Autonomic arousal and attentional orienting to visual threat are predicted by awareness.

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Abstract

The rapid detection and evaluation of threat is of fundamental importance for survival. Theories suggest that this evolutionary pressure has driven functional adaptations in a specialized visual pathway that evaluates threat independently of conscious awareness. This is supported by evidence that threat-relevant stimuli rendered invisible by backward masking can induce physiological fear responses and modulate spatial attention. The validity of these findings has since been questioned by research using stringent, objective measures of awareness. Here, we use a modified continuous flash suppression paradigm to ask whether threatening images induce adaptive changes in autonomic arousal, attention or perception when presented outside of awareness. In trials where stimuli broke suppression to become visible, threatening stimuli induced a significantly larger skin conductance response than non-threatening stimuli and attracted spatial attention over scrambled images. However, these effects were eliminated in trials where observers were unaware of the stimuli. Additionally, concurrent behavioural data provided no evidence that threatening images gained prioritised access to awareness. Taken together, our data suggest that the evaluation and spatial detection of visual threat are predicted by awareness.

Keywords: vision, threat; emotion; awareness; suppression; attention

Given capacity limits, a critical function of vision is to direct resources in order to promote efficient detection and evaluation of threat in the environment. Additionally, it is widely held by neurocognitive theories that threatening stimuli are processed in the absence of conscious awareness, possibly via a subcortical visual pathway to the amygdala (for a review, see Tamietto & de Gelder, 2010), a structure implicated in mediating adaptive fear responses (Adolphs, 2013).

Empirical support for such theories comes predominantly from studies employing backward masking, a technique in which a briefly presented (typically ~30 ms) target stimulus is rendered invisible via masking by a subsequent, co-located stimulus (Esteves & Ohman, 1993). Threatening stimuli presented under these conditions can nonetheless elicit responses in both central and autonomic nervous systems consistent with fear arousal. For example, images of threatening stimuli increase amygdala activity (Morris, Ohman, & Dolan, 1999; Nomura et al., 2004) and autonomic skin conductance responses (SCRs) when rendered invisible by masking (Esteves, Dimberg, & Ohman, 1994). In addition, masked threat stimuli are suggested to selectively direct spatial attention to enhance threat appraisal and behavioral response selection. The masked visual probe paradigm provides evidence for this effect: an observer’s detection of a peripheral target is enhanced when co-located with a preceding masked threatening image, relative to a neutral image (e.g. Carlson, Fee, & Reinke, 2009; Fox, 2002; Mogg & Bradley, 2002). Together, these findings suggest that signals of threat are registered independently of awareness and influence adaptive changes in behavior and physiology.

The debate concerning the most valid assessment of awareness has an extended history. In the main, this centers on a tension between measures that index subjective vs. objective awareness (Cheesman, & Merikle, 1984; Merikle, Smilek, & Eastwood, 2001). One approach is to use an observer’s subjective report to index whether a stimulus is perceived.

This *subjective* approach is rooted in the intuitive idea that only the observer can give reliable information about their conscious experience, since awareness is subjective in nature (Wiens, 2006). The subjective approach has been challenged however, on the basis of signal detection models, which state that observers may be reluctant to report weak or brief percepts (Green & Swets, 1966). Accordingly, a more stringent approach relies on *objective* measures: observers are deemed unaware of a stimulus only when performance is at chance in a forced choice discrimination task (e.g. determining the presence or location of the stimulus, see Pessoa, Japee & Ungeleider, 2006). A current view is that both objective and subjective measures have conceptual and practical limitations and thus should be used in combination to comprehensively characterize visual awareness (Szcepanowski & Pessoa, 2007; Wiens, 2006).

It is in the context of this objective approach that more recent evidence has questioned the ability of the backward masking paradigm to reliably suppress stimuli from awareness. For example, studies using signal detection criteria to assess awareness revealed that the majority of observers can reliably detect stimuli masked after 33ms (Pessoa, Japee, Sturman & Ungerleider, 2006). Furthermore, exposure durations of 17-25ms may result in above chance discrimination of masked threat stimuli, even when subjective reports indicate unawareness (Szczepanowski & Pessoa, 2007). Such findings are important, given that physiological and behavioural threat responses observed in studies employing ~30 ms presentation durations (Carlson, Reinke, & Habib, 2009; Morris, Ohman, & Dolan, 1999; Whalen et al., 1998) are cited as concomitants of “unconscious” processing. Thus, it has been suggested that many previous studies reporting unconscious responses to threat may be explained by sub-optimal measures of awareness (Pessoa, 2005). Consistent with this stance, Coldispoti, Mazzetti and Bradley (2009) showed that physiological responses to emotionally salient stimuli (including SCRs) require exposures of at least 80 ms to be reliably measurable (a duration at which stimuli are also reliably detected) and that exposure durations of 25 ms or less eliminate all physiological reactions. Furthermore, it has recently been suggested that other methodological limitations of masking studies, such as temporally inaccurate presentation methods (Hannula, Simons, & Cohen, 2005; Wiens et al., 2004) and trial order confounds (Wiens, Katkin, & Ohman, 2003) could explain the physiological responses to briefly presented stimuli observed in previous studies. Thus, although previous physiological studies suggest that threat can be evaluated without awareness of the eliciting stimulus, the limitations of the masking paradigms employed require that such findings are re-examined. Similar concerns apply to the masked visual probe literature, which is characterised by a number of studies that do not include an explicit awareness check (Carlson & Reinke, 2008; Fox, Cahill & Zougkou, 2010; Sutton & Altarriba, 2011;Writh & Schultheiss, 2007). Instead assumptions are made about the efficacy of the masking procedure based on previous literature. Again, therefore, the associated claims about unconscious threat processing should be revisited.

