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Accepted Version

Hedger, N. ORCID: <https://orcid.org/0000-0002-2733-1913>, Adams, W. J. and Garner, M. (2015) Autonomic arousal and attentional orienting to visual threat are predicted by awareness. *Journal of Experimental Psychology-Human Perception and Performance*, 41 (3). pp. 798-806. ISSN 0096-1523 doi: <https://doi.org/10.1037/xhp0000051> Available at <https://centaur.reading.ac.uk/87283/>

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To link to this article DOI: <http://dx.doi.org/10.1037/xhp0000051>

Publisher: APA PsycNET

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

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Word count =3990 (excluding title, author affiliations, references).

1 Abstract

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

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

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

7 Empirical support for such theories comes predominantly from studies employing
8 backward masking, a technique in which a briefly presented (typically ~30 ms) target
9 stimulus is rendered invisible via masking by a subsequent, co-located stimulus (Esteves &
10 Ohman, 1993). Threatening stimuli presented under these conditions can nonetheless elicit
11 responses in both central and autonomic nervous systems consistent with fear arousal. For
12 example, images of threatening stimuli increase amygdala activity (Morris, Ohman, & Dolan,
13 1999; Nomura et al., 2004) and autonomic skin conductance responses (SCRs) when
14 rendered invisible by masking (Esteves, Dimberg, & Ohman, 1994). In addition, masked
15 threat stimuli are suggested to selectively direct spatial attention to enhance threat appraisal
16 and behavioral response selection. The masked visual probe paradigm provides evidence for
17 this effect: an observer's detection of a peripheral target is enhanced when co-located with a
18 preceding masked threatening image, relative to a neutral image (e.g. Carlson, Fee, & Reinke,
19 2009; Fox, 2002; Mogg & Bradley, 2002). Together, these findings suggest that signals of
20 threat are registered independently of awareness and influence adaptive changes in behavior
21 and physiology.

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

1 This *subjective* approach is rooted in the intuitive idea that only the observer can give reliable
2 information about their conscious experience, since awareness is subjective in nature (Wiens,
3 2006). The subjective approach has been challenged however, on the basis of signal detection
4 models, which state that observers may be reluctant to report weak or brief percepts (Green
5 & Swets, 1966). Accordingly, a more stringent approach relies on *objective* measures:
6 observers are deemed unaware of a stimulus only when performance is at chance in a forced
7 choice discrimination task (e.g. determining the presence or location of the stimulus, see
8 Pessoa, Japee & Ungerleider, 2006). A current view is that both objective and subjective
9 measures have conceptual and practical limitations and thus should be used in combination to
10 comprehensively characterize visual awareness (Szcepanowski & Pessoa, 2007; Wiens,
11 2006).

12 It is in the context of this objective approach that more recent evidence has questioned
13 the ability of the backward masking paradigm to reliably suppress stimuli from awareness.
14 For example, studies using signal detection criteria to assess awareness revealed that the
15 majority of observers can reliably detect stimuli masked after 33ms (Pessoa, Japee, Sturman
16 & Ungerleider, 2006). Furthermore, exposure durations of 17-25ms may result in above
17 chance discrimination of masked threat stimuli, even when subjective reports indicate
18 unawareness (Szcepanowski & Pessoa, 2007). Such findings are important, given that
19 physiological and behavioural threat responses observed in studies employing ~30 ms
20 presentation durations (Carlson, Reinke, & Habib, 2009; Morris, Ohman, & Dolan, 1999;
21 Whalen et al., 1998) are cited as concomitants of “unconscious” processing. Thus, it has been
22 suggested that many previous studies reporting unconscious responses to threat may be
23 explained by sub-optimal measures of awareness (Pessoa, 2005). Consistent with this stance,
24 Coldispoti, Mazzetti and Bradley (2009) showed that physiological responses to emotionally
25 salient stimuli (including SCRs) require exposures of at least 80 ms to be reliably measurable

