for intact faces but not for phase-scrambled faces. However, if the N2pc is driven by low-level visual properties that characterise angry faces, then an N2pc should be observed both when the faces are intact and when they are phase-scrambled. Based on previous research suggesting that capture of attention by threat-related facial expressions depends on the perception of emotional expressions (Ikeda et al., 2013), it was expected that no such effects would be observed when the bilateral face cues were phase-scrambled.

The design of the present study also enabled me to examine the amplitude of the occipital P1 component elicited by intact versus phase-scrambled faces. The occipital P1 is sensitive to emotional facial expressions, with larger amplitudes typically observed for threat-related expressions than for neutral expressions (Batty & Taylor, 2003; Holmes, Neilsen, & Green, 2008; Pizzagalli, Regard, & Lehmann, 1999;

Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005). This finding is usually taken to represent enhanced processing of emotional stimuli because the P1 component is thought to reflect visual gain in extrastriate cortex, with increases in amplitude indicating an increase in visual gain (Hillyard, Vogel, & Luck, 1998; Luck & Kappenman, 2012). I examined the difference in P1 amplitudes when the task-irrelevant faces were intact compared to when they were phase-scrambled. It was expected that intact faces would elicit a larger P1 than phase-scrambled faces due to their emotional significance. However, because the intact and phase-scrambled angry-neutral face pairs differed not only in terms of the presence versus absence of an emotion signal but also in terms of the presence versus absence of intact faces to perceive, such differences cannot necessarily be attributed to emotion. Regardless, the P1 serves as a useful indicator of early sensory processing of the task-irrelevant stimuli.

Finally, it is known that attentional processing to threat-related stimuli is abnormal in depressed and anxious individuals (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, van Ijzendoorn, 2007; Kircanski, Joormann, & Gotlib, 2012), and the N2pc is sensitive to such individual differences (at least in anxiety; Fox, Derakshan, & Shoker, 2008). Participants in the present experiment completed questionnaires to screen for depression and anxiety at the time of testing, and participants with high scores on either measure were excluded from the sample. Participants were screened in this way to ensure that the sample was free of emotional disorder. This was done because the threat-capture hypothesis posits that capture of attention is driven by fundamental properties of the threat-detection system and should therefore be observed in healthy individuals, free of emotional disorder.

Method

Participants

Participants were 20 undergraduate students from Victoria University of Wellington (VUW). Participants' depression and anxiety were assessed using the Beck Depression Inventory II (BDI-II; Beck, Steer, & Brown, 1996) and the Mini Mood and Anxiety Symptom Questionnaire (Mini MASQ; Clark & Watson, 1995), respectively. Participants were excluded if their scores on the BDI-II were indicative of clinically significant depression (i.e. a score greater than 29) or if their score on the Mini MASQ was greater than two standard deviations above the mean score. Three participants were excluded because their BDI-II score exceeded 29, leaving 17 participants (13 women, 13 right handed, mean age: 18.5 years, *SD* = 1.2) in the sample. Mean score on the BDI-

II was 10.6 (*SD* = 6.6, range = 0-24) and on the Mini MASQ was 48.4 (*SD* = 8.9, range = 33-67). All participants reported normal or corrected-to-normal vision, no history of neurological disorder, and no history of treatment for depression (either through counselling or prescribed Selective Serotonin Reuptake Inhibitor [SSRI] medications). The experiment was conducted with the approval of the Human Ethics Committee of the School of Psychology, VUW, under delegated authority of the VUW Human Ethics Committee. All participants gave written informed consent before participating in the experiment.

Procedure and Apparatus

Participants completed a two hour session. Testing took place in a dimly lit, electrically-shielded chamber. Participants were fitted with a Lycra Quik-Cap (Compumedics NeuroMedical Supplies) embedded with Ag/AgCl electrodes. The experiment consisted of three tasks, completed in the same order by all participants. First, participants completed the dot-probe task. Next, they rated the emotional intensity of the face stimuli presented in the dot-probe task. Finally, they completed the BDI-II followed by the Mini MASQ. At the end of the session participants were verbally debriefed and provided with a written debriefing statement.

During the dot-probe task, a chin rest maintained head position and a constant viewing distance of 60 cm to the computer screen. The experiment was presented on a Dell Optiplex 760 computer with a Dell 19” LCD monitor (1280 × 1024 pixels, 60 Hz refresh rate). E-prime software (Schneider, Eschman, & Zuccolotto, 2002a, 2002b) was used to control stimulus presentation and to record responses. The electroencephalogram (EEG) was amplified with Professional BrainAmps and digitised using Brain-Vision Recorder software (Brain Products, Gilching, Germany).

Dot-probe Task

Face stimuli. The face stimuli consisted of greyscale photographs of angry (open mouth, with teeth exposed) and neutral (closed mouth) facial expressions for eight male actors, all of European decent, taken from the NimStim set of facial expressions (Tottenham et al., 2009). These actors were selected because of high concordance between raters’ labels and the intended expressions for angry and neutral faces (Cohen’s kappas > 0.75; Tottenham et al.). Each face was trimmed to include only the face and hair, and scaled so that it subtended ~12° vertically. Finally, trimmed faces were superimposed on a grey rectangle subtending 10.0° × 12.8° visual angle, so that the point between the eyes was at the centre of the rectangle. Mann-Whitney U tests revealed that these neutral and angry face stimuli did not differ significantly in average pixel luminance (*p* = 0.27) or RMS contrast (*p* = 0.11).

Fourier phase-scrambled versions of the face stimuli were generated using the Image Processing Toolbox for MATLAB (The MathWorks, Natick, MA). Phase-scrambled images were generated by applying the 2-D Fast Fourier Transform to identify the spatial frequency components of the images, followed by phase randomization and reconstruction using the 2-D amplitude spectrum of the original image. This phase-scrambling procedure randomised the phase (i.e., the position) of all spatial frequency components. Phase scrambling therefore eliminated emotional/semantic content of the image but preserved the global low-level properties of the original image (i.e., average pixel luminance, RMS contrast, and the Fourier amplitude spectrum). See Figure 2 for an example of the intact and phase-scrambled face stimuli used in this experiment.

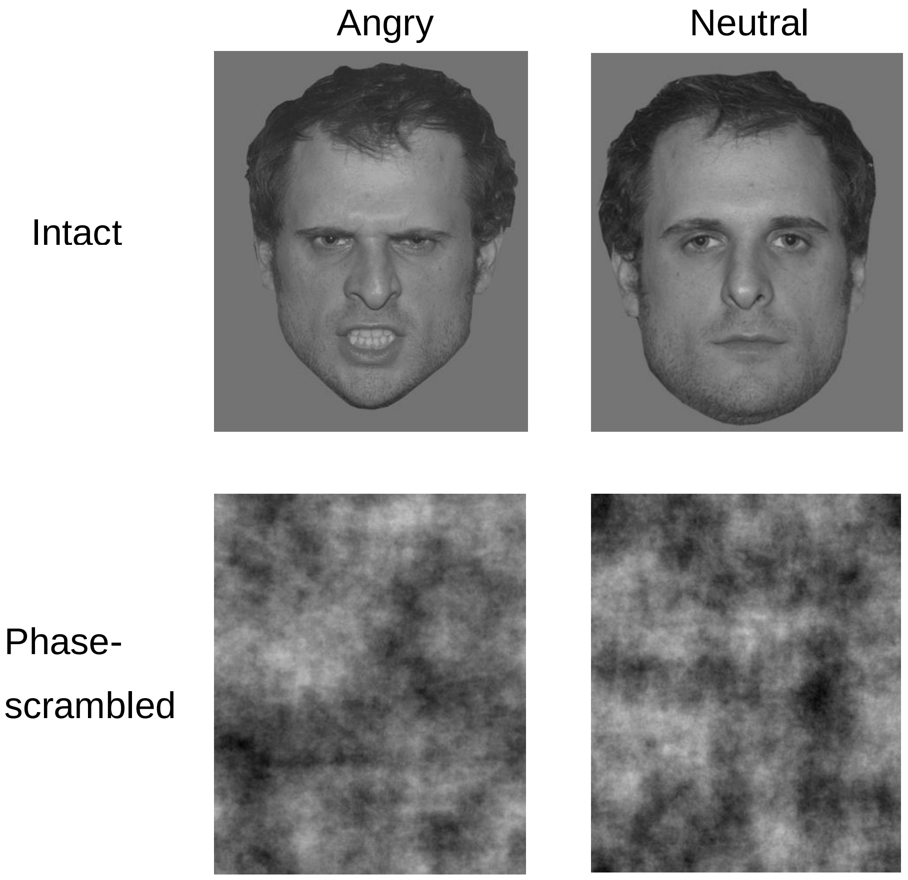

Figure 2. Examples of intact angry and neutral faces and their Fourier phase-scrambled counterparts used in the present experiments.

Procedure and design. Participants performed a go/no-go dot-probe task (see Figure 3). Stimuli were presented on a black background. Each trial began with a white fixation cross (subtending 2.0° × 2.0°; each bar was 0.1° thick), which remained on screen for the duration of the trial. After a random interval between 400 and 800 ms, a bilateral face display was presented for 200 ms (i.e., too brief for saccades), consisting of one angry and one neutral face from the same actor, one presented in the left visual field (LVF) and one presented in the right visual field (RVF). The face stimuli were centred 9.5° to the left and right of the vertical meridian, with the inner edge located 4.5° from the vertical meridian, and were centred 4.6° below the horizontal meridian. The bilateral face pairs were centred below the horizontal meridian because the amplitude of the N2pc component is larger when elicited by stimuli presented in the lower visual field (Hilimire et al., 2011; Luck, Girelli, McDermott, Ford, 1997). Both faces were either intact or phase-scrambled. After offset of the faces, the fixation cross remained onscreen for a random interval between 100 and 200 ms before a lateral probe was presented for 150 ms in the LVF or RVF. This jittered delay ensured that the ERPs within the N2pc time-range were not contaminated by ERPs evoked by the probe display. The lateral probe was a white rectangular bar (either horizontal or vertical), subtending 5.8° × 0.4°, and centred 9.5° to the left or right of the vertical meridian, and 4.6° below the horizontal meridian. The lateral probe was presented in the same location as the angry face on *valid trials* or the neutral face on *invalid trials*. Concurrently with the onset of the lateral probe, one of the bars of the fixation cross (either the horizontal or vertical bar) increased in thickness (0.3°) for 150 ms. Participants made a speeded response with the index finger of their dominant hand (on the “0” key of the number-pad on a standard keyboard) when the orientation of the lateral probe matched that of the thicker bar of the fixation cross. No response was required when the orientation of these bars differed. Because participants were required to make a match versus non-match discrimination of the lateral probe and the fixation cross, the task ensured that participants maintained fixation at the central fixation cross throughout the dot-probe task (Pourtois et al., 2004). After the probe display, the screen remained blank for the remainder of a 1500-ms response window (i.e., for 1350 ms), or until a response was made. Failure to respond within the response window on go trials was considered an incorrect response. Responses made on no-go trials were also considered incorrect. Finally, feedback indicating whether the response was correct (a green fixation cross) or incorrect (a red fixation cross) was presented for 500 ms after a response was made, or after the response window if the participant failed to respond. The next trial began immediately after feedback. All participants were instructed to ignore the bilateral face display and to keep their eyes fixated on the fixation cross for the full duration of each block of trials. Participants were instructed to respond as quickly as possible on go trials and to keep responses on no-go trials (i.e., false alarms) to a minimum.

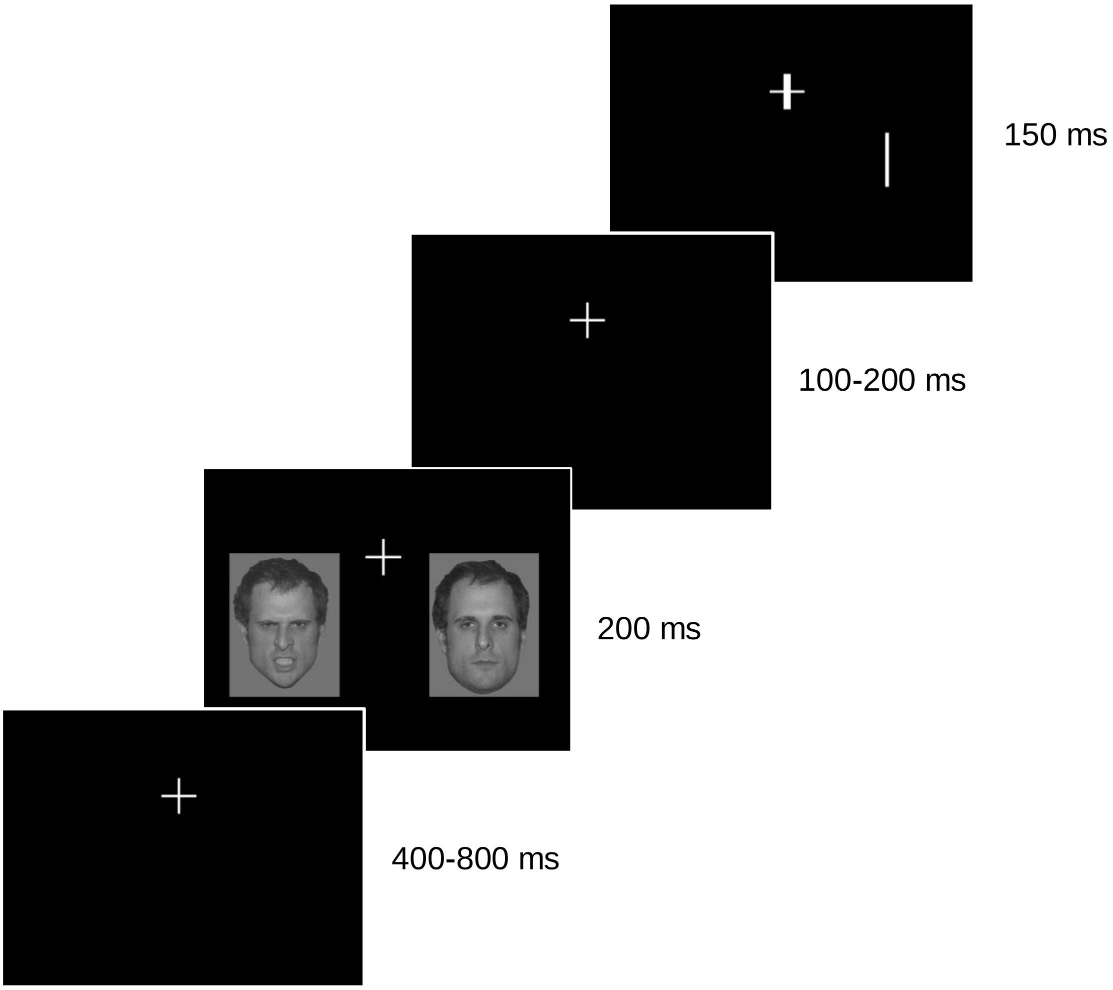

Figure 3. The sequence of events in a trial of the dot-probe task used in Experiment 1. This figure is for illustrative purposes only. Stimuli are not presented to scale.