Continuous flash suppression (CFS) is an increasingly popular technique that allows longer and more robust manipulations of awareness than backward masking (Lin & He, 2009). A stereoscope or anaglyph is used to present a dynamic masking pattern to one eye, which suppresses conscious perception of stimuli presented to the other. Despite continuous input to both retinae, the observer may perceive only the masking pattern for long durations, sometimes up to several minutes (Tsuchiya & Koch, 2005).

A rapidly growing body of studies employing CFS has demonstrated that emotionally salient stimuli suppressed from awareness can induce changes in neural activity indicative of threat processing. For instance, studies employing CFS in conjunction with functional magnetic resonance imaging (fMRI) have recorded differential amygdala responses to invisible fearful and neutral faces (Jiang & He, 2006; Vizueta, Patrick, Jiang, Thomas, & He, 2012). However, these studies did not report convergent changes in behaviour or autonomic physiological arousal that characterise functional threat responses. Although the amygdala is responsive to threat, contemporary models propose that it also sensitive to a broader range of stimulus properties (e.g. unpredictability, value, subjective preference) that modulate cognition and behaviour (Bar & Neta, 2007; Herry et al., 2007; Pessoa, 2010). Moreover, patients with amygdala lesions nonetheless exhibit selective prioritisation of threat in a range of behavioural tasks (Piech et al., 2011; Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009). Thus, it is unclear whether differential amygdala responses to suppressed stimuli can be directly related to functional threat responses, without measures of behavioural performance or autonomic arousal.

Psychophysical studies indicate that both spatial and feature-based attention may modulate the processing of low-level properties of simple stimuli (e.g. Gabor patch orientation) rendered invisible by CFS (Bahrami, Carmel, Walsh, Rees, & Lavie, 2008; Kanai, Tsuchiya, & Verstraten, 2006; Shin, Stolte, & Chong, 2009). In addition, the relative salience of invisible Gabor stimuli may drive eye movement responses (Rothkirch, Stein, Sekutowicz, & Sterzer, 2012). These observations have shaped the modal view that that attention and awareness are dissociable processes (Koch & Tsuchiya, 2007). By extension, conscious perception of the threat stimuli may not be required for their attentional selection. However, the extent to which threatening stimuli modulate spatial attention under CFS has not yet been investigated.

A variant of CFS: breaking continuous flash suppression (bCFS) has also been used to assess visual processing without awareness. The initial suppression duration is used as a correlate of a stimulus' unconscious processing advantage. For example, fearful faces are detected more quickly than neutral faces from invisibility induced by CFS (Yang, Zald, & Blake, 2007), suggesting they are prioritised at unconscious stages of processing. However, recent research suggests that these differences in detection times may be better explained by low-level stimulus variations such as contrast (Gray, Adams, Hedger, Newton, & Garner, 2013) or by criterion effects (Stein, Hebart, & Sterzer, 2011) rather than by unconscious processes sensitive to threat. The extent to which signals of threat are evaluated under CFS, therefore, remains a matter of debate.

In the present study, we assessed the extent to which unconsciously presented visual threat evokes adaptive changes in physiology and behavioural performance. To investigate this, we recorded SCRs to stimuli rendered invisible by CFS. With two concurrent behavioural tasks, we additionally examined whether threatening stimuli presented outside of awareness i) gain prioritised access to awareness or ii) modulate spatial attention.

Method

Stimulus images from the International Affective Picture System (IAPS; Lang, Bradley & Cuthbert, 2008) were chosen on the basis of their high emotional validity. Four images depicted biologically relevant threats (images of animal attack, e.g. a snake in a striking pose, IAPS numbers: 1050, 1300, 1726, 1930) and 4 depicted non-threatening animals (e.g. a deer, IAPS numbers: 1440, 1610, 1630, 1710) (mean valence and arousal ratings on a scale of 1-9 for images of animal attack: 3.90 and 6.59 respectively, non-threat images: 7.90 and 4.61 respectively – see Lang et al., 2008). We used images of animal attack as threat stimuli because they elicit the most robust SCRs of all image categories in the IAPS set (Bradley, Codispoti, Cuthbert, & Lang, 2001). All images were matched for root mean squared (RMS) contrast and mean luminance. Each image subtended 6.2 x 4.1 degrees of visual angle (DVA) at the viewing distance of 60 cm. Stimuli were prepared using MATLAB (Mathworks, Natick, MA) and presented using Inquisit 2 software (Millisecond Software) on a Sony Trinitron (1280 x 1024 pixel resolution, 60 Hz) monitor.