1 (a duration at which stimuli are also reliably detected) and that exposure durations of 25 ms
2 or less eliminate all physiological reactions. Furthermore, it has recently been suggested that
3 other methodological limitations of masking studies, such as temporally inaccurate
4 presentation methods (Hannula, Simons, & Cohen, 2005; Wiens et al., 2004) and trial order
5 confounds (Wiens, Katkin, & Ohman, 2003) could explain the physiological responses to
6 briefly presented stimuli observed in previous studies. Thus, although previous physiological
7 studies suggest that threat can be evaluated without awareness of the eliciting stimulus, the
8 limitations of the masking paradigms employed require that such findings are re-examined.
9 Similar concerns apply to the masked visual probe literature, which is characterised by a
10 number of studies that do not include an explicit awareness check (Carlson & Reinke, 2008;
11 Fox, Cahill & Zougkou, 2010; Sutton & Altarriba, 2011; Writh & Schultheiss, 2007). Instead
12 assumptions are made about the efficacy of the masking procedure based on previous
13 literature. Again, therefore, the associated claims about unconscious threat processing should
14 be revisited.

15 Continuous flash suppression (CFS) is an increasingly popular technique that allows
16 longer and more robust manipulations of awareness than backward masking (Lin & He,
17 2009). A stereoscope or anaglyph is used to present a dynamic masking pattern to one eye,
18 which suppresses conscious perception of stimuli presented to the other. Despite continuous
19 input to both retinae, the observer may perceive only the masking pattern for long durations,
20 sometimes up to several minutes (Tsuchiya & Koch, 2005).

21 A rapidly growing body of studies employing CFS has demonstrated that emotionally
22 salient stimuli suppressed from awareness can induce changes in neural activity indicative of
23 threat processing. For instance, studies employing CFS in conjunction with functional
24 magnetic resonance imaging (fMRI) have recorded differential amygdala responses to
25 invisible fearful and neutral faces (Jiang & He, 2006; Vizueta, Patrick, Jiang, Thomas, & He,

1 2012). However, these studies did not report convergent changes in behaviour or autonomic
2 physiological arousal that characterise functional threat responses. Although the amygdala is
3 responsive to threat, contemporary models propose that it also sensitive to a broader range of
4 stimulus properties (e.g. unpredictability, value, subjective preference) that modulate
5 cognition and behaviour (Bar & Neta, 2007; Herry et al., 2007; Pessoa, 2010). Moreover,
6 patients with amygdala lesions nonetheless exhibit selective prioritisation of threat in a range
7 of behavioural tasks (Piech et al., 2011; Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs,
8 2009). Thus, it is unclear whether differential amygdala responses to suppressed stimuli can
9 be directly related to functional threat responses, without measures of behavioural
10 performance or autonomic arousal.

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

21 A variant of CFS: breaking continuous flash suppression (bCFS) has also been used to
22 assess visual processing without awareness. The initial suppression duration is used as a
23 correlate of a stimulus' unconscious processing advantage. For example, fearful faces are
24 detected more quickly than neutral faces from invisibility induced by CFS (Yang, Zald, &
25 Blake, 2007), suggesting they are prioritised at unconscious stages of processing. However,

1 recent research suggests that these differences in detection times may be better explained by
2 low-level stimulus variations such as contrast (Gray, Adams, Hedger, Newton, & Garner,
3 2013) or by criterion effects (Stein, Hebart, & Sterzer, 2011) rather than by unconscious
4 processes sensitive to threat. The extent to which signals of threat are evaluated under CFS,
5 therefore, remains a matter of debate.