Task instructions were read by participants and were further emphasised by the experimenter. The experimenter supervised each participant while they completed a block of 24 practice trials to ensure they fully understood the task. Face-type (intact, phase-scrambled) and probe validity (valid, invalid) were manipulated within subjects. After the practice trials, participants completed six blocks of 128 trials (768 total; 192 valid probe trials and 192 invalid probe trials for each level of face type). Half of the trials were go trials and half were no-go trials. Thus, each block included 64 go trials and 64 no-go trials that comprised all combinations of face type (intact or phase-scrambled), location of angry face (left or right visual field), and probe validity (valid or invalid) for each of the eight face identities (2 × 2 × 2 × 8 = 64 trials). The trial order within each block was random. The orientation of the lateral probe (and hence the orientation of the wide bar at fixation) was determined randomly on a trial-by-trial basis.

Emotion-rating Task

Participants rated the emotional intensity of each of the intact face stimuli presented during the dot-probe task. The same 16 face stimuli used in the dot-probe task were presented one at a time, and participants rated, on a 9-point scale, how angry and how threatening each face seemed to them. The face stimuli were presented on a black background in the centre of the monitor. For each face, the question “How angry does this facial expression seem?” was presented below the face accompanied by a row of evenly spaced grey boxes labelled “1” to “9” from left to right. The phrase “Not angry at all” was presented above the leftmost box, and the phrase “Extremely angry” was presented above the rightmost box. Participants responded with a mouse click on one of the nine boxes. Once a response was made the question and these labels were replaced. The question “How threatening does this facial expression seem?” was presented below the face, the phrase “Not threatening at all” was presented above the leftmost box, and the phrase “Extremely threatening” was presented above the rightmost box. Again, participants responded with a mouse click on one of the nine boxes. Ratings were self-paced; each face remained onscreen until a response was made. The order in which the faces were presented was randomised.

ERP Recording and Analysis

EEG was recorded while participants completed the dot-probe task. The EEG was recorded from 28 scalp sites (FP1, FP2, F7, F3, FZ, F4, F8, FT7, FC3, FC4, FT8, T7, C3, CZ, C4, T8, TP7, CP3, CP4, TP8, P7, P3, PZ, P4, P8, O1, OZ, and O2, according to the modified 10-20 system; American Electroencephalographic Society, 1994). To detect eye movements and blinks, the electrooculogram (EOG) was recorded from electrodes placed at the outer canthus of each eye and above and below the left eye. All channels were referenced online to the left mastoid. Impedances at all electrodes were kept below 10 kΩ. EEG and EOG were filtered online with a bandpass filter of 0.02 to 1000 Hz, and digitised at a sampling rate of 500 Hz.

Electrophysiological data were analysed using Brain-Vision Analyzer 2.0 (Brain Products, Gilching, Germany). Offline, all channels were re-referenced to the algebraic average of the left and right mastoids. The four EOG channels were re-referenced into bipolar vertical (VEOG) and horizontal (HEOG) derivations. All channels were notch filtered at 50 Hz, and bandpass filtered from 0.1 to 30 Hz using a zero phase-shift Butterworth filter (12 dB/oct). EEG was then segmented into 600 ms epochs, beginning 200 ms before onset of the bilateral face display and continuing 400 ms after stimulus onset. Segments were baseline corrected by subtracting the average signal recorded during the 200 ms pre-stimulus baseline. Segments containing muscular artefacts (voltage exceeding ±100 µV at any scalp site) or eye blinks (a change in voltage exceeding 100 µV in the VEOG channel, within any 200 ms period) were eliminated. A two-step procedure was employed to exclude horizontal eye movements (for a similar procedure, see Hilimire, Hickey, & Corballis, 2012). First, segments with a change in voltage exceeding 50 µV in the HEOG channel, within any 200 ms period, were considered artefacts and rejected. This step eliminated large eye movements or saccades. A second step was taken to identify participants who might have systematically made small eye movements that went undetected in the first step[2]. Average HEOG waveforms were created separately for trials on which the angry face was presented in the left and right visual fields. These average waveforms were created separately for the intact and phase-scrambled conditions. Participants were to be excluded from all analyses if the averaged HEOG activity exceeded ±5 µV in any condition. However, no participants were excluded based on this criterion. The grand average HEOG activity of the remaining participants did not exceed ±3.2 µV (which corresponds to a systematic eye movement of 0.2°) for any condition. Therefore, systematic eye movements did not exceed 0.2°, with propagated voltage at posterior sites less than 0.1 µV, in either the intact or phase-scrambled conditions (Lins et al., 1993a, 1993b). Incorrect responses and EEG/EOG artefacts led to the rejection of an average of 7.2% of trials per participant (*SD* = 5.0%, range = 0.9-18.1%).

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[2] It is important to ensure that small but systematic eye movements are excluded when examining the N2pc component because they will generate lateralised electrical activity that will propagate to posterior sites (Lins, Picton, Berg, & Sherg, 1993a, 1993b). This activity may be mistaken for an N2pc component.

Results and Discussion

Emotion-rating Task

One participant did not complete the emotion-rating task due to time constraints. Thus, the analysis was based on the remaining 16 participants. Mean anger and threat ratings for angry and neutral faces are presented separately for each of the eight actors in Table A1 of the appendix. Anger ratings range from 1 *(not angry at all*) to 9 (*extremely angry*), and threat ratings ranged from 1 (*not threatening at all*) to 9 (*extremely threatening*). To ensure that angry faces were perceived as angrier and as more threatening than the neutral faces, paired-samples *t*-tests were used to compare the mean anger and threat ratings for angry and neutral faces collapsed across the eight actors. These analyses confirmed that angry faces (*M* = 7.05, *SD* = 0.93) were rated as angrier than neutral faces (*M* = 1.47, *SD* = 0.65), *t*(15) = 22.993, *p* < .001, *d* = 3.133[3]. Similarly, angry faces (*M* = 5.68, *SD* = 1.40) were rated as more threatening than neutral expressions (*M* = 1.52, *SD* = 0.54), *t*(15) = 11.159, *p* < .001, *d* = 2.790[4]. These results confirmed that the stimuli used in the dot-probe task are appropriate to examine capture of attention by angry facial expressions.

Dot-probe Task Performance

RTs. RTs were analysed for go trials on which a response was made within the 1500-ms response window. Failure to respond within the response window led to the exclusion of an average of 1.4% of trials per participant (*SD* = 1.1%, range = 0.5-3.8%) from the analysis. Median RTs are presented in Figure 4 as a function of face type and probe validity. These data were analysed in a 2 (face type: intact, phase-scrambled) × 2 (probe validity: invalid, valid) repeated-measures ANOVA. There was no main effect of face type, *F*(1, 16) = .592, *p* = .453, η_p^2 = .036, indicating that RTs to probe displays did not vary depending on whether the bilateral face display consisted of intact or phase-

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[3] For all paired-samples *t*-tests in this thesis, Cohen's d was calculated by dividing the population mean difference score by the standard deviation of the difference score (Gibbons, Hedeker & Davis, 1993).

[4] Additionally, both anger and threat ratings were analysed in a 2 (intended expression: anger, neutral) × 8 (actor identity) repeated-measures analysis of variance (ANOVA). Both of these analyses yielded a significant Intended expression × Actor identity interaction [anger ratings: *F*(7, 105) = 4.536, *p* < .001, η_p^2 = .232; threat ratings: *F*(7, 105) = 8.200, *p* < .001, η_p^2 = .353], indicating that the difference in ratings between the intended angry and neutral faces varied by actor. However, Bonferroni corrected *t*-tests confirmed that the angry face for each of the eight actors was rated as angrier and as more threatening than its neutral counterpart.

scrambled faces. More importantly, inconsistent with the threat-capture hypothesis, there was no main effect of probe validity, *F*(1, 16) = .142, *p* = .712, η_p^2 = .009, nor was there a Probe validity × Face type interaction, *F*(1, 16) = .066, *p* =.800, η_p^2 = .004. Therefore, RTs on go trials were not faster when the probe replaced the angry face than when it replaced the neutral face, and this was the case when the face cues were intact and phase-scrambled. This finding suggests that angry faces did not capture attention.

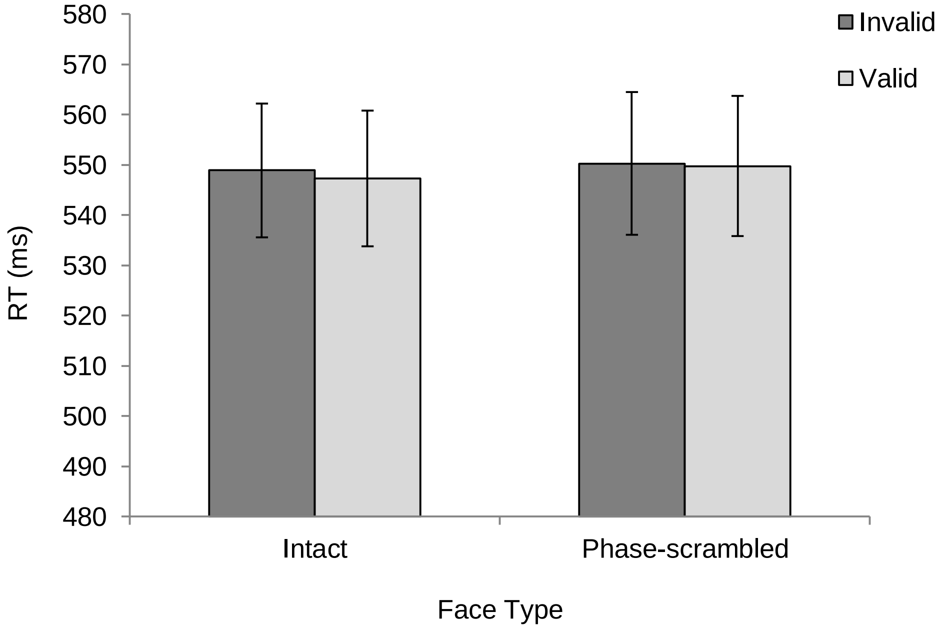

Figure 4. Mean RTs on go trials for valid and invalid probe displays following intact and phase-scrambled bilateral face displays in Experiment 1. Error bars represent standard error of the mean.

Sensitivity (*d'*). Because the go/no-go discrimination was essentially a signal detection task, accuracy was transformed into a measure of sensitivity (*d'*), which provides an index of the participant's ability to discriminate between go and no-go signals. Sensitivity (*d'*) was calculated on the basis of each participant's hit rate (the proportion of go trials on which a response was made within the response window) and false alarm rate (the proportion of no-go trials on which a response was made within the response window) according to the formula:

$$d' = z(\text{Hit Rate}) - z(\text{False Alarm Rate})$$

Rates of 0 and 1 were corrected to 0.005 and 0.995, respectively (Macmillan & Creelman, 1991), such that *d'* scores had a maximum value of 5.152. Sensitivity (*d'*) scores are presented in Figure 5 as a function of face type and probe validity. Overall, *d'* scores were very high (*M* = 3.97, *SD* = .60), suggesting that the task was relatively easy. These data were analysed in a 2 (face type: intact, phase-scrambled) × 2 (probe validity: invalid, valid) repeated-measures ANOVA. There was no main effect of face type, *F*(1, 16) = .148, *p* = .706, η_p^2 = .009, indicating that sensitivity on the go/no-go task did not vary depending on whether the bilateral face display consisted of intact or phase-scrambled faces. More importantly, as in the RT analysis, there was no main effect of probe validity, *F*(1, 16) = .640, *p* = .435, η_p^2 = .038, and no Face type × Probe validity interaction, *F*(1, 16) = .272, *p* = .609, η_p^2 = .017. Thus, sensitivity to the go/no-go signal was not greater when the probe replaced the angry face than when it replaced the neutral face. This was the case when faces were both intact and phase-scrambled. As with the RT data, these data are inconsistent with the predictions derived from the threat-capture hypothesis, and suggest that the face cues did not influence attention. However, it must be noted that sensitivity (*d'*) was very high on this task (*M* = 3.97, *SD* = .60) and RTs were relatively quick for a discrimination task (*M* = 549 ms, *SD* = 56 ms). Therefore, it may be the case that the go/no-go task was not sufficiently difficult to be sensitive to attentional effects produced by the face cues.

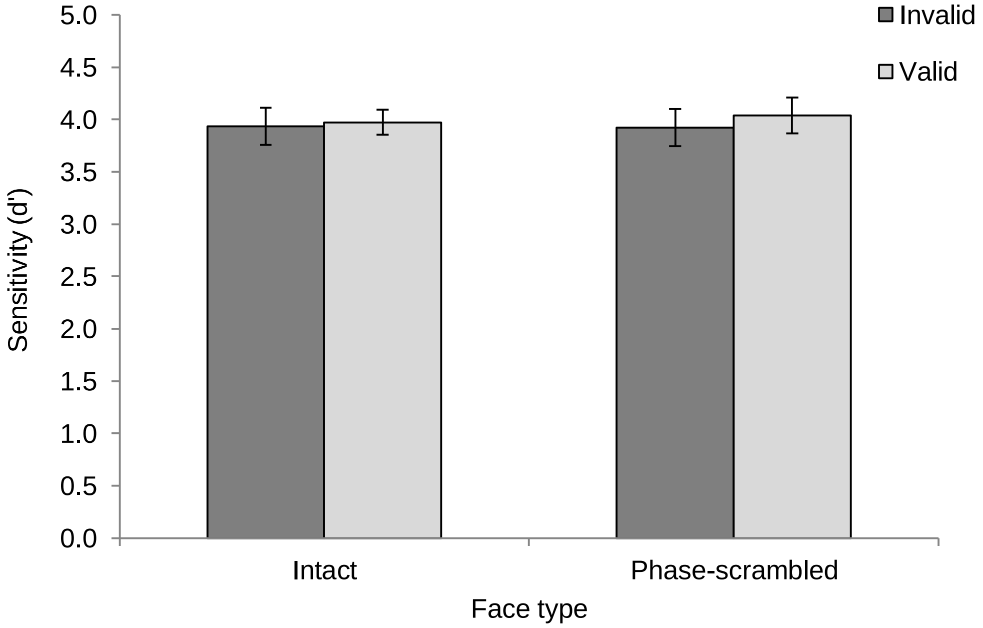

Figure 5. Sensitivity (*d'*) on the go/no-go task for valid and invalid probe displays following intact and phase-scrambled bilateral face displays in Experiment 1. Error bars represent standard error of the mean.