In the *experimental* block, we employed a CFS paradigm that closely mirrored that of Jiang, Costello, Fang, Huang and He (2006). Figure 1 shows a schematic of the trial sequence. (i) At the beginning of each trial, a central fixation cross was presented to each eye. (ii) Subsequently, observers viewed a CFS display via a mirror stereoscope, in which one eye viewed a pair of dynamic masks (random patterns of red-tinted, high contrast ellipses), which updated at 10Hz. The other eye viewed intact and block-scrambled (block size 0.17 x 0.17 DVA) versions of one IAPS image, which were presented simultaneously at 1.4 DVA to the left and right of a central fixation cross. Each eye's display was framed by a random dot surround (9.5 x 11.4 DVA) to assist fusion. The IAPS images (and their scrambled versions) were slowly introduced by linearly increasing contrast from 0-100% over the 800ms presentation period to reduce the risk of onset transients breaking suppression. (iii) This display was followed by an inter-stimulus interval (ISI) of 100ms during which only the fixation cross and random dot surround were presented. (iv) To measure the allocation of spatial attention, a Gabor patch (2.5 x 2.5 DVA, 4 cycles per degree) was briefly displayed (100ms) at the location preceded by the intact (valid) or scrambled image (invalid). The Gabor was oriented 1° clockwise or counter-clockwise from the vertical axis. The observer reported the orientation (clockwise or counter-clockwise) of the Gabor via key press "as quickly and accurately as possible". (v) At the end of each trial, observers were prompted to indicate (via key press) whether "*anything other than the mask*" had been visible during the CFS presentation, thereby providing a subjective awareness check. Importantly, this awareness check did not rely on recognition of the target stimulus, which could be influenced by criterion effects. Moreover, the uniform colour of the mask allowed observers to use any deviation from this colour as a cue to aid stimulus detection. The inter-trial interval of 8 seconds was sufficiently long to enable SCRs from consecutive stimuli to be differentiated (Boucsein et al., 2012; Breska, Maoz, & Ben Shakhar, 2011).

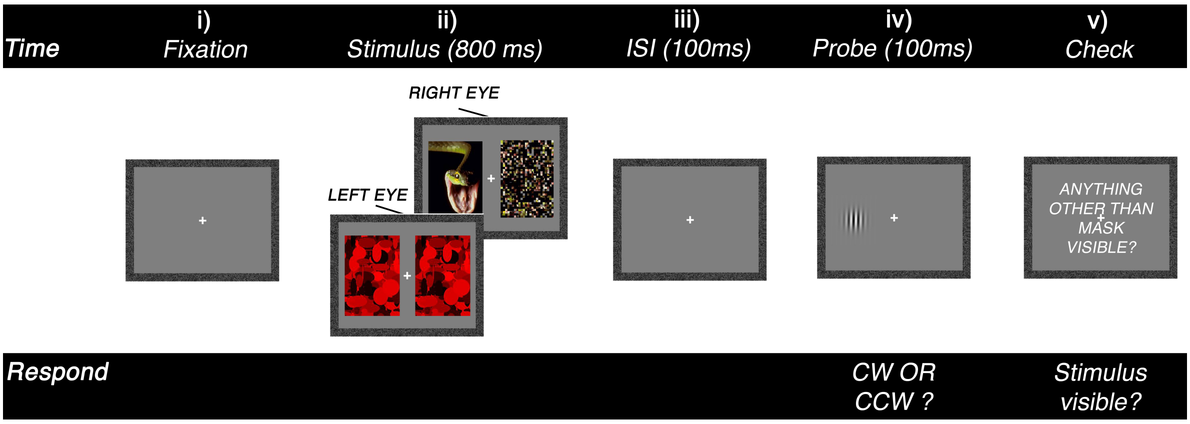

Figure 1. Schematic of trial sequence from the experimental block. Observers viewed a CFS display for 800 ms. The allocation of attention was measured by discrimination of a subsequent probe. Subjective awareness was measured by forced choice responses at the end of each trial.

The University of Southampton’s local ethics committee approved the study and all observers gave informed consent. Twenty-nine naive undergraduate students (11 male) each completed 128 randomly ordered experimental trials (2 stimulus categories (threatening, non-threatening) x 4 images x 16 repetitions), counterbalanced across probe position (valid, invalid), location of the intact image (left, right) and eye of suppressed images (left, right). Observers also completed a separate block of 128 *control* trials as an objective awareness check. Control trials were identical to the experimental trials, except that after each stimulus presentation, rather than viewing a Gabor, observers reported whether the intact stimulus had appeared to the left or right of fixation (2AFC). Observers whose performance significantly exceeded chance level (binomial limit= 74 correct responses) were classified as being objectively aware of (at least some of) the stimuli; their data were not included in analyses of ‘unaware’ trials – see below. An *a priori* calculation confirmed that this task provided adequate statistical power (> 80 %) to detect even small (> Cohen's $h = 0.22$) deviations from chance performance.