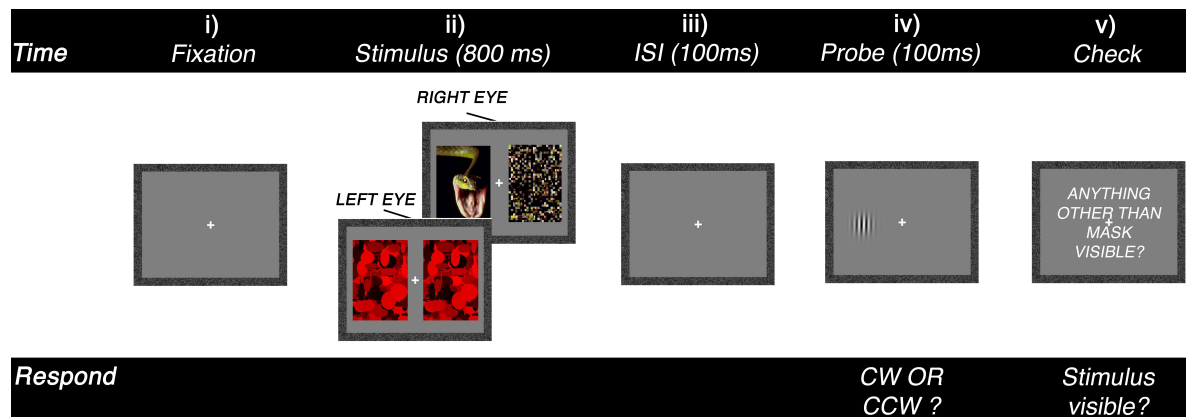
6 In the present study, we assessed the extent to which unconsciously presented visual
7 threat evokes adaptive changes in physiology and behavioural performance. To investigate
8 this, we recorded SCRs to stimuli rendered invisible by CFS. With two concurrent
9 behavioural tasks, we additionally examined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

11 **Method**

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

1 In the *experimental* block, we employed a CFS paradigm that closely mirrored that of
2 Jiang, Costello, Fang, Huang and He (2006). Figure 1 shows a schematic of the trial
3 sequence. (i) At the beginning of each trial, a central fixation cross was presented to each eye.
4 (ii) Subsequently, observers viewed a CFS display via a mirror stereoscope, in which one eye
5 viewed a pair of dynamic masks (random patterns of red-tinted, high contrast ellipses), which
6 updated at 10Hz. The other eye viewed intact and block-scrambled (block size 0.17 x 0.17
7 DVA) versions of one IAPS image, which were presented simultaneously at 1.4 DVA to the
8 left and right of a central fixation cross. Each eye's display was framed by a random dot
9 surround (9.5 x 11.4 DVA) to assist fusion. The IAPS images (and their scrambled versions)
10 were slowly introduced by linearly increasing contrast from 0-100% over the 800ms
11 presentation period to reduce the risk of onset transients breaking suppression. (iii) This
12 display was followed by an inter-stimulus interval (ISI) of 100ms during which only the
13 fixation cross and random dot surround were presented. (iv) To measure the allocation of
14 spatial attention, a Gabor patch (2.5 x 2.5 DVA, 4 cycles per degree) was briefly displayed
15 (100ms) at the location preceded by the intact (valid) or scrambled image (invalid). The
16 Gabor was oriented 1° clockwise or counter-clockwise from the vertical axis. The observer
17 reported the orientation (clockwise or counter-clockwise) of the Gabor via key press "as
18 quickly and accurately as possible". (v) At the end of each trial, observers were prompted to
19 indicate (via key press) whether "*anything other than the mask*" had been visible during the
20 CFS presentation, thereby providing a subjective awareness check. Importantly, this
21 awareness check did not rely on recognition of the target stimulus, which could be influenced
22 by criterion effects. Moreover, the uniform colour of the mask allowed observers to use any
23 deviation from this colour as a cue to aid stimulus detection. The inter-trial interval of 8
24 seconds was sufficiently long to enable SCRs from consecutive stimuli to be differentiated
25 (Boucsein et al., 2012; Breska, Maoz, & Ben Shakh, 2011).

1



2

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

7

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

1 adequate statistical power ($> 80\%$) to detect even small ($> \text{Cohen's } h = 0.22$) deviations from
2 chance performance.