ERPs

P1. The P1 component elicited by the bilateral face displays was quantified as the mean amplitude in a 40-ms window (110-150 ms) at occipital-temporal electrodes P7 and P8, over the left and right hemispheres respectively. The P1 time window was chosen based on the most positive peak in the grand average waveform across both levels of face type (intact, phase-scrambled) and electrode (P7, P8). As expected, P1 amplitudes were larger for trials on which the faces where intact than for trials on which they were phase-scrambled (Figure 6). Larger P1 amplitudes were also observed at electrode P8 than at electrode P7. This pattern of results was confirmed in a 2 (face type: intact, phase-scrambled) × 2 (electrode: P7, P8) repeated-measures ANOVA, with P1 amplitudes as the dependent measure. This analysis yielded significant main effects of face type, $F(1, 16) = 26.9$, $p < .01$, $\eta_p^2 = 0.627$, and electrode, $F(1, 16) = 19.74$, $p < .01$, $\eta_p^2 = .552$. The Face type × Electrode interaction was not significant, $F(1, 16) = 0.33$, $p = .33$, $\eta_p^2 = .060$. The finding that P1 amplitudes were greater for intact than for phase-scrambled faces indicates that the early stages of visual processing in extrastriate cortex that are indexed by the occipital P1 were sensitive to differences between the intact and phase-scrambled faces. One possibility is that the enhanced P1 to intact faces versus phase-scrambled faces were driven by the emotional information portrayed by these stimuli. Indeed, the P1 is known to be sensitive to emotional facial expressions (Batty & Taylor, 2003; Holmes et al., 2008; Pourtois et al., 2005). However, in this experiment, the intact and phase-scrambled stimuli did not differ only in terms of the emotional information conveyed. These stimuli also differed in the presence versus absence of a face to be perceived. For this reason, it cannot be concluded that the enhanced P1 to intact faces necessarily reflects sensitivity to emotional information. Nevertheless, the fact that the P1 was larger for intact than phase-scrambled faces indicates that early stage visual processing were sensitive to some difference between intact and phase-scrambled faces.

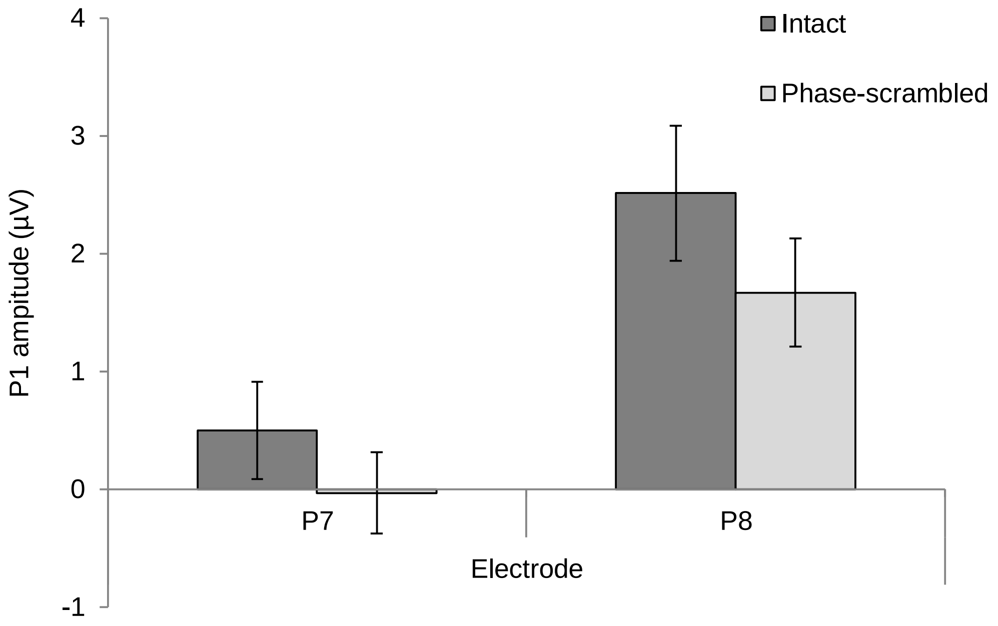

Figure 6. Amplitude of the occipital P1 component (mean voltage 110-150 ms post-stimulus) at occipital-temporal electrodes P7 and P8 elicited by intact and phase-scrambled bilateral face displays in Experiment 1. Error bars represent standard error of the mean.

N2pc. The N2pc component manifests as a more negative wave over the contralateral side of the head than over the ipsilateral side at occipito-temporal scalp sites (Luck, 2012). The N2pc was quantified at occipito-temporal electrodes P7 and P8 (according the modified 10-20 system; American Electroencephalographic Society, 1994). A significantly more negative contralateral than ipsilateral waveform (in the N2pc time window) is indicative of an N2pc component. ERP waveforms at electrodes P7/P8 contralateral and ipsilateral to the angry face are presented in Figure 7A for intact (upper) and phase-scrambled (lower) bilateral face displays. An enhanced negativity was observed contralateral to the angry face (i.e., an N2pc for the angry face) approximately 200-300 ms after onset of the bilateral face displays. This effect was of similar magnitude for intact and phase-scrambled displays. The scalp distribution of the contralateral negativities were centred at occipital-temporal sites (see Figure 7B), a distribution that is typical of the N2pc component (Luck, 2012). The N2pc elicited by both intact and phase-scrambled angry faces can be clearly seen in the contralateral - ipsilateral difference waveforms presented in Figure 7C. These observations were confirmed by statistical analysis. The N2pc was quantified in a 120-ms window (200-320 ms after onset of the bilateral face display). This window was chosen based on the peak in the grand average contralateral - ipsilateral difference waveform across both levels of face type. Mean amplitudes at electrodes P7 and P8 were analysed in a 2 (face type: intact, phase-scrambled) × 2 (electrode laterality: contralateral, ipsilateral) repeated-measures ANOVA. This analysis revealed a significant main effect of electrode laterality, $F(1, 16) = 25.66$, $p < .01$, $\eta_p^2 = .616$. Thus, mean voltage was significantly more negative at the contralateral electrode than at the ipsilateral electrode, indicative of a significant N2pc component. The Face type × Electrode laterality interaction was not significant, $F(1, 16) = 0.66$, $p = .43$, $\eta_p^2 = .040$, indicating that the amplitude of the N2pc component did not differ for intact and phase-scrambled faces. These N2pc effects suggest that attention was captured by the angry face in the bilateral face display, consistent with the predictions of the threat-capture hypothesis.

The fact that an N2pc was observed even when faces were phase-scrambled suggests that attention capture by angry faces is driven by global low-level visual properties that are preserved in the Fourier phase-scrambled stimuli. However, while the angry and neutral face stimuli (and the corresponding phase-scrambled stimuli) did not significantly differ in average pixel luminance or RMS contrast, they were not matched for these parameters. Thus, it is possible that the N2pc effects reported are driven by sensory differences between the neutral and angry face stimuli. However, this is unlikely for two reasons. First, average pixel luminance and RMS contrast were higher for neutral faces than for angry faces on average. Therefore, if the N2pc effects observed were driven by sensory imbalance, one would expect the opposite pattern of results. That is, attention should have been captured by the neutral stimuli, which were slightly (though not significantly) brighter and higher in contrast. Second, the effect of sensory differences between the angry neutral faces on lateralised ERP waveforms should be greatest at short latencies because sensory differences should predominantly impact on early stages of processing (Mazza et al., 2007). Therefore, if the N2pc effect is driven by sensory differences between the neutral and angry faces, the lateralised ERP activity should occur earlier than the N2pc time window. To examine this possibility, mean amplitudes at electrodes P7/P8 in the P1 time window (110-150 ms) were subjected to an additional 2 (face type: intact, phase-scrambled) × 2 (electrode laterality: contralateral, ipsilateral) repeated-measures ANOVA. Critically, this analysis yielded no main effect of electrode laterality, $F(1, 16) = .078$, $p = .784$, $\eta_p^2 = .005$, and no Face type × Electrode laterality interaction, $F(1, 16) = 3.518$, $p = .079$, $\eta_p^2 = .180$[5], indicating that sensory differences between the angry and neutral faces did not influence lateralised ERP activity in the P1 time window when faces were intact nor when they were phase-scrambled. Therefore, the N2pc effects are unlikely to be driven by sensory imbalances.

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[5] Because the type × electrode interaction was marginally significant, paired-samples *t*-tests were conducted to ensure that there was no significant contralateral vs. ipsilateral difference in the P1 time window. These analyses confirmed that no such differences were present for normal, $t(16) = 1.492$, $p = .155$, $d = .362$, or phase-scrambled, $t(16) = -1.577$, $p = .134$, $d = .382$, bilateral face displays.

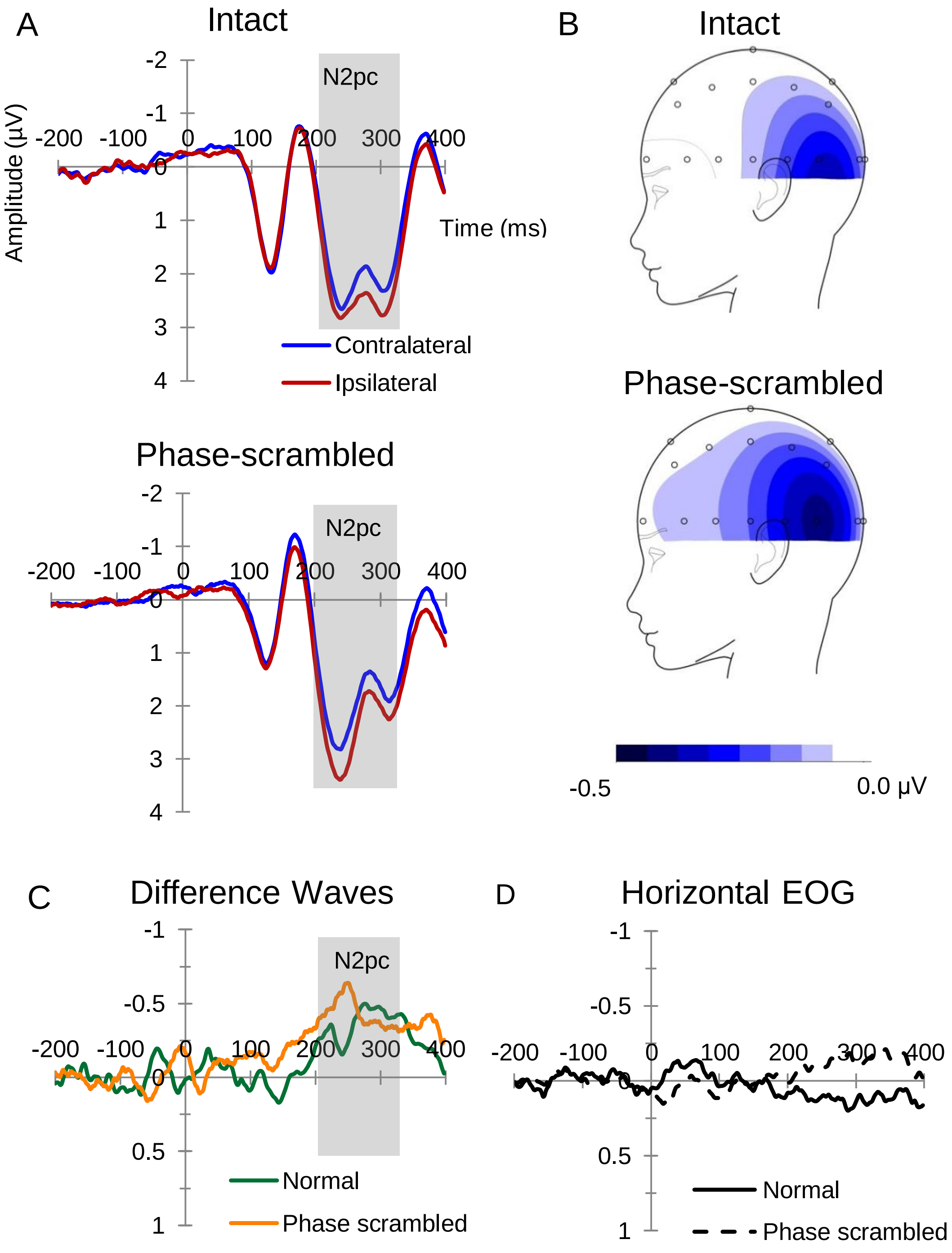


Figure 7. A: Grand averaged ERP waveforms at electrodes P7/P8 contralateral (blue) and ipsilateral (red) contralateral to the angry face for intact and phase-scrambled bilateral face displays. B: Scalp distributions of the N2pc for intact and phase-scrambled faces. C: Contralateral - ipsilateral difference waveforms at electrodes P7/P8. D: Grand averaged HEOG waveforms, recalculated such that a negative voltage indicates eye movement towards the angry face.

Summary

To summarise, rating data confirmed that the angry faces were perceived as being angrier and more threatening than the neutral faces. A larger occipital P1 was observed for intact faces than for phase-scrambled faces, indicating that these stimuli were discriminated at the early stages of visual processing indexed by the P1 component. The N2pc data suggests that angry faces capture attention in a dot-probe paradigm in which the faces themselves are irrelevant. This finding is not surprising; it is consistent with the threat-capture hypothesis, as well as with previous research (Grimshaw et al., 2013; Holmes et al., 2009). Importantly, this finding confirms that the set of face stimuli used here effectively produce threat capture when presented at the size, eccentricity, and timing parameters used in the present experiment, confirming that these stimuli (at the present parameters) can be used to examine whether angry faces capture attention when it is engaged elsewhere in the following experiments.

Curiously, the N2pc elicited by angry faces was preserved when the face stimuli were phase-scrambled, and this effect cannot be attributed to differences between the sensory differences between the angry and neutral faces. Although the N2pc has been observed for threat-related facial expressions in previous studies (e.g., Grimshaw et al., 2013; Holmes et al., 2009), this is the first study to use Fourier phase-scrambled faces to control for global low-level visual properties. The finding that the N2pc remained when faces were phase-scrambled suggests that attention capture by angry faces may be driven by properties of the Fourier amplitude spectrum (i.e., the relative intensities of spatial frequency components across orientations) that are unaffected by phase-scrambling, rather than by the emotional expression *per se*. This point will be considered further in the general discussion.