Throughout the experiment, skin conductance responses were sampled at 1000Hz using a BioPac MP150 amplifier (Goleta, CA). SCRs were collected by applying Ag-AgCl electrodes with conductive gel to the medial phalanges of the second and third fingers of the observer's non-dominant hand. Data from 6 observers were removed from the SCR analyses due to recording failure.

SCR data were reduced by submitting the raw amplitudes to a low pass filter (cut-off frequency: > 25 hz). Responses were defined as the maximum peak-to-peak amplitude in a pre-defined window 1-4 seconds after stimulus onset, measured in microsiemens (Cacioppo, Tassinary, & Berntson, 2007). We did not define a lower limit to demarcate a "non-response" (Dawson, Schell, & Filion, 2000), to avoid masking potentially small differences in trials where stimuli were successfully suppressed. To correct for individual differences in reactivity, these amplitudes were normalised by dividing by the individual's mean SCR amplitude (Lyken & Vennables, 1971). SCR outliers were identified as lying beyond 3 standard deviations from the mean following a log transformation to correct for skew. Visual review of these outliers revealed large, abrupt changes in amplitude consistent with movement or recording artefacts. These accounted for 0.72% of the data and were excluded from further analyses. SCRs for each observer were summarised by a "threat effect" score: the differential response to threatening vs. non -threatening stimuli (*Normalised SCR to threatening images- Normalised SCR to non-threatening images*). A positive score represents a larger SCR to threatening than non-threatening images and indicates fear arousal.

Results

Trials in the *experimental block* were separated into those in which observers were not aware of the target stimulus ('*unaware*') vs. those in which at least some part of the stimulus was detected (‘*aware’*). Trials were classified as *unaware* (1638 trials) when the observer (i) indicated that no stimulus was visible in the subjective report for that trial and (ii) the observer performed at chance level in the 2AFC objective control task (*N*=14). Conversely, *aware* trials (829 trials) were taken from all observers (*N*=23), and included all trials on which the subjective report indicated that the stimulus had broken suppression.[1] Data in each trial category were pooled across observers and analysed with a standard bootstrap resampling procedure (Efron & Tibshirani, 1993; Howell, 2013).

Figure 2 depicts the SCR data from the *experimental block*, separated by trial category. Aware trials induced significantly larger SCRs to threatening than non-threatening images ($M = 0.159$, 95% CI [0.004, 0.309], $p = .041$). However, this differential response was eliminated in unaware trials ($M = -0.070$, 95% CI [-0.159, 0.022], $p = .140$). Thus, when observers were unaware of stimuli, as determined by subjective and objective criteria, we found no evidence that SCRs were modulated by visual threat. Furthermore, the SCR threat effect was significantly larger in aware than unaware trials ($p = .010$).