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

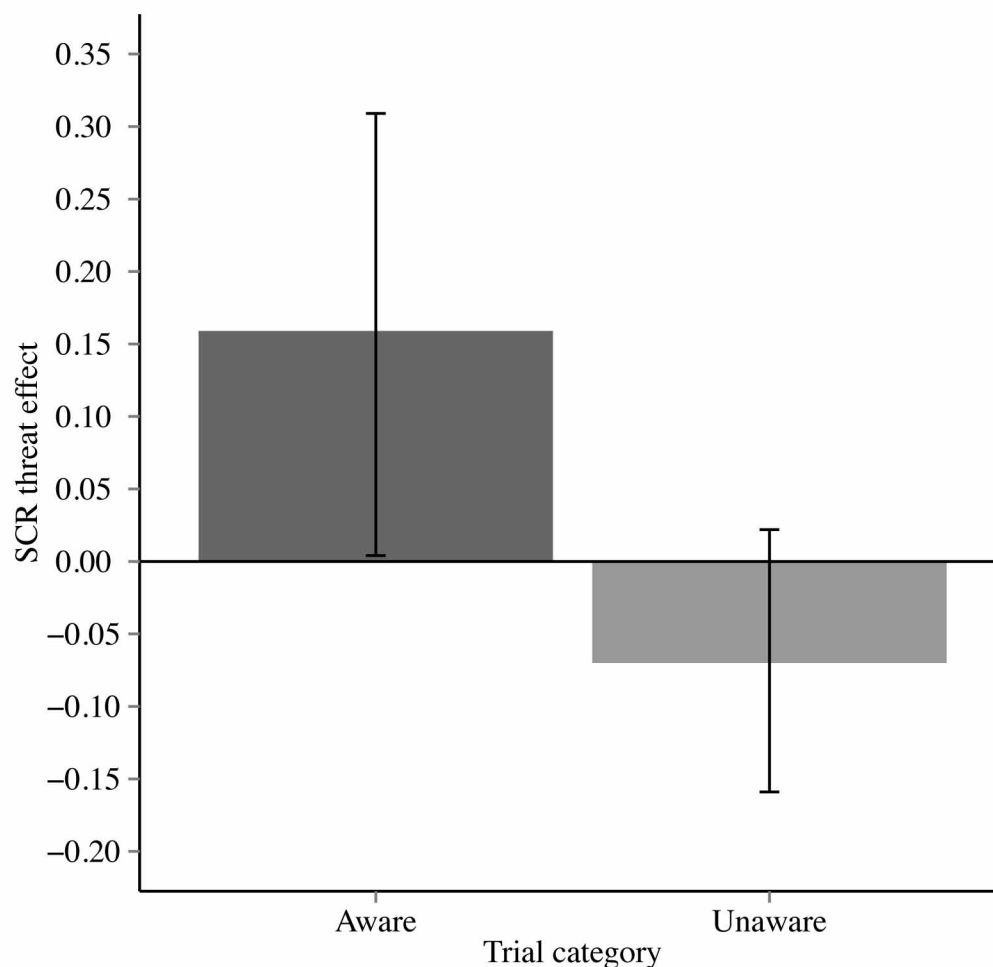
8 SCR data were reduced by submitting the raw amplitudes to a low pass filter (cut-off
9 frequency: $> 25 \text{ Hz}$). Responses were defined as the maximum peak-to-peak amplitude in a
10 pre-defined window 1-4 seconds after stimulus onset, measured in microsiemens (Cacioppo,
11 Tassinary, & Berntson,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

23 **Results**

24 Trials in the *experimental block* were separated into those in which observers were
25 not aware of the target stimulus ('*unaware*') vs. those in which at least some part of the

1 stimulus was detected ('*aware*'). Trials were classified as *unaware* (1638 trials) when the
2 observer (i) indicated that no stimulus was visible in the subjective report for that trial and (ii)
3 the observer performed at chance level in the 2AFC objective control task ($N=14$).
4 Conversely, *aware* trials (829 trials) were taken from all observers ($N=23$), and included all
5 trials on which the subjective report indicated that the stimulus had broken suppression.¹ Data
6 in each trial category were pooled across observers and analysed with a standard bootstrap
7 resampling procedure (Efron & Tibshirani, 1993; Howell, 2013).