The N2pc effects provide clear evidence that angry faces captured attention. However despite this, face cues did not influence performance on the go/no-go task (both in terms of RTs and sensitivity to the go/no-go signal). The absence of attentional effects in performance of the dot-probe task may be due to the delay from offset of the face cues to onset of the probe display (of a random duration between 100-200 ms). This delay was included in the present experiment to ensure that the N2pc data was not contaminated by the ERPs evoked by the probe display. Consistent with this possibility, in a similar dot-probe paradigm, Grimshaw et al. (2013) also observed an N2pc for an angry face in the absence of any effects on task performance. Likewise, in that study there was a delay between offset of the face cues and onset of the probe stimuli. It may be the case that participants were able to redistribute their attention across the whole display once the face stimuli offset, before the probe stimuli were presented. However, other studies have found face cues to influence task performance on a very similar go/no-go dot-probe task with a similar delay between offset of face cues and onset of the probe (e.g., Pourtois et al., 2004). Therefore, a more likely explanation for the lack of attention effects in task performance is that the go/no-go task was simply not sufficiently difficult to detect such effects. This limitation could be addressed by reducing the stimulus duration and the luminance of the lateral probe.

Experiment 2A

Experiment 1 established that task-irrelevant angry faces elicit an N2pc in a dot-probe paradigm, suggesting that they capture attention when it is broadly distributed, even when they are irrelevant to the task. However, the threat-capture hypothesis predicts that angry faces should capture attention when it is engaged elsewhere. Experiment 2A tested this prediction. Participants performed a letter-identification task in which they searched for a target letter (an X or N) among non-target letters. The perceptual load of this task was varied between blocks of trials. In low-load blocks the non-target letters where homogeneous (all Os), while in high-load blocks the non-target letters were heterogeneous (i.e., a variety of letters). This is a common and effective manipulation of perceptual load (Lavie, 2010). Bilateral face pairs were presented concurrently with the task-relevant letter stimuli, and were presented at the same size, eccentricity, and timing parameters as in Experiment 1, which were confirmed to be effective in eliciting threat capture. This experiment was designed to examine the behavioural consequences of capture of attention by task-irrelevant angry faces. On some trials, the bilateral face stimuli consisted of two neutral faces (*neutral-neutral trials*) while on other trials they consisted of one angry and one neutral face (*angry-neutral trials*). If an angry face captures attention, then responses on the letter-identification task should be slower on trials in which an angry face is present (i.e. slower on angry-neutral trials than on neutral-neutral trials). According to the threat-capture hypothesis, threat-related stimuli such as angry faces capture attention because a preattentive threat-detection system automatically directs attention to their location. The threat-capture hypothesis therefore predicts that threat capture should not be influenced by the perceptual load of a primary task because the preattentive threat-detection system is theorised not to rely on attentional resources. It was therefore predicted that an angry face should produce a cost in RT for the letter-identification task, and that this cost should not be affected by the perceptual load of the task. As in Experiment 1, control trials were included in which the bilateral face stimuli were Fourier phase-scrambled. Given the results of Experiment 1, which suggest that capture of attention by angry faces is driven by visual properties that are preserved in phase-scrambled stimuli, it was expected that phase-scrambled angry faces should also disrupt task performance (i.e., slow RTs), regardless of the perceptual load of the primary task. Finally, as in Experiment 1, participants with high scores on measures of depression and anxiety were excluded from the sample.

Method

Participants

Participants were 25 undergraduate students from VUW. Participants' depression and anxiety were assessed using BDI-II and the Mini MASQ. As in Experiment 1, participants were excluded if their scores on the BDI-II were indicative of clinically significant depression (i.e. a score greater than 29) or if their score on the Mini MASQ was greater than two standard deviations above the mean score. No participants were excluded based on these criteria. One participant was removed due to a high error rate on the letter-identification task (more than three standard deviations above the mean), resulting in a sample of 24 participants (19 women; 22 right-handed; mean age: 18.5 years, *SD* = 2.0 years). Mean score on the BDI-II was 11.9 (*SD* = 6.4, range = 1-27) and on the Mini MASQ was 51.1 (*SD* = 10.7, range = 35-72). All participants reported normal or corrected-to-normal vision, no history of neurological disorder, and no history of treatment for depression (either through counselling or prescribed SSRI medications). The experiment was conducted with the approval of the Human Ethics Committee of the School of Psychology, VUW, under delegated authority of the VUW Human Ethics Committee. All participants gave written informed consent prior to participation in the experiment.

Procedure and Apparatus

Participants completed a one hour session. Testing took place in a dimly lit room. The experiment consisted of three tasks, completed in the same order by all participants. First, participants completed the letter-identification task. During this task a chin rest maintained head position and a constant viewing distance of 60 cm to the computer screen. Next, they completed the emotion-rating task described in Experiment 1. Finally, they completed the BDI-II followed by the Mini MASQ. Participants were verbally debriefed and provided with a written debriefing statement at the end of the session. The apparatus was identical to that used in Experiment 1 with the exception that the experiment was presented on a Dell Optiplex 745 computer. As in Experiment 1, stimuli were presented on a Dell 19” LCD monitor (1280 × 1024 pixels, 60 Hz refresh rate).

Letter-identification Task

Participants performed a letter-identification task, in which they searched a vertical column of letters for a target letter. The column was flanked by a bilateral face display. Stimuli were presented on a black background. Each trial began with a white fixation cross (subtending 0.3° × 0.3°). After a random duration between 400 and 800 ms, a stimulus display was presented for 200 ms (i.e., too brief for saccades). This display consisted of a vertical column of six white, uppercase letters, centred at fixation, and a bilateral pair of face stimuli (see Figure 8). The column of letters comprised a target letter (X or N), and five non-target letters (U, F, S, P, and J in the high perceptual load condition, and Os in the low perceptual load condition). Each letter subtended 0.3° × 0.4° and was separated from its neighbours by 0.2°. The bilateral face stimuli were taken from the set of face stimuli described in Experiment 1, and were the same size and presented at the same eccentricity as the face stimuli presented in the bilateral face displays in Experiment 1. The stimulus display was followed by a blank screen for 1800 ms or until a response was made. Participants made a speeded response, pressing the “1” key for “X” or the “2” key for “N” with the index and middle fingers of their dominant hand, respectively. Responses were immediately followed by feedback presented for 500 ms indicating whether the response was correct (a green fixation cross) or incorrect (“Incorrect” presented in red text). On trials in which participants did not respond within 2 s of onset of the stimulus display, the feedback “Please respond faster” was presented in red text for 500 ms. Participants were instructed to ignore the face stimuli and to maintain fixation at the location of the fixation cross throughout the blocks of trials and to respond as quickly and accurately as possible. Unlike in Experiment 1, all of the task-relevant stimuli (i.e., the letters) were presented near fixation, so there was no motivation for participants to distribute their attention across the display.

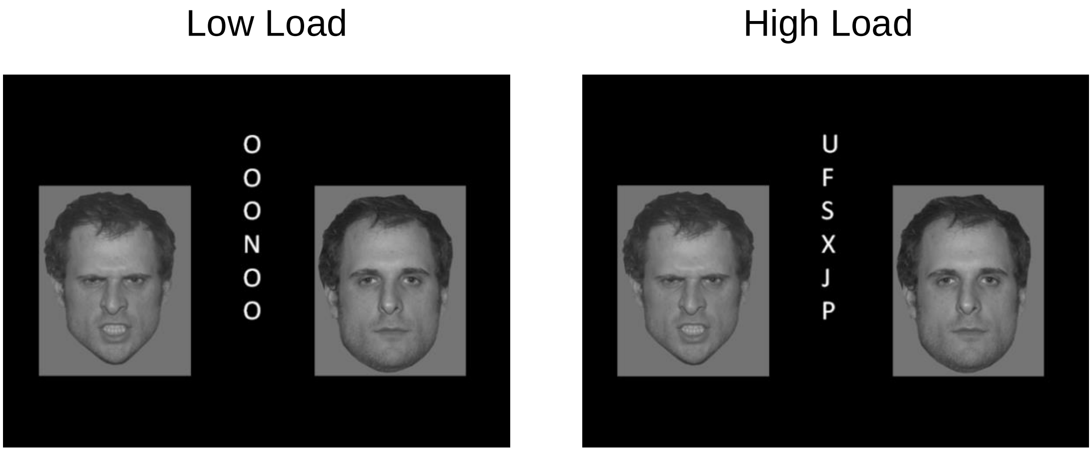


Figure 8. Examples of low and high perceptual load stimulus displays presented in Experiments 2A and 2B. This figure is for illustrative purposes only. Stimuli are not presented to scale.

The bilateral face stimuli could consist of two identical neutral expressions (*neutral-neutral* trials) or an angry and a neutral expression from the same individual (*angry-neutral* trials), and these could be intact or phase-scrambled. The independent variables were therefore perceptual load (low or high), face type (intact or phase-scrambled), and emotion (angry-neutral or neutral-neutral). Face type and emotion were manipulated within blocks of trials and perceptual load was manipulated between blocks of trials. Participants read task instructions, which were further emphasised by the experimenter. The task began with a practice block of 24 low perceptual load trials followed by a practice block of 24 high perceptual load trials. The experimenter supervised each participant while they completed the practice trials to ensure they fully understood the task. Participants then completed 12 blocks of 64 trials (768 total; 96 trials for each of the eight conditions of the 2 × 2 × 2 factorial design), alternating between high perceptual load blocks and low perceptual load blocks. The perceptual load of the first block was counterbalanced across participants. Each target letter (X or N) was presented equally often (i.e., 32 repetitions) in each block of trials, and the position of the target within the column of letters was random. Each block of 64 trials comprised two repetitions of each combination of face type (intact or phase-scrambled) and emotion (neutral-neutral or angry-neutral) for each of the eight actors (2 × 2 × 2 × 8 = 64). For angry-neutral trials, the angry face appeared in the left and right visual fields equally often for all 16 combinations of actor and face type within each block of trials. The trial order within each block was random.

Results and Discussion

Emotion-rating Task

Mean anger and threat ratings for angry and neutral faces are presented separately for each of the eight actors in Table A2 of the appendix. Paired-samples *t*-tests were used to compare the mean anger and threat ratings for angry and neutral faces collapsed across the eight actors. As in Experiment 1, paired samples *t*-tests confirmed that angry faces (*M* = 6.34, *SD* = 1.37) were rated as angrier than neutral faces (*M* = 1.54, *SD* = 0.56), *t*(23) = 15.351, *p* < .001, *d* = 3.133. Similarly, angry faces (*M* = 5.45, *SD* = 1.57) were rated as more threatening than neutral faces (*M* = 1.85, *SD* = 0.89), *t*(23) = 9.893, *p* < .001, *d* = 2.019.

Letter-identification Task

RTs. Trials with incorrect responses or with RTs less than 200 ms (taken to be indicative of anticipatory responding) were excluded from the analysis, leading to the rejection of an average of 6.4% of trials per participant (*SD* = 4.3%, range = 1.3-20.6%). Mean RTs are presented in Figure 9 as a function of face type, perceptual load, and emotion. Median RTs were analysed in a 2 (face type: intact, phase-scrambled × 2 (perceptual load: low load, high load) × 2 (emotion: angry-neutral, neutral-neutral) repeated-measures ANOVA. This analysis yielded a significant main effect of perceptual load, *F*(1, 23) = 113.775, *p* < .001, η_p^2 = .832, indicating that RTs were slower on high-load trials than on low-load trials. This effect indicates that the high-load task was indeed more difficult than the low-load task. The main effects of face type, *F*(1, 23) = .352, *p* = .559, η_p^2 = .015, and emotion, *F*(1, 23) = 2.738, *p* = .112, η_p^2 = .106, were not significant. There was a significant Face type × Emotion interaction, *F*(1, 23) = 6.182, *p* = .021, η_p^2 = .212, indicating that RTs were slower on angry-neutral trial than neutral-neutral trials when the faces were phase-scrambled, *t*(23) = 2.902, *p* = .008, *d* = 0.592, but not when they were intact, *t*(23) = -.110, *p* = .914, *d* = .022. Thus, angry faces appeared to capture attention and disrupt task performance but only when they were phase-scrambled. The Face type × Perceptual load interaction was not significant, nor was the Face type × Perceptual load × Emotion interaction (*F*s < 1).

Most pertinent to the hypothesis, there was a significant Perceptual load × Emotion interaction, *F*(1, 23) = 6.131, *p* = .021, η_p^2 = .210, indicating that RTs were slower on angry-neutral trials than neutral-neutral trials under conditions of high perceptual load, *t*(23) = 3.007, *p* = .006, *d* = .614, but not under conditions of low perceptual load, *t*(23) = -.275, *p* = .768, *d* = .056. This finding suggests that angry faces captured attention in the high-load condition but not low-load condition. Therefore, the perceptual load manipulation had a clear impact on attention capture by task-irrelevant angry faces. This result is partially inconsistent with the threat-capture hypothesis, which predicts that angry faces should capture attention, and therefore disrupt task performance, regardless of perceptual load. However, angry faces did capture attention in the high perceptual load condition, suggesting that they capture attention when it is engaged elsewhere. This pattern of results was clearly inconsistent with load theory (Lavie, 1995, 2005), which posits that task-irrelevant distractors should be more likely to influence behaviour when perceptual load is low because surplus attentional resources are involuntarily devoted to the processing of such stimuli. On the other hand, when perceptual load is high, processing of task-relevant stimuli should exhaust attentional resources meaning that none are available for the processing of distractors. Load theory therefore predicts that the task-irrelevant faces in the present experiment should be more likely to interfere with task performance under conditions of low perceptual load. Despite this, the task-irrelevant faces influenced RTs under high but not low perceptual load.

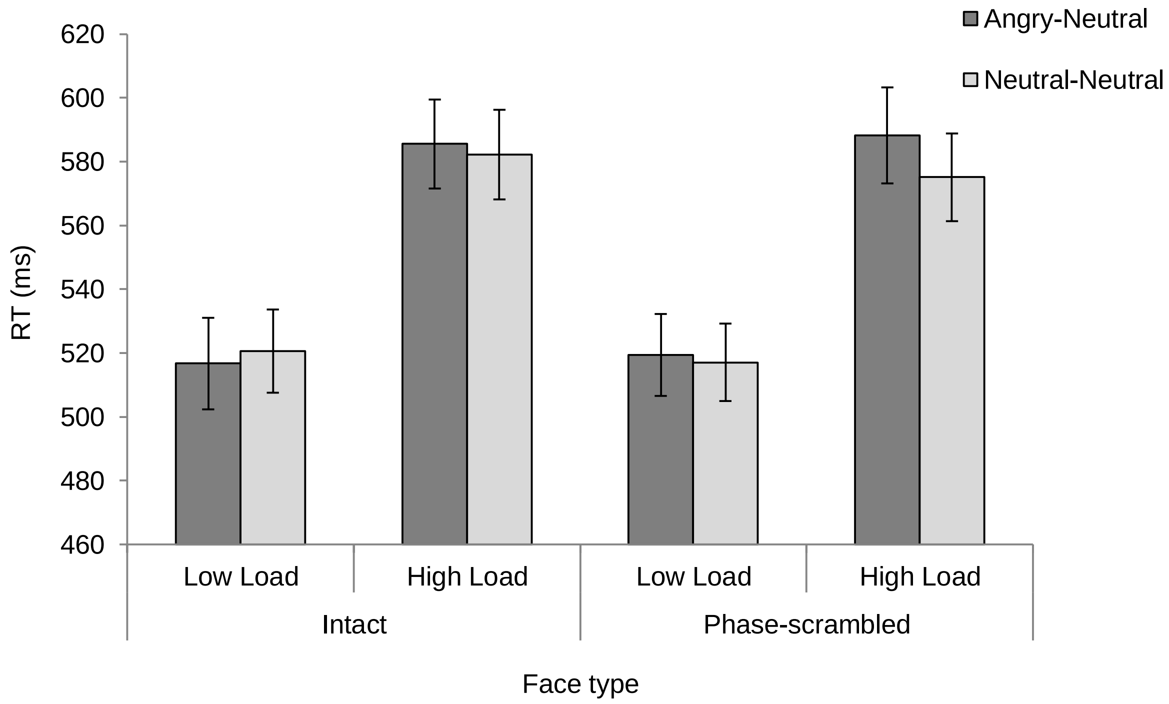


Figure 9. Mean RTs on the letter-identification task as a function of face type, perceptual load, and emotion. Error bars represent standard error of the mean.