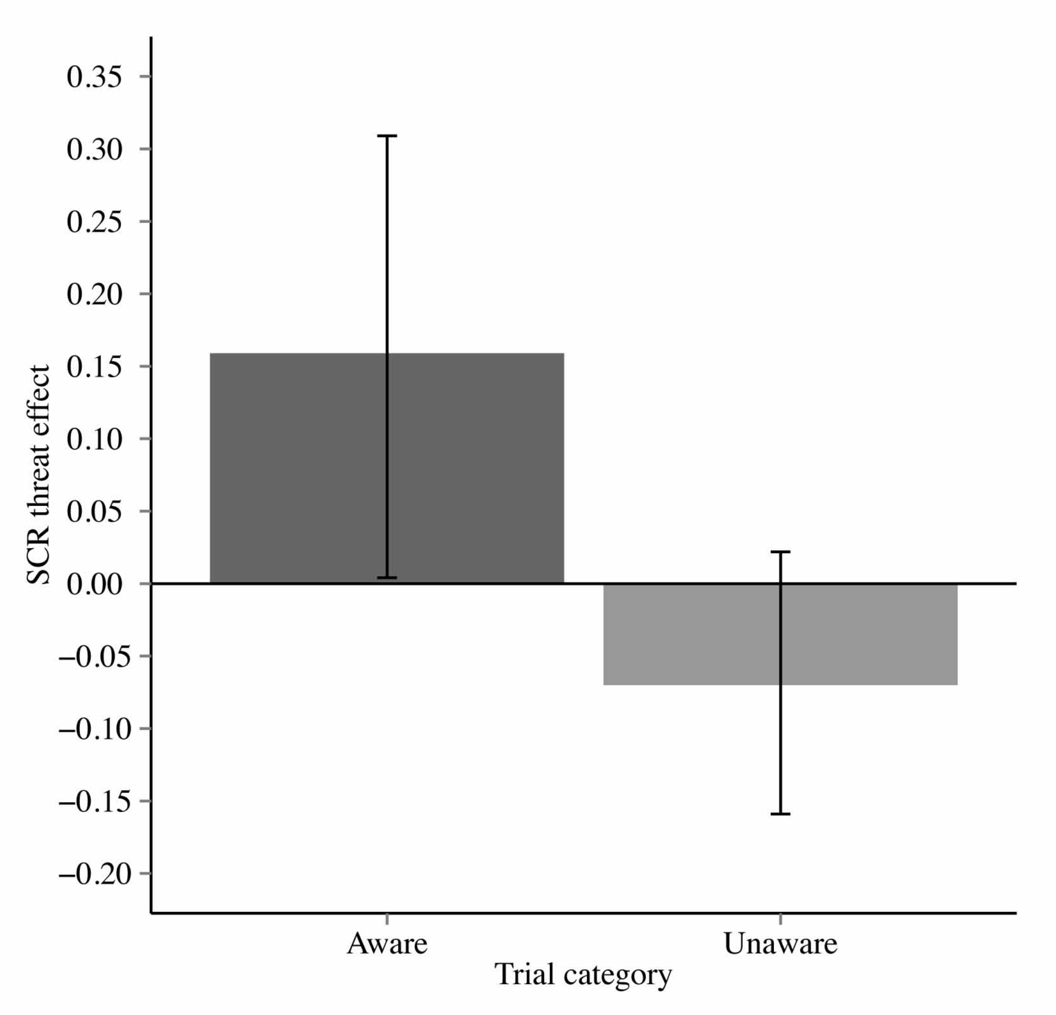

Figure 2. SCR data from the CFS block, plotted as a function of trial category. Error bars give 95% confidence intervals obtained via bootstrapping.

To assess the effect of threat on target visibility, we determined the percentage of trials in which stimuli broke suppression (bCFS) as a function of stimulus category, as indexed by forced choice decisions at the end of each trial. In contrast to previous findings with emotional face stimuli (Gray et al., 2013; Yang, et al., 2007), we found no evidence that threatening and non-threatening images differed in visibility, $t(28) = .736$, $p = .468$ (threatening images: $M = 32.17\%$, non-threatening images: $M = 30.50\%$, $d = 0.05$), suggesting no unconscious prioritisation of threat, relative to non-threat images.

To measure the effect of threat on spatial attention, we used the data from the attentional cueing task to compute an accuracy difference score. In this challenging probe discrimination task, modulation of spatial attention is reflected in differences in discrimination accuracy, rather than response time[2] (Jiang et al., 2006). Attention was thus measured by subtracting the probe discrimination accuracy in invalid trials from accuracy in valid trials. A positive score reflects greater discrimination accuracy at the location of the target stimulus (vs. the scrambled image) suggesting that attention has been allocated to the target (Chica, Martin-Arevalo, Botta, & Lupiáñez, 2014).

Figure 3 shows substantial differences in attentional allocation between aware and unaware trials. We first compared the accuracy difference scores in each condition to zero (no accuracy difference between valid and invalidly cued trials). In aware trials, threatening images attracted spatial attention (*M* = 8.95%, 95% CI [1 13, 16.80], *p* = .027), but non-threatening images did not: observers did not show significantly enhanced probe discrimination following non-threatening images (*M* = 6.03%, 95% CI [-2.35, 14.25], *p* = .153). In contrast, in unaware trials, neither threatening (*M* = 0.96%, 95% CI [-5.71, 7.74], *p* = .783), nor non-threatening images (*M* =1.14%, 95% CI [-5.57, 7.89], *p* = .748) attracted spatial attention. In other words, in the absence of awareness, there is no attentional preference for intact images of either category, relative to their scrambled counterparts. Next, we directly compared stimulus categories (threat vs. non-threat) in terms of attentional allocation. The difference in attention to threatening and non-threatening images was not significant in aware trials (*p* = .640) or unaware trials (*p* = .944). When collapsing accuracy difference scores across stimulus categories, overall attentional allocation to intact vs. scrambled images was significantly greater in aware than unaware trials (*p* = .047), consistent with an increased attentional preference for intact / behaviourally relevant images in aware trials, irrespective of stimulus type. Finally, to decompose the effect of awareness on attentional orienting to intact images, we compared the accuracy difference scores for aware vs. unaware trials for each stimulus category (e.g. threat stimuli in aware trials compared to threat stimuli in unaware trials). This analysis revealed that the overall enhanced attending to intact images in aware trials, relative to unaware trials was 1.6 times greater for threatening (mean difference = 7.99, *p* = .065), than non-threatening stimuli (mean difference =4.89, *p* = .188). In summary, consistent with the physiological measures, the data suggest that threat stimuli only modulate attention when they are available to awareness.