Error rates. Mean error rates are presented in Figure 10 as a function of face type, perceptual load, and emotion. Error rates were analysed in a 2 (face type: intact, phase-scrambled) × 2 (perceptual load: low load, high load) × 2 (emotion: angry-neutral, neutral-neutral) repeated-measures ANOVA. This analysis yielded no significant main effects or interactions (all *F*s < 1). Thus, the RT effects cannot be attributed to speed-accuracy trade-offs. Critically, because slower RTs were observed under high perceptual load than under low perceptual load and error rates did not differ between perceptual load conditions, it can be concluded that the perceptual load manipulation was effective; the high-load condition was more difficult than the low-load condition.

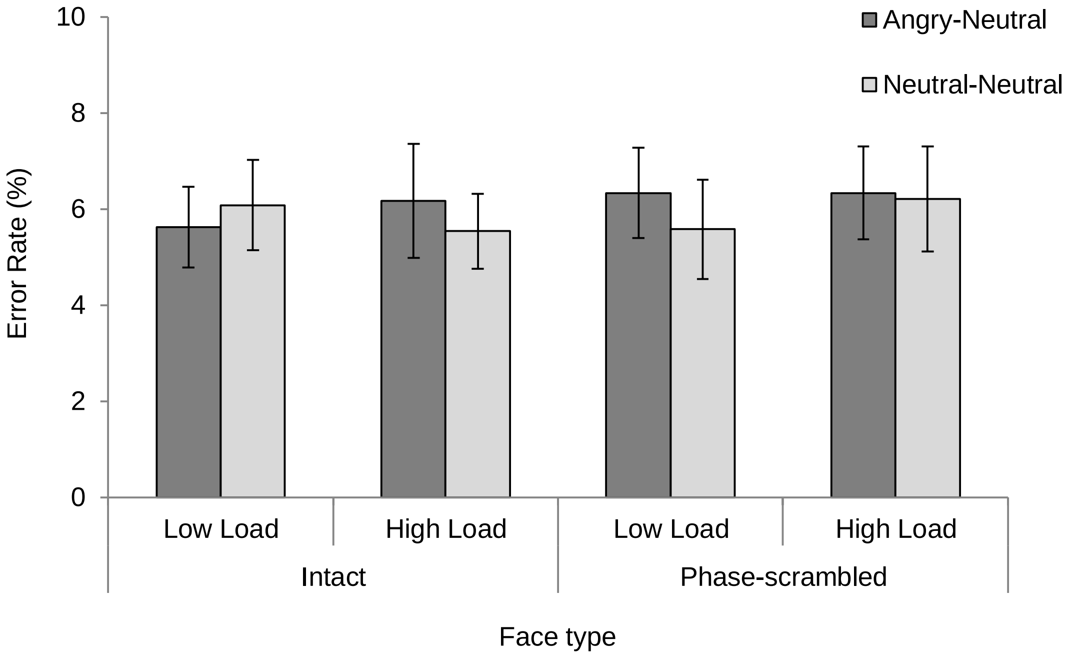


Figure 10. Mean error rates on the letter-identification task as a function face type, perceptual load, and emotion in Experiment 2A. Error bars represent standard error of the mean.

Summary

The results of the present study were partially inconsistent with the threat-capture hypothesis. It was found that RTs were slower on angry-neutral trials than on neutral-neutral trials when perceptual load was high, regardless of whether the faces were intact or phase-scrambled. However, no such effect was observed when perceptual load was low. Therefore, the presence of an angry face interfered with task performance when perceptual load was high but not low. This finding suggests that angry faces captured attention but only under conditions of high perceptual load. These results are partially inconsistent with the threat-capture hypothesis, which predicts that the influence of an angry face should capture attention even when it is engaged elsewhere. The finding that RTs were slowed by the presence of an angry face in the high-load condition is consistent with this prediction. However, the lack of such an effect in the low-load condition is not. This pattern of results is entirely inconsistent with load theory (Lavie, 1995, 2005), according to which task-irrelevant stimuli should influence performance when perceptual load is low but not when it is high. One might argue that the fact that angry faces influenced task performance in the high perceptual load condition but not in the low load condition suggests that the perceptual load manipulation was ineffective. However, RTs were significantly longer in the high-load than in the low-load condition and no difference in error rates was observed between these conditions, indicating that the perceptual load manipulation was indeed effective.

The second interesting finding of this study was that RTs were slower on angry-neutral trials than on neutral-neutral trials only when the faces were phase-scrambled. Thus it appears that capture of attention by angry faces was more resistant to perceptual load when faces were phase-scrambled than when they were intact. No significant three-way interaction was present in the current experiment. However, inspection of the data suggests that this may be due to a lack of statistical power, with the only clear angry-neutral versus neutral-neutral RT difference present when faces were phase-scrambled and presented under conditions of high perceptual load. This finding is consistent with the results of Experiment 1 and suggests that attention capture by angry faces may be driven by visual properties within the Fourier amplitude spectrum that characterises angry faces, rather than by perception of an angry facial expression.

Experiment 2B

Like Experiment 2A, Experiment 2B was intended to test the prediction of the threat-capture hypothesis that angry faces capture attention when it is engaged elsewhere. This experiment was similar in design to Experiment 2A but was adapted to examine the effect of perceptual load on the N2pc elicited by task-irrelevant angry faces. Participants performed the same letter-identification task as participants in Experiment 2A. Because this experiment was designed to examine the N2pc component, rather than behavioural interference produced by a task-irrelevant angry face, only angry-neutral face pairs were presented (as in Experiment 1); neutral-neutral trials were excluded to maximise the number of critical angry-neutral trials from which an N2pc can be isolated. As in the previous two experiments, trials in which faces were phase-scrambled were included as a control condition. Based on the threat-capture hypothesis, it was predicted that an N2pc, indicating attention capture by angry faces, would be observed regardless of perceptual load. Furthermore, based on the findings of Experiment 1, it was expected that an N2pc would be observed for angry faces when they were phase-scrambled. As in Experiment 1, the amplitude of the occipital P1 was compared when the faces were intact versus phase-scrambled to determine whether there was evidence for early processing of these stimuli. Finally, participants who scored highly on measures of depression and anxiety were excluded from the sample, as in the previous two experiments.

Method

Participants

Participants were 24 undergraduate students from VUW. Participants' depression and anxiety were assessed using the BDI-II and the Mini MASQ. As in the previous experiments, participants were excluded if their scores on the BDI-II were indicative of clinically significant depression (i.e., a score greater than 29) or if their score on the Mini MASQ was greater than two standard deviations above the mean score. Two participants were excluded because their score on the BDI-II was in the clinically significant range. Two further participants were removed because of excessive ERP trial loss for the letter-identification task due to incorrect responses and EEG/EOG artefacts (see the ERP Recording and Analysis section below), leaving 20 participants (12 women, 18 right-handed, mean age: 18.5 years, *SD* = 1.8) in the sample. Mean score on the BDI-II was 9.4 (*SD* = 7.4, range = 1-25) and on the Mini MASQ was 48.5 (*SD* = 13.3, range = 28-81). All participants reported normal or corrected-to-normal vision, no history of neurological disorder, and no history of treatment for depression (either through counselling or prescribed SSRI medications). The experiment was conducted with the approval of the Human Ethics Committee of the School of Psychology, VUW, under delegated authority of the VUW Human Ethics Committee. All participants gave written informed consent prior to participation in the experiment.

Procedure and Apparatus

Participants completed a two hour session. Testing took place in a dimly lit, electrically-shielded chamber. Participants were fitted with an EEG cap and were made comfortable with the testing situation. The experiment consisted of three tasks, completed in the same order by all participants. First, participants completed a similar letter-identification task to participants in Experiment 2A. Next, they completed the emotion-rating task described in Experiment 1. Finally, they completed the BDI-II followed by the Mini MASQ. Participants were verbally debriefed and provided with a written debriefing statement at the end of the session. The apparatus was identical to that used in Experiment 1.

Letter-identification Task

Participants performed the same letter-identification task as participants in Experiment 2A, with the only difference being the task-irrelevant face pairs presented. The face stimuli were the same as those used in the previous experiments. However, unlike in Experiment 2A, face pairs were always angry-neutral. The independent variables were therefore perceptual load (low or high) and face type (intact or phase-scrambled), which were both manipulated within subjects. Perceptual load was manipulated between blocks of trials and face type was manipulated within blocks. Task instructions were read by participants and were further emphasised by the experimenter. The task began with a practice block of 24 low perceptual load trials followed by a practice block of 24 high perceptual load trials. The experimenter supervised each participant while they completed the practice trials to ensure they fully understood the task. Participants then completed 12 blocks of 64 trials (768 total; 192 intact trials and 192 phase-scrambled trials under each condition of perceptual load), alternating between high perceptual load blocks and low perceptual load blocks. The perceptual load of the first block was counterbalanced across participants. Each target letter (X or N) was presented equally often in each block of trials, and the position of the target in the column of letters was random. Each block of 64 trials comprised two repetitions of each combination of face type (intact or phase-scrambled), and location of angry face (left or right visual field) for each of the eight actors (2 × 2 × 2 × 8 = 64 trials). The trial order within each block was random.

ERP Recording and Analysis

EEG recording, offline re-referencing, and filtering was conducted as in Experiment 1. Impedances at all electrodes were kept below 5 kΩ while participants performed the letter-identification task. EEG was segmented into 600 ms epochs, beginning 200 ms before onset of the stimulus display and continuing 400 ms after stimulus onset. Segments were baseline corrected by subtracting the average signal recorded during the 200 ms pre-stimulus baseline. Segments containing EEG/EOG artefacts were excluded using the same artefact rejection procedures as used in Experiment 1. No participants were excluded from the analyses on the basis of the two-step procedure used to exclude horizontal eye movements described in Experiment 1. Two participants were excluded from all analyses because of excessive ERP trial loss (more than 20% of trials) due to incorrect responses and EEG/EOG artefacts. In the remaining 20 participants, the grand average HEOG activity did not exceed ±3.2 μV in any condition (which corresponds to a systematic eye movement of 0.2°), ensuring that systematic eye movements did not exceed 0.2°, with propagated voltage at posterior sites of less than 0.1 μV (Lins et al., 1993a, 1993b). In these participants, incorrect responses and EEG/EOG artefacts led to the rejection of an average of 10.3% of trials per participant (*SD* = 3.3%, range = 5.5-19.8%).

Results and Discussion

Emotion-rating Task

Mean anger and threat ratings for angry and neutral faces are presented separately for each of the eight actors in Table A3 of the appendix. As in the previous experiments, paired-samples *t*-tests were used to compare the mean anger and threat ratings for angry and neutral faces collapsed across the eight actors. These analyses confirmed that angry expressions (*M* = 6.51, *SD* = 1.06) were rated as angrier than neutral expressions (*M* = 1.52, *SD* = 0.49), $t(19) = 24.861$, $p < .001$, $d = 5.559$. Similarly, angry expressions (*M* = 5.72, *SD* = 1.34) were rated as more threatening than neutral expressions (*M* = 1.68, *SD* = 0.67), $t(19) = 13.458$, $p < .001$, $d = 3.009$.

Letter-identification Task

Task performance.

RTs. Trials with incorrect responses or with RTs less than 200 ms (taken to be indicative of anticipatory responding) were excluded from the analysis, leading to the rejection of an average of 6.4% of trials per participant (*SD* = 2.4%, range = 2.6-12.1%). Mean RTs are presented in Figure 11 as a function of perceptual load and face type. Median RTs were analysed in a 2 (perceptual load: low load, high load) × 2 (face type: intact, phase-scrambled) repeated-measures ANOVA. This analysis yielded a significant main effect of perceptual load, $F(1, 19) = 89.909$, $p < .001$, $\eta_p^2 = .826$, indicating that RTs were longer for high perceptual load trials than for low perceptual load trials. There was no significant main effect of face type, $F(1, 19) = 3.017$, $p = .099$, $\eta_p^2 = .137$, and no significant Perceptual load × Face type interaction, *F*(1, 19) = .003, $p = .959$, $\eta_p^2 < .001$.

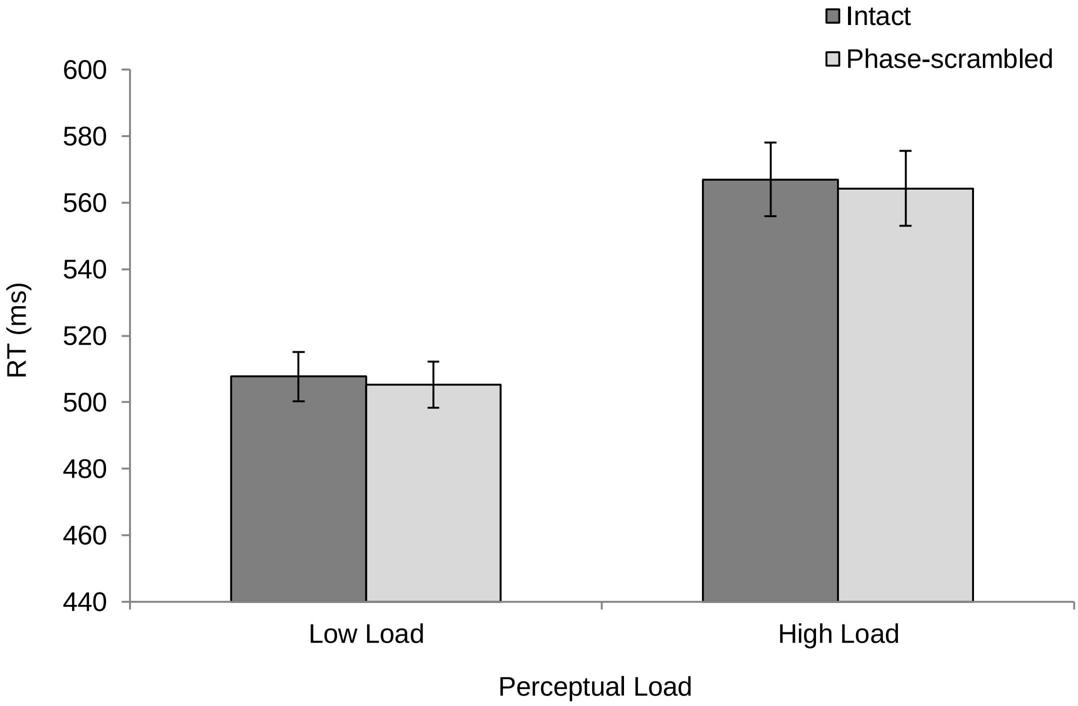


Figure 11. Mean RTs on the letter-identification task as a function of face type and perceptual load in Experiment 2B. Error bars represent standard error of the mean.