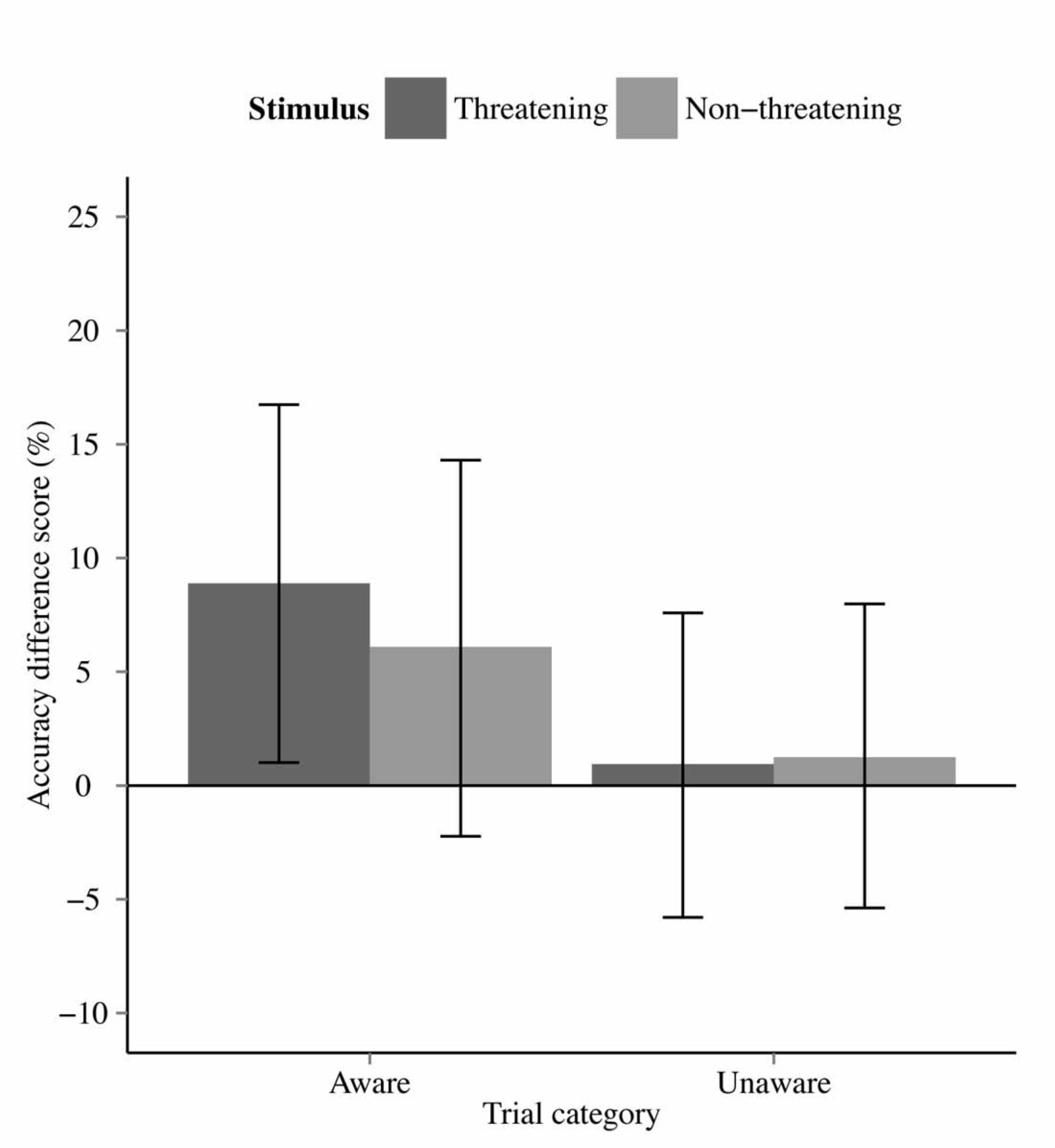

Figure 3. Data from the attentional cueing task, plotted as a function of stimulus and trial category. Error bars are 95% confidence intervals obtained via bootstrapping.

Discussion

In the present study, we used a CFS paradigm to assess physiological and behavioural concomitants of threat processing under conscious and unconscious viewing conditions. Under conscious processing, threat stimuli induced robust physiological responses and captured spatial attention over scrambled images. However, we found no evidence of threat evaluation without awareness: in unconscious presentations we found (i) no threat-related autonomic responses, (ii) no enhanced salience as measured by bCFS and (iii) no greater attentional allocation to threat (or non-threat) images relative to scrambled images. Notably, these null findings in unaware trials were coupled with robust positive effects under aware conditions, making it unlikely that a lack of sensitivity in our task or analyses can account for the null effects. Moreover, our own meta-analyses suggest that attentional effects for animal attack stimuli in subliminal cueing paradigms are medium (*dz*=0.51) and that biases for threatening stimuli (fearful faces) in *b*CFS paradigms are large (*dz*=0.71) (Hedger, Adams, & Garner, 2014). Consequently, our sample size provided good statistical power (.85 and .98 respectively) to detect similar effects of this magnitude. How can we reconcile our findings with previous studies that have reported evidence of emotion / threat processing without awareness?

Many previous demonstrations of selective responses to unconsciously presented threat stimuli have primarily used backward masking to prevent briefly presented stimuli from reaching awareness. However, some of these studies did not assess objective awareness on an individual basis (e.g. Carlson & Reinke, 2008; Dimberg, Thunberg, & Elmehed, 2000; Esteves et al., 1994; Fox et al., 2010; Morris et al., 1999; Writh & Schultheiss, 2007), or extrapolated objective 2AFC data from one sample of observers to another (e.g. Carlson et al., 2009; Nomura et al., 2004; Ohman & Soares, 1994; Phillips et al., 2004; Sutton & Altarriba, 2011). Moreover, some objective awareness checks may have lacked sufficient statistical power to establish above-chance detection performance, leaving open the possibility of awareness on at least some trials (e.g. Katkin, Wiens, & Ohman, 2001; Wiens et al., 2003). For these reasons, it is unclear whether these studies can unequivocally support claims of unconscious perception. Here, we assessed awareness at the individual level by using both subjective and objective criteria and found no evidence for physiological or behavioural threat responses under unaware conditions. Our results are thus more consistent with other lines of evidence that suggest that responses to threatening stimuli are strongly modulated by their conscious detection (Hoffman, Lipka, Mothes-Lasch, Miltner, & Straube, 2012; Mayer et al., 1999; Peira, Golkar, Ohman, Anders & Wiens, 2012).

It is important to note that two recent studies with stringent awareness measures have reported SCR's to conditioned (Raio, Carmel, Carasco, & Phelps, 2012) and unconditioned fearful faces presented under CFS (Lapate, Bokers, Li, & Davidson, 2013). It is possible therefore, that fearful faces, but not animals in attack postures, are able to modulate autonomic responses independently of awareness (notably, Lapate and colleagues also observed that physiological responses to threatening animal stimuli were dependent on awareness). However, to maximise ecological benefit, an effective threat-detection system should mediate adaptive responses to a wide range of threat stimuli in a variety of viewing conditions. For instance, the fear expression is only an *indicator* of threat in the environment, rather than being a *direct* threat to survival and wellbeing. It seems unlikely that humans would have evolved unconscious sensitivity to an indicator of unspecified threat in the environment (fear), without sensitivity to the classes of directly threatening stimuli (e.g. animal attack). Indeed, single cell recordings indicate that the amygdala contains large populations of neurons that are highly selective to both face (Rutishauser et al., 2011) and animal stimuli (Mormann et al., 2011). Moreover, human neuroevolutionary models claim that unconscious vision remains particularly sensitive to snakes, due to the deadly threat they posed to early mammals (Cook & Mineka, 1991; Ohman & Mineka, 2001). Future studies should therefore directly compare autonomic and behavioural responses to a broader range of threat stimuli to investigate the source of this discrepancy.

Our data do not, of course, preclude unconscious processing of other types of threat stimuli. In addition, it is important to note that other dependent measures, such as event related potentials (ERPs) may reveal selective threat responses in the absence of the physiological and behavioural responses that we measured. This consideration is particularly important given that even when behavioural correlates of semantic processing are eliminated, electrophysiological correlates may still be present (Heil, Rolke, & Pecchinenda, 2004). Similarly, studies have reported differential amygdala activation to threatening and neutral stimuli under binocular rivalry (e.g. Jiang & He, 2006; Pasely, Mayes, & Schultz, 2004; Vizueta et al., 2012). With both these ERP and fMRI measures it is important to consider that any pair of stimuli may induce differential activation at the neural level. However, what is the functional purpose of sensitivity to threat at the neural level if this does not cause adaptive changes in physiology and perception? Our study provides no evidence that threatening visual stimuli induce adaptive physiological or behavioural responses when reliably suppressed from awareness via CFS. Thus, combining our paradigm with neuroimaging methods would help further clarify the role of the amygdala in fear behaviour during conscious and unconscious threat processing.

Recently, concerns have been raised regarding the measurement of awareness in binocular rivalry paradigms (including CFS). The boundary between aware and unaware states in rivalry may be graded rather than discrete (Pessoa, 2005), and involve “mixed” states of “piecemeal” rivalry (Alais & Blake, 2005). For this reason, an observer’s perceptual report of awareness is likely to be influenced by their response criteria. These concerns apply to bCFS studies that use suppression duration (indexed by response time) as a measure of differential unconscious processing (as in Gray et al., 2013; Sylvers, Brennan, & Lilienfeld, 2011; Yang et al., 2007). This response time comprises both an unconscious component that reflects “pure” suppression duration, but is also confounded by the time observers take to use visible information to report a stimulus (Stein et al., 2011). It may therefore be inappropriate to conceptualise differential response times in these studies as genuine differences in unconscious processing. We obviated these issues by using fixed presentation durations and a more conservative forced choice task to evaluate awareness and found no advantage for threatening images in breaking suppression. In addition, work from our lab shows that the widely reported “fear advantage” in which fear faces emerge quickly from CFS (Yang et al., 2007) can be explained entirely by the low-level characteristics of fear faces; stimuli with the same low-level properties (i.e. spatial frequency content) but whose emotional expressions are unrecognizable are similarly detected faster following CFS (Gray et al., 2013; Hedger, Adams, & Garner, 2013). Critically, this finding is explained without reference to a sub-cortical pathway that prioritises threat during the suppression phase of CFS and is thus consistent with the present data.