Error rates. Mean error rates are presented in Figure 12 as a function of perceptual load and face type. Error rates were analysed in a 2 (perceptual load: low load, high load) × 2 (face type: intact, phase-scrambled) repeated-measures ANOVA. There was no significant main effect of perceptual load, *F*(1, 19) = .737, $p = .401$, $\eta_p^2 = .037$, or face type, *F*(1, 19) = 3.353, $p = .083$, $\eta_p^2 = .150$, nor was there a significant Perceptual load × Face type interaction, *F*(1, 19) = .010, $p = .920$, $\eta_p^2 = .001$. Thus, the slower RTs under high perceptual load than under low perceptual load cannot be attributed to a speed-accuracy trade-off, confirming that the high perceptual load condition was more difficult than the low perceptual load condition.

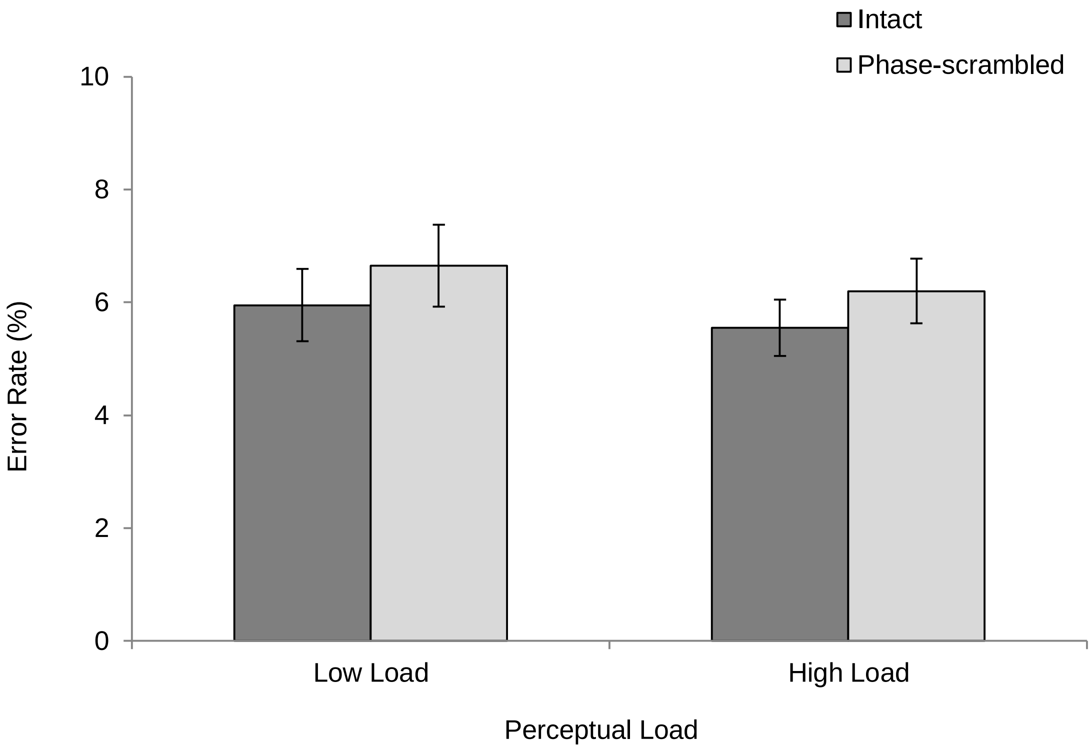


Figure 12. Mean error rates on the letter-identification task as a function of face type and perceptual load in Experiment 2B. Error bars represented standard error of the mean.

ERPs.

P1. As in Experiment 1, the P1 component elicited by the bilateral face displays was quantified as the mean amplitude in a 40-ms window (100-140 ms) at occipital-temporal electrodes P7 and P8, over the left and right hemispheres, respectively. The P1 time-window was chosen based on the most positive peak in the grand average waveform collapsed across perceptual load (low load, high load), face type (intact, phase-scrambled), and electrode (P7, P8). As in Experiment 1, P1 amplitudes were larger on trials in which the faces were intact than on trials in which the faces were phase-scrambled, except for at electrode P8 under conditions of low perceptual load (see Figure 13). P1 amplitudes were analysed in a 2 (perceptual load: low load, high load) × 2 (face type: intact, phase-scrambled) × 2 (electrode: P7, P8) repeated-measures ANOVA. There was a significant main effect of face type, $F(1, 19) = 5.639$, $p = .028$, $\eta_p^2 = .229$, indicating that P1 amplitudes were significantly greater for intact than for phase-scrambled faces. However, no other main effects or interactions were significant (Fs < 3).These results indicate that intact and phase-scrambled faces were differentiated at the early stages of visual processing indexed by the P1 component, regardless of perceptual load.

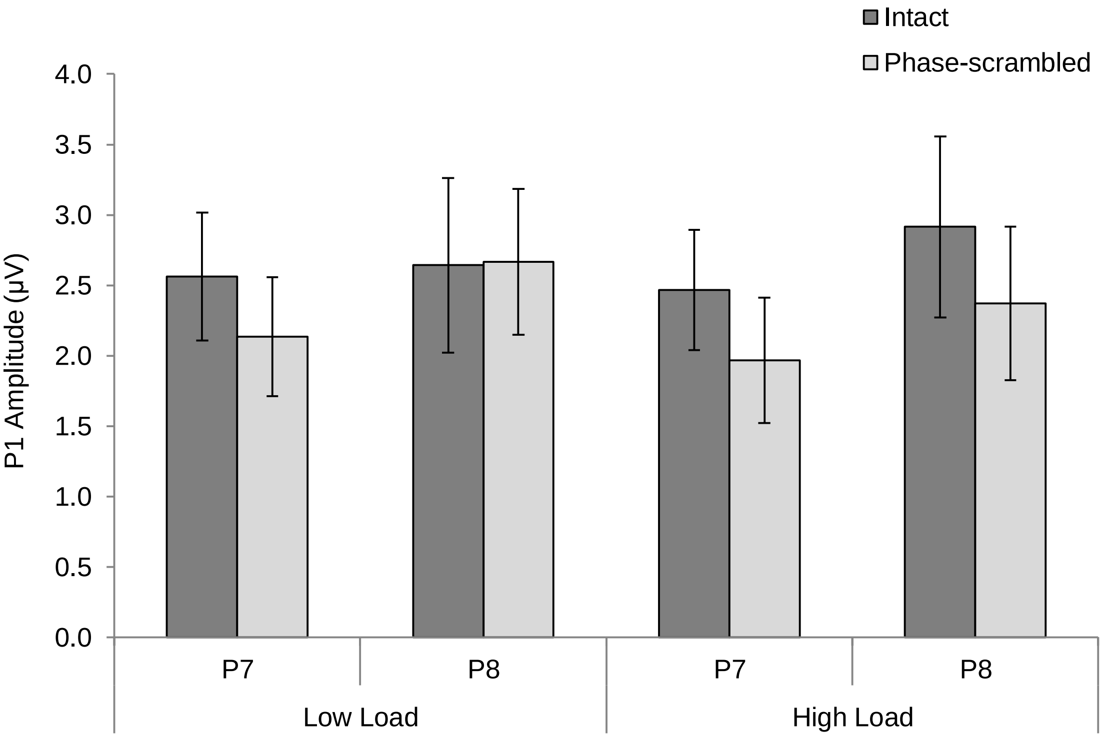
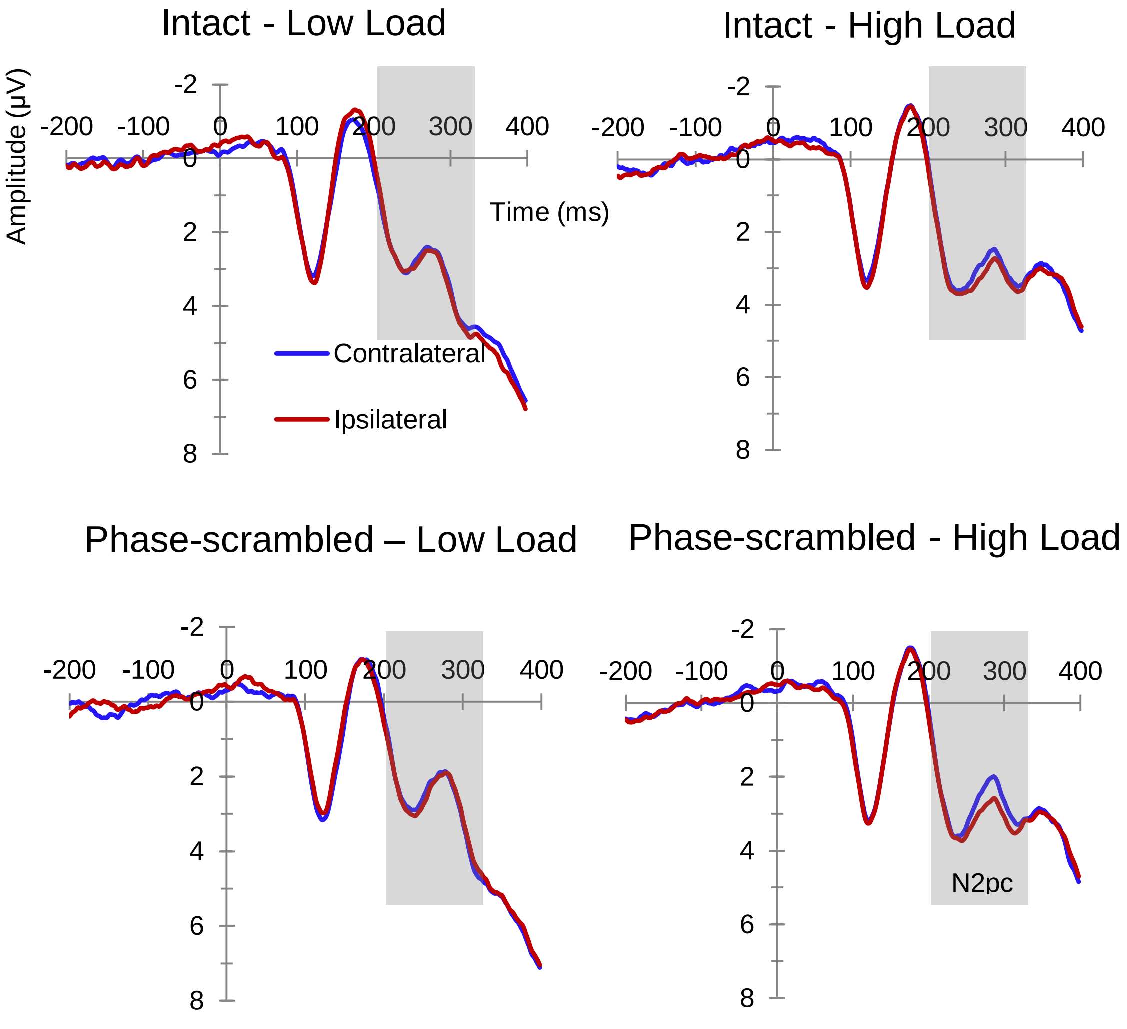


Figure 13. Amplitude of the occipital P1 component (mean voltage 100-140 ms post-stimulus) at occipital-temporal electrodes P7 and P8 elicited by intact and phase-scrambled stimulus displays under conditions of low and high perceptual load in Experiment 2B. Error bars represent standard error of the mean.

N2pc. As in Experiment 1, the N2pc was quantified at occipito-temporal electrodes P7 and P8. ERP waveforms at electrodes P7/P8 contralateral and ipsilateral to the angry face are presented in Figure 14 for intact (upper panel) and phase-scrambled (lower panel) faces, under conditions of low (left) and high (right) perceptual load. An enhanced negativity was observed contralateral to the angry face when the faces were both intact and phase-scrambled in the high perceptual load condition but not in the low perceptual load condition. These contralateral negativities can be seen more clearly in the contralateral - ipsilateral difference waves presented in Figure 15.A (right panel). These observations were confirmed by statistical analysis. The N2pc was quantified in a 120-ms window (200-320 ms after onset of the stimulus display). This window was chosen based on the peak in the grand average contralateral - ipsilateral difference waveform, collapsed across all conditions. Mean amplitudes at electrodes P7 and P8 were analysed in a 2 (perceptual load: low load, high load) × 2 (face type: intact, phase-scrambled) × 2 (electrode laterality: contralateral, ipsilateral) repeated-measures ANOVA. This analysis yielded a significant main effect of electrode laterality, $F(1, 19) = 6.411$, $p = .020$, $\eta_p^2 = .252$, indicating that the contralateral waveform was more negative in the N2pc time window than the ipsilateral waveform, and a marginally significant Perceptual load × Electrode laterality interaction, $F(1, 19) = 3.845$, $p = .065$, $\eta_p^2 = .168$. Given the relevance of the Perceptual load × Electrode laterality interaction to the threat-capture hypothesis, which predicts that the N2pc elicited by angry faces should not be affected by perceptual load, this interaction was followed up with paired-samples *t*-tests to compare the mean voltage in the N2pc window at contralateral and ipsilateral electrodes, for each level of perceptual load. These *t*-tests indicated that a contralateral negativity was present under high, $t(19) = .440$, $p = .665$, $d = .098$, but not low, $t(19) = 2.830$, $p = .011$, $d = .633$, perceptual load. No other main effects or interactions were significant (*F*s < 1.2).

The scalp distributions of the contralateral negativities for intact and phase-scrambled displays under high perceptual load are presented in Figure 16. The scalp distribution of the contralateral negativity observed on phase-scrambled trials is centred over occipito-temporal sites. Although this distribution is slightly superior to those observed in Experiment 1 (see Figure 7B), it is typical of the N2pc component. In contrast, the contralateral negativity elicited by intact faces had a temporal scalp distribution, which does not resemble the well-documented topography of the N2pc component (see Luck, 2012). Thus, it is unlikely that the lateralised ERP activity elicited by intact faces represents an N2pc component.

As in Experiment 1, to ensure these lateralised ERP effects did not reflect sensory differences between the angry and neutral face stimuli (i.e., differences in average pixel luminance and RMS contrast), lateralised ERP activity at electrodes P7/P8 within the P1 window (100-140 ms) was examined because sensory factors should predominantly influence early stages of processing. These data were analysed in a 2 (perceptual load: low load, high load) × 2 (face type: intact, phase-scrambled) × 2 (electrode laterality: contralateral, ipsilateral) repeated-measures ANOVA. This analysis yielded a significant main effect of face type, $F(1, 19) = 5.639$, $p = .028$, $\eta_p^2 = .229$, indicating that P1 amplitudes were bigger in response to intact faces as compared with phase-scrambled faces (as reported above). Critically, all other main effects and interactions were not significant (*F*s < 3), indicating that sensory differences between angry neutral faces did not influence lateralised ERP activity in the P1 time window. Thus the contralateral negativities observed for intact and phase-scrambled face displays in the N2pc time window on high perceptual load trials are unlikely to be the result of sensory differences between the neutral and angry face stimuli.



Intact - Low Load

Intact - High Load

Phase-scrambled – Low Load

Phase-scrambled - High Load

Figure 14. Grand averaged ERP waveforms at electrodes P7/P8 contralateral (blue) and ipsilateral (red) contralateral to the angry face for intact (upper panel) and phase-scrambled (lower panel) faces under conditions of low (left) and high (right) perceptual load.

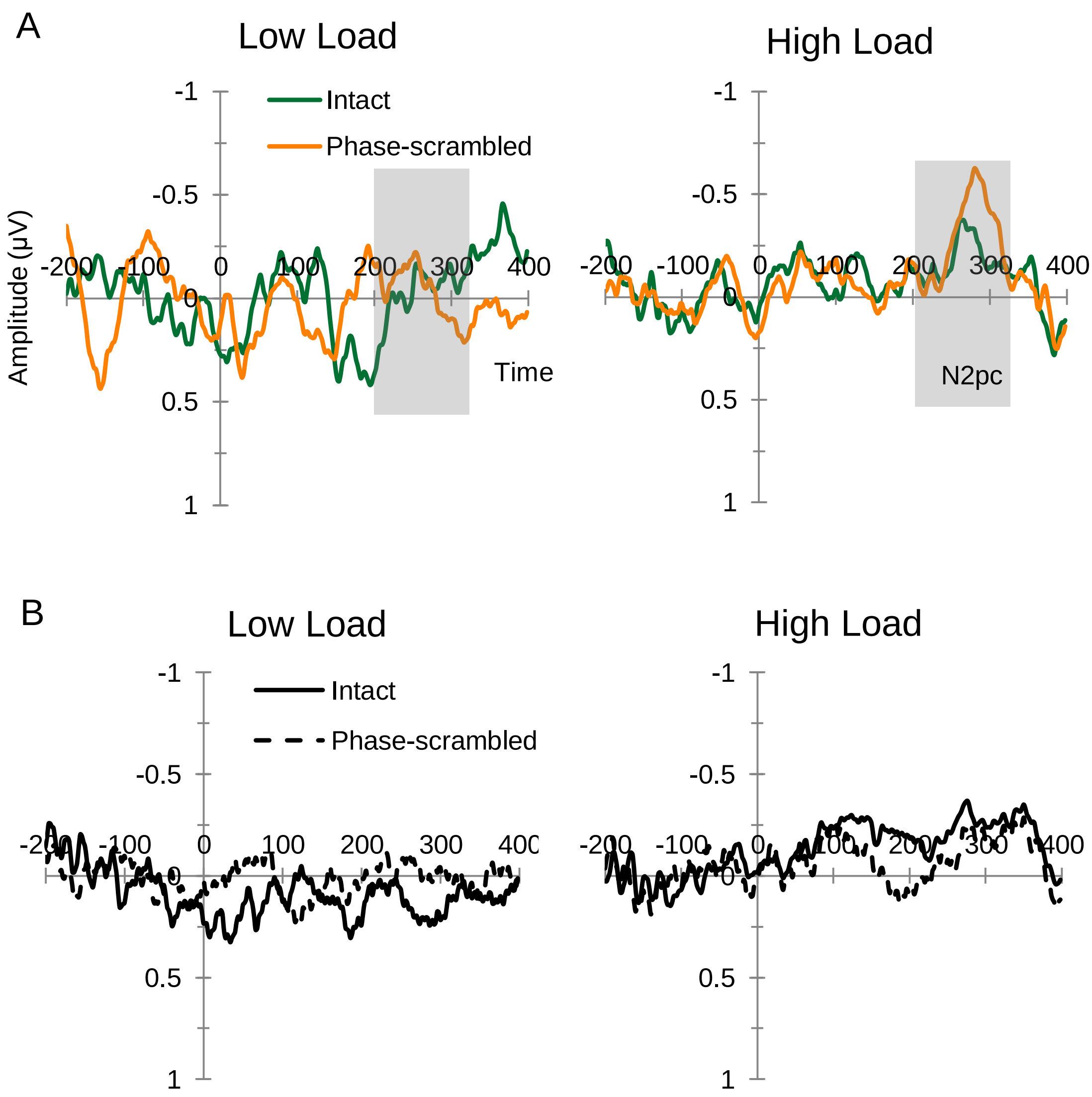


Figure 15. A: Contralateral - ipsilateral difference waveforms at electrodes P7/P8 for intact and phase-scrambled faces under conditions of low (left) and high (right) perceptual load trials. B: Grand averaged HEOG waveforms, recalculated such that a negative voltage indicates eye movement towards the angry face.

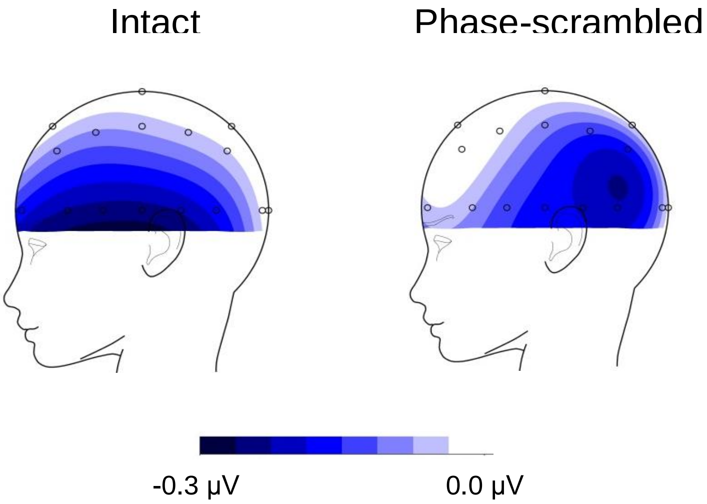


Figure 16. Scalp distributions of the contralateral negativities observed under conditions of high perceptual load for intact and phase-scrambled faces.

Summary

Significant contralateral negativities in the N2pc window were observed for both intact and phase-scrambled faces on high perceptual load trials but not on low perceptual load trials. However, the contralateral negativity for phase-scrambled faces, but not for intact faces, had a scalp distribution that resembled a typical N2pc component. Thus, it is unlikely that the lateralised activity observed for intact faces was an N2pc. Moreover, these effects appeared not to be driven by sensory differences between the angry and neutral face stimuli, as no lateralised ERP activity was observed earlier, within the P1 time window. This pattern of results mirrors those of Experiment 2A, suggesting that phase-scrambled but not intact angry faces captured attention, and that they did so only under conditions of high perceptual load. Of course, this pattern of results is entirely inconsistent with load theory, which predicts that attentional capture should occur under conditions of low load but not high perceptual load. This pattern of results is partially inconsistent with the threat-capture hypothesis, which predicts that an N2pc should be seen for angry faces, regardless of perceptual load. However, the N2pc under conditions of high perceptual load for phase-scrambled angry faces suggests that these stimuli capture attention when it is engaged elsewhere. It is unclear why no corresponding N2pc was observed for intact angry faces.

A larger occipital P1 component was observed when faces were intact than when they were phase-scrambled, indicating that these stimuli were differentiated at early stages of visual processing in extrastriate cortex indexed by this component. Thus, under conditions of low perceptual load, the P1 and N2pc components dissociated, such that a P1 but not an N2pc was observed. This finding is inconsistent with the threat-capture hypothesis because it suggests that the task-irrelevant angry faces were processed in visual cortex yet failed to capture attention.

General Discussion

The threat-capture hypothesis posits a preattentive threat-detection system that automatically directs attention to threat-related stimuli, facilitating the processing of these stimuli (Feldmann-Wüstefeld et al., 2011; Ikeda et al., 2013; Öhman & Mineka 2001). However, compelling empirical support for this hypothesis has been limited, with strong support for the hypothesis coming from a single study (Ikeda et al., 2013). The present experiments tested two key predictions of the threat-capture hypothesis. Experiment 1 tested the prediction that angry faces capture attention when they are task-irrelevant, while Experiments 2A and 2B tested the prediction that angry faces should capture attention even when it is engaged elsewhere.

Participants in Experiment 1 performed a dot-probe task, in which bilateral cue displays, consisting of one neutral and one angry face, preceded a lateralised probe. Importantly, this probe could appear in either visual field, encouraging a broad distribution of attention. As expected, a larger occipital P1 was observed for intact faces than for phase-scrambled faces. Because the P1 is thought to reflect visual gain in extrastriate visual areas (Hillyard et al., 1998), this finding suggests that participants processed the face stimuli to the extent that intact and phase-scrambled faces were differentiated in extrastriate cortex. Consistent with the threat-capture hypothesis, angry faces elicited an N2pc despite being completely task-irrelevant. This finding was not unexpected and is consistent with previous dot-probe studies that have reported an N2pc for angry faces (Grimshaw et al., 2013; Holmes et al., 2009). Therefore, this experiment adds to a growing literature that suggests that threat-related facial expressions compete for attention when it is broadly distributed (Grimshaw et al., 2013; Hodsoll et al., 2011; Holmes et al., 2009; Pourtois et al., 2004). To determine whether threat capture was driven by the perception of an emotional facial expression or by low-level visual properties, trials were included in which the faces were Fourier phase-scrambled. Curiously, the N2pc for angry faces remained when faces where phase-scrambled, suggesting that capture of attention was driven by low-level visual properties that were preserved when the faces were phase-scrambled. Because similar effects were observed in Experiments 2A and 2B, the implications of this finding will be discussed further below. Finally, the N2pc for angry faces (and phase-scrambled angry faces) in Experiment 1 confirmed that the face stimuli and stimulus parameters such as size, eccentricity, and stimulus duration used in the present series of experiments are effective at eliciting attention capture by angry faces. This finding is important because the same stimuli and stimulus parameters were used in the following experiments while participants performed a primary task to engage attention.

Participants in Experiments 2A and 2B performed a letter-identification task in which they searched a column of letters at fixation for a target letter while task-irrelevant bilateral face pairs were presented. In these experiments, the perceptual load of the letter-identification task was manipulated to investigate whether capture of attention by angry faces, as established in Experiment 1, depends on the availability of attentional resources. Experiment 2A was designed to examine the behavioural cost (in RTs) produced by task-irrelevant angry faces, while Experiment 2B was designed to examine the N2pc produced by the same stimuli. It was found that the very same angry faces presented in Experiment 1 produced a cost in RT and an N2pc. However, this was the case only when they were phase-scrambled and only under conditions of high perceptual load. These findings are partially inconsistent with the threat-capture hypothesis, which predicts that angry faces should capture attention even when it is engaged elsewhere. It is unclear why attention capture effects were seen under conditions of high but not low perceptual load, and for phase-scrambled but not intact angry faces. More problematic for the threat-capture hypothesis, the N2pc and the occipital P1 dissociated in Experiment 2B. Specifically, under conditions of low perceptual load, a larger P1 was observed for intact than for phase-scrambled faces. However, no N2pc was observed. These data suggest that attention was not captured by angry faces despite these stimuli being processed to the extent that intact and phase-scrambled stimuli were differentiated at the early stages of processing in visual cortex that are indexed by the P1 component.

The finding that angry-faces influenced RTs and produced an N2pc under high but not low load was unexpected to say the least. Load theory (Lavie, 1995, 2005) predicts that task-irrelevant stimuli should influence performance to a greater extent under conditions of low perceptual load than under conditions of high perceptual load. According to load theory, under conditions of low perceptual load, “spare” attentional resources are involuntarily devoted to the processing of these stimuli. In contrast, under conditions of high perceptual load, attentional resources should be exhausted such that none (or at least fewer) attentional resources remain for the processing of task-irrelevant stimuli. Indeed, there is considerable evidence that task-irrelevant distractors are processed to a lesser extent as perceptual load increases, and this is true for both emotional (Lim et al., 2008; Pessoa et al., 2002, 2005; Silvert et al., 2007; Yates et al., 2010) and non-emotional (Lavie, 1995; Lavie & Cox, 1997; Pinsk et al., 2004; Rees et al., 1997; Schwartz et al., 2005; Yi et al., 2004) distractors. In Experiment 2B, it was found that the occipital P1 had greater amplitude when the faces were intact than when they were phase-scrambled, indicating that task-irrelevant faces were processed to the extent that they were differentiated in extrastriate cortex. Importantly, this effect was not influenced by perceptual load. This finding could be taken to indicate that the perceptual load manipulation was not effective. However, task performance clearly indicated that the high load condition was more difficult than the low load condition; RTs were slower in the high perceptual load condition in Experiments 2A and 2B, and this was not accounted for by a speed-accuracy trade-off. To the best of my knowledge, there is no theoretical framework that can explain why angry faces influenced attention under high but not low perceptual load. Perhaps the most straightforward account of this finding is that it is spurious. However, it must be acknowledged that this finding was consistent across behavioural and electrophysiological experiments.

The present findings are inconsistent with the recent study of Ikeda et al. (2013) that provided support for the threat-capture hypothesis. Ikeda et al. found that task-irrelevant fearful facial expressions elicited an N2pc, regardless of the perceptual load of a primary task. There are no major differences between the present Experiments 2A and 2B and those of Ikeda et al. However, there are a number of subtle methodological differences between these experiments. For example, Ikeda et al. used fearful faces rather than angry faces and the task-irrelevant faces were presented nearer to the task-relevant stimuli than in the present experiments. Thus, it remains unclear what factors might influence capture of attention by threat-related expressions. A systematic evaluation of the stimulus factors (e.g., stimulus duration, size, eccentricity, and properties of the emotional facial expressions such as exposed versus non-exposed teeth) that influence attention capture by emotional facial expressions is necessary.