One other important issue in the measurement of awareness is whether an observer’s attempts to monitor their detection of a target may interfere with any unconscious processing that may have otherwise taken place. As Koudier, de Gardelle, Sackur and Dupoux (2010) note, this is conceptually similar to an “observer effect”, in which an observer’s attempt to monitor the state of a system may alter the processes of that system. For instance, in the masked priming literature, Carr and Dagenbach (1990) found that asking observers to make semantic judgements about a masked stimulus could disrupt priming effects. Is it possible that, in the current study, unconscious processing was similarly disrupted by observers' concurrent monitoring of target visibility? We think this is unlikely for several reasons. Firstly, our awareness check required a simple, low-level perceptual judgement (i.e. "was anything other than the mask visible?"), which contrasts with the more demanding, semantic judgement employed by Carr and Dagenbach. Our dynamic mask was a uniform hue, which was easily differentiated from the target stimulus: observers were not required to identify the target and could detect it purely on the basis of hue. The cognitive and attentional resources required to monitor target visibility were thus minimised, making it unlikely that our concurrent awareness measures muted any unconscious processing. In fact, one recent eye tracking study has shown that, despite observers actively trying (and failing) to detect a suppressed Gabor patch, attention was nonetheless driven to its location (Rothkirch et al., 2012). Furthermore, in our study, effects in unaware trials were not simply reduced in magnitude, but were in the opposite direction predicted by the unconscious prioritisation of threat: in unaware trials SCRs and attentional cueing effects were greater to *non-threatening* images (this is also opposite to the pattern found in aware trials, where effects were consistent with enhanced threat processing). Lastly, in our study, CFS was used in all trials and thus observers monitored target visibility in all trials. Trials were classified as 'aware' or 'unaware' post hoc on the basis of target detection. Thus, the process of monitoring awareness would equally affect both aware and unaware trials.

Finally, on a cautionary note, we must consider the limitations of CFS and other paradigms used to manipulate awareness. To assess the role of awareness in threat processing, an optimal paradigm would modulate only awareness, and not any other aspect of visual processing. However, current methods for rendering sensory inputs invisible create stimulus conditions that may not be commonly encountered during everyday visual experience (Kim & Blake, 2005), or require conclusions to be generalized from small samples of individuals with brain damage (e.g. Tamietto et al., 2009). Indeed, neuroimaging data suggest that suppression via both backward masking and CFS disrupts neural activity representing the suppressed stimulus at early stages of visual processing (Rolls, Tovee & Panzeri, 1999; Tong, 2003; Yuval-Greenberg & Heeger, 2013) and differentially affects activity in the ventral and dorsal processing stream (Almeida, Mahon, Nakayama, & Caramazza, 2008; Fang & He, 2005). It remains possible, therefore, that suppression paradigms with different underlying mechanisms, such as motion induced blindness (Bonneh, Cooperman, & Sagi, 2001), or visual crowding (Koudier, Berthet, & Faivre, 2011) may eliminate awareness but spare visual processing to the extent that threat-responses remain effective.

To summarise, using a CFS paradigm, we found no evidence for physiological or behavioural responses to threat when awareness is eliminated according to stringent subjective and objective criteria. Our data compliment other lines of evidence (see Pessoa, 2005; Pessoa & Adolphs, 2010) that challenge current claims that threat is identified unconsciously to direct processing resources.

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[1] We used conservative criteria to define ‘unaware’ trials, excluding data from observers performing above chance in the objective awareness check. This minimised chances of unreported partial awareness being included in the ‘unaware’ category. However, partitioning the data into ‘aware’ and ‘unaware’ trials based solely on subjective reports of awareness (so all data from all observers was used) produced results that were nearly indistinguishable to those reported in the main text.

[2] Enhanced probe discrimination in aware trials was not the product of a speed accuracy trade-off; probe validity did not modulate reaction times in any condition (ps >.18). Raw accuracy scores for each of the eight conditions were also statistically above chance (binomial limit =68%), suggesting null effects were not due to floor effects. In aware trials: (threatening valid: 82%, threatening invalid: 73% non-threatening valid: 74%, non-threatening invalid: 68%) and in unaware trials: (threatening valid: 76%, threatening invalid: 75%, non-threatening valid: 77%, non-threatening invalid: 76%).