Future Directions

The role of low-level visual properties in threat capture.

To determine what properties of threat-related facial expressions cause them to capture attention, it is essential to use control conditions that rule out certain factors that may be responsible for attention capture. Many studies examining capture of attention by emotional expressions have not used control stimuli (e.g., Eimer & Kiss, 2007; Fenker et al., 2010; Grimshaw et al., 2013; Holmes et al., 2009; Pourtois et al., 2004). As a result, these studies can tell us that threat-related facial expressions do capture attention but not *why* they capture attention. Previous research has sought to rule out the possibility that attention capture by threat-related expressions is driven by low-level visual factors (e.g., luminance, contrast, and configural properties of the stimulus). To control for these factors, researchers have typically used inverted faces (e.g., Eastwood et al., 2001; Holmes, Green, & Vuilleumier, 2005; Ikeda et al., 2013) because inversion disrupts the perception of emotional expressions while preserving low-level properties (de Gelder et al., 1997; Eimer & Holmes, 2002; Searcy & Bartlett, 1996). These studies have often found that emotional facial expressions influence attention when they are upright but not inverted (e.g., Eastwood et al., 2001; Holmes et al., 2005; Ikeda et al., 2013). Such findings have led researchers to conclude that capture of attention by emotional facial expressions relies on perception of the emotional expression rather than on low-level visual properties (e.g., Eastwood et al., 2001; Ikeda et al., 2013). In the present experiments, I used phase-scrambled faces to control for low-level factors. I chose to use these stimuli because phase scrambling does not alter the global low-level properties (i.e., the Fourier amplitude spectrum, average pixel luminance, and RMS contrast) of the original face stimulus but, unlike inversion, completely eliminates the perception of an emotional expression.

Interestingly, findings across all three of the current experiments suggest that capture of attention by angry faces does not rely on perception of the emotional facial expression *per se*. Instead, Fourier phase-scrambled angry faces appear to contain the critical properties of angry faces that capture attention. Phase scrambling randomises the phase (i.e., the position) of the spatial frequency components of an image but does not alter the Fourier amplitude spectrum (i.e., the relative intensities of the spatial frequency components across orientations). The findings of the present experiments suggest that it is the Fourier amplitude spectrum that characterises angry facial expressions that captures attention. This *low-level capture hypothesis* is consistent with previous research that suggests that the Fourier amplitude spectrum is important in early stages of face perception (e.g., Honey et al., 2008; Rossion & Caharel, 2011). For example, saccades are made much more quickly and accurately to faces than to non-face stimuli, even when stimuli are Fourier phase-scrambled. However, when faces are scrambled in a way that randomises the orientation of the spatial frequency components, and therefore alters the Fourier amplitude spectrum, no such effect is observed (Honey et al., 2008).

Although it has often been argued that the perception of emotional expressions drives their influence on attention (e.g., Eastwood et al., 2001; Ikeda et al., 2013), I am not the first to suggest that specific low-level visual properties of emotional expressions may play a particularly important role in attracting attention. For example, it has been argued that the low spatial frequency (LSF) components of fearful facial expressions play a crucial role in attention capture (Holmes et al., 2005). It is not surprising that the LSF of emotional facial expressions may be important for attracting attention given that the amygdala appears to respond selectively to LSF components of these stimuli (Vuilleumier, Armony, Driver, & Dolan, 2003), and that modulation of activity in face-selective regions of visual cortex by emotional expressions is driven by LSF information (Winston, Vuilleumier, & Dolan, 2003). In a dot-probe paradigm, Holmes et al. (2005) found an attentional bias for fearful faces (as indicated by faster RTs to probes that replaced fearful faces than to probes replacing the neutral face of a fearful-neutral cue) that remained when the faces were filtered to include only LSF components. In contrast, when faces were filtered to include only high spatial frequency (HSF) components, no attentional bias was observed. Thus, LSF components of fearful faces appear to play a key role in their effect on attention. This finding, together with the results of the current experiments, suggests that the LSF components within the Fourier amplitude spectrum may play a particularly important role in capture of attention by emotional expressions.

While the N2pc for phase-scrambled angry faces generates an interesting hypothesis, it is important that this effect is interpreted with caution. The present experiments used a relatively small set of phase-scrambled stimuli (one phase-scrambled version of each of the eight neutral and eight angry face stimuli). Consequently, it is possible that these effects may have been driven by artefacts of some of these stimuli (e.g., regions of high contrast). Therefore, it is important that this effect is replicated with a different set of phase-scrambled face stimuli. One approach might be to generate a large set of angry and neutral phase-scrambled faces and randomly sample from this set so that any effects cannot be attributed to a select few stimuli but only to the general properties that characterise phase-scrambled angry faces.

Fortunately, the low-level capture hypothesis proposed here generates straightforward predictions and can therefore be easily tested. If it is the Fourier amplitude spectrum that drives attention capture by emotional expressions, then emotional expression should capture attention when faces are phase-scrambled but not when they are processed in ways that alter the Fourier amplitude spectrum. For example, inverted phase-scrambled angry faces should fail to capture attention because inversion changes the orientation of the spatial frequency components of a stimulus, and therefore alters the Fourier amplitude spectrum. This prediction is particularly interesting given that Ikeda et al. (2013) found no N2pc for fearful faces when they were inverted. Their findings are therefore consistent with the idea that it is the Fourier amplitude spectrum that drives attention capture by threat-related facial expressions. Based on the low-level capture hypothesis, one would also expect no attention capture by angry faces that have been wavelet scrambled. This procedure is similar to phase-scrambling in that it produces cloudy images devoid of semantic content. However, wavelet scrambling essentially provides the opposite manipulation to phase-scrambling. Whereas phase-scrambling preserves the Fourier amplitude spectrum but randomises the phase of spatial frequency components, wavelet scrambling disrupts to Fourier amplitude spectrum (by randomising the orientation of spatial frequency components) but preserves the phase of these components (Honey et al., 2008). Future research should use such stimuli to isolate the specific low-level visual properties that are involved in attention capture by emotional facial expressions.

Individual differences in anxiety.

In the present experiments, participants that scored highly on questionnaire measures of anxiety and depression were excluded because they are known to show atypical responses to threat stimuli (Bar-Haim et al., 2007; Kircanski et al., 2012). Anxiety is particularly important because it is associated with an early attentional bias to threat (Bar-Haim et al., 2007). This hyper-vigilance for threat seen in anxious individuals is thought to be underpinned by a hypersensitive bottom-up threat-detection system (Bishop, 2007; Bishop, Duncan, & Lawrence, 2004) coupled with deficits recruiting cognitive control mechanisms to suppress emotional but irrelevant stimuli (Bishop, Duncan, Brett, & Lawrence, 2004). Recent studies have revealed that early attentional selection of threat stimuli, as indexed by the N2pc, is modulated by anxiety. Specifically, these studies have revealed that higher levels of anxiety are associated with a larger N2pc for angry facial expressions (Fox et al., 2008). However, both of these studies used dot-probe paradigms in which task demands promoted a broad distribution of attention. It therefore remains to be determined how anxiety influences the N2pc for task-irrelevant angry faces when attention is engaged elsewhere. Although individual differences in anxiety were beyond the scope of the present study, it will be an important factor to consider in future research. Investigating the role of individual differences will not only inform our understanding of interactions between attention and emotion but will also shed light on the cognitive underpinnings of anxiety.

Limitations

Of course, the current experiments are not without limitations. One important limitation concerns the extent to which angry faces were repeatedly presented. This level of repetition was necessary to examine the N2pc because the ERP technique relies on averaging across many trials to detect a small event-related signal contained within the relatively noisy EEG (Luck, 2005). This repetition may have led to habituation of responses to the emotional stimuli. Indeed, neuroimaging studies have revealed rapid habituation in the response of the amygdala (Breiter et al., 1996) and fronto-parietal attention network (Feinstein, Goldin, Stein, Brown, & Paulus, 2002) to emotional facial expressions. Moreover, these regions are thought to play a key role in directing attention to threat (Vuilleumier & Driver, 2007). Clearly, habituation was not a problem when attention was broadly distributed, as in Experiment 1, as an N2pc for angry faces was observed in this experiment. However, it may be that the response of neural systems that are responsible for directing attention to threat was attenuated due to habituation. Consequently, these systems may have failed to respond sufficiently strongly to override goal-directed signals and direct attention to the angry faces when it was engaged elsewhere, as in the low perceptual load conditions of Experiments 2A and 2B. One solution to the potential problem of habituation is to present angry facial expressions infrequently. This would likely involve having participants complete a number of sessions to obtain a sufficient number of critical trials on which angry faces are present to examine the N2pc component.

A second and related limitation of the current experiments was that the emotional salience of the angry faces may have been inadequate to capture attention when it was engaged elsewhere. These stimuli lack ecological validity because they convey no real threat. One solution to this problem is to explicitly manipulate the emotional salience of the angry faces. This can be achieved through an aversive conditioning procedure whereby stimuli are repeatedly paired with an unpleasant stimulus such as a mild electric shock (e.g., Lim et al., 2008). Previous research has found that aversively conditioned distractor faces interfere with task performance to a greater extent (Yates et al., 2010) and produce a greater amygdala response (Lim et al., 2008) than non-conditioned stimuli. However, these studies did not examine direct measures of attentional selection, as the N2pc provides. Therefore, future research should examine how perceptual load and emotional salience interact to determine whether task-irrelevant emotional stimuli elicit an N2pc. It may be that when the emotional salience of a distractor is sufficiently high, it successfully competes for attention, regardless of the perceptual load of the task.

Conclusions

This thesis tested the predictions of the threat-capture hypothesis that threat-related facial expression capture attention when they are task-irrelevant, even when attention is engaged elsewhere. Experiment 1 tested the prediction that angry faces capture attention when they are task-irrelevant. It was found that task-irrelevant angry faces produced an N2pc. In this experiment, task demands promoted a broad distribution of attention. This finding therefore adds to a growing literature that suggests that threat-related facial expressions preferentially attract attention when it is broadly distributed (e.g., Grimshaw et al., 2013; Hodsoll et al., 2011; Holmes et al., 2009; Pourtois et al., 2004). Experiments 2A and 2B tested the prediction of the threat-capture hypothesis that angry faces capture attention when it is engaged elsewhere. The results of these experiments were not clear cut. Consistent evidence for attention capture by angry faces was found across these two experiments when the perceptual load of the primary task was high but not low. Thus, it is not entirely clear whether angry faces capture attention when attention is engaged elsewhere. However, it was found that task-irrelevant angry faces failed to elicit an N2pc in Experiment 2B despite evidence for some degree of processing of these stimuli in extrastriate cortex. Taken together, these findings are seemingly inconsistent with the threat-capture hypothesis, and suggest that threat-related facial expressions do not necessarily capture attention when it is engaged elsewhere. Finally, the finding that Fourier phase-scrambled angry faces attract attention across all three experiments suggest that the low-level properties within the Fourier amplitude spectrum that characterises angry faces may drive attention capture by these stimuli, rather than perception of an emotional facial expression *per se*. These findings are consistent with previous research that suggests specific low-level visual properties are important in guiding attention to emotional facial expressions (e.g., Holmes et al., 2005). Future research is necessary to identify the precise properties within the Fourier amplitude spectrum that are important for capture of attention by threat-related facial expressions.

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Appendix

Emotional Ratings of Facial Expressions

Table A1.

Mean (SD) anger and threat ratings by intended expression and actor identity in Experiment 1.

Actor identity	Anger Ratings				Threat Ratings			
	Angry		Neutral		Angry		Neutral	
Actor 1	7.56	(1.41)	1.50	(0.89)	6.25	(1.81)	1.69	(1.01)
Actor 2	6.19	(1.42)	1.38	(0.89)	4.63	(1.86)	1.44	(0.89)
Actor 3	7.25	(1.18)	1.06	(0.25)	7.25	(1.06)	1.19	(0.54)
Actor 4	6.38	(1.67)	1.31	(0.47)	4.63	(2.06)	1.13	(0.34)
Actor 5	7.00	(0.97)	1.63	(1.36)	5.31	(1.99)	1.62	(1.09)
Actor 6	7.81	(1.17)	1.13	(0.34)	6.63	(2.13)	1.25	(0.45)
Actor 7	6.75	(1.44)	1.31	(0.87)	4.94	(2.02)	1.31	(0.70)
Actor 8	7.44	(1.09)	2.44	(1.75)	5.81	(1.87)	2.50	(1.86)

Table A2.

Mean (SD) anger and threat ratings by intended expression and actor identity in Experiment 2A.

Actor identity	Anger Ratings				Threat Ratings			
	Angry		Neutral		Angry		Neutral	
Actor 1	6.88	(1.87)	1.54	(1.06)	5.71	(1.99)	1.75	(1.33)
Actor 2	5.71	(2.03)	1.54	(1.02)	5.38	(2.34)	1.88	(1.33)
Actor 3	6.33	(1.90)	1.46	(0.72)	5.75	(2.09)	1.92	(1.69)
Actor 4	5.58	(1.77)	1.38	(1.06)	4.17	(2.01)	1.67	(1.31)
Actor 5	6.00	(2.06)	1.50	(0.83)	6.13	(1.65)	1.45	(0.66)
Actor 6	7.08	(1.77)	1.29	(0.75)	5.96	(2.27)	1.42	(0.78)
Actor 7	6.00	(1.89)	1.54	(0.88)	4.58	(2.21)	1.88	(1.60)
Actor 8	7.13	(1.45)	2.04	(1.12)	5.88	(2.51)	2.79	(2.06)

Table A3.

Mean (SD) anger and threat ratings by intended expression and actor identity in Experiment 2B.

Actor identity	Anger Ratings				Threat Ratings			
	Angry		Neutral		Angry		Neutral	
Actor 1	7.05	(1.43)	1.50	(0.76)	6.30	(1.81)	1.50	(0.89)
Actor 2	5.75	(1.29)	1.45	(0.69)	4.75	(1.59)	1.60	(0.94)
Actor 3	6.55	(1.73)	1.20	(0.52)	6.85	(1.69)	1.25	(0.64)
Actor 4	5.40	(1.93)	1.40	(0.68)	4.15	(1.93)	1.45	(0.89)
Actor 5	6.85	(1.23)	1.50	(1.00)	6.35	(1.73)	1.80	(1.06)
Actor 6	7.45	(1.28)	1.25	(0.44)	6.75	(1.77)	1.40	(0.68)
Actor 7	6.30	(2.03)	1.80	(1.24)	4.75	(2.38)	2.15	(1.69)
Actor 8	6.75	(1.55)	2.05	(0.83)	5.80	(1.99)	2.25	(1.55)