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



1

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

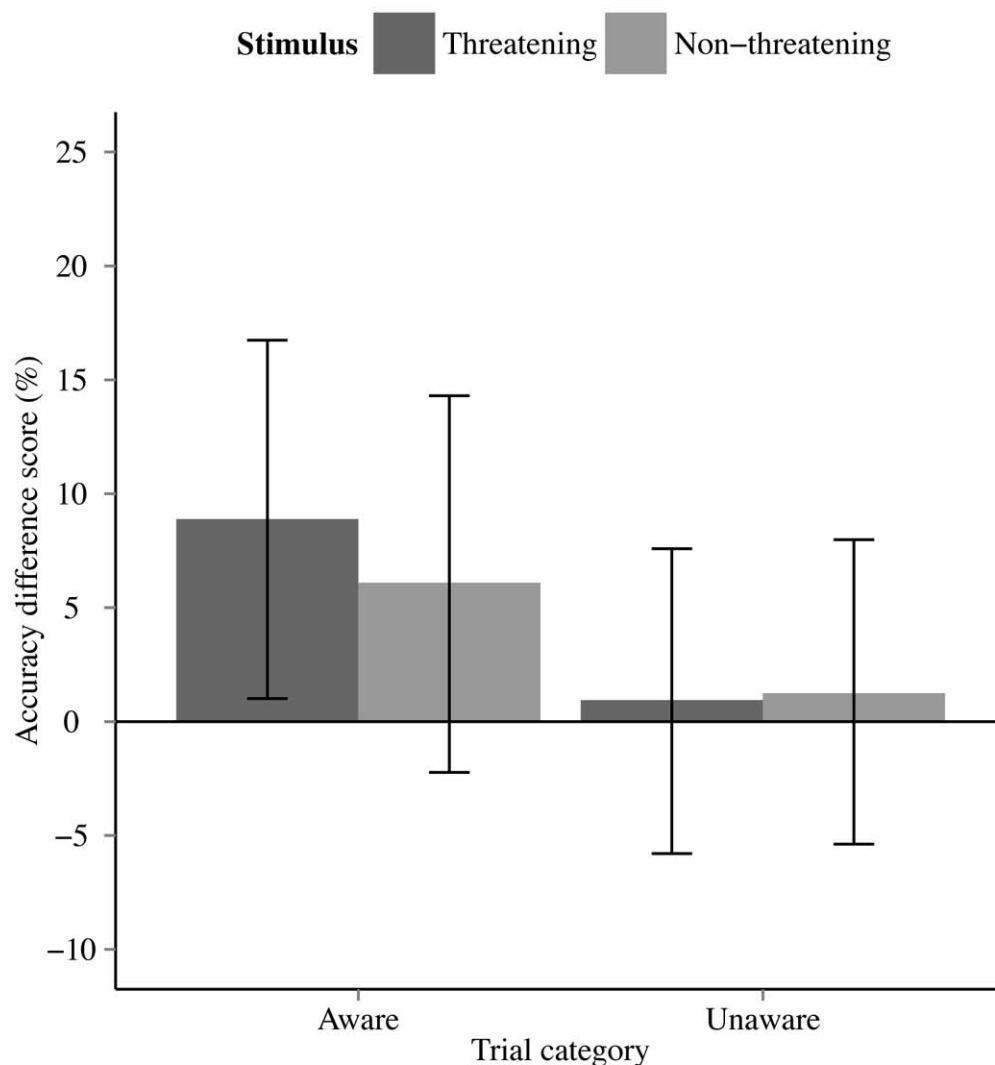
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5 To assess the effect of threat on target visibility, we determined the percentage of
6 trials in which stimuli broke suppression (bCFS) as a function of stimulus category, as
7 indexed by forced choice decisions at the end of each trial. In contrast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

1 To measure the effect of threat on spatial attention, we used the data from the
2 attentional cueing task to compute an accuracy difference score. In this challenging probe
3 discrimination task, modulation of spatial attention is reflected in differences in
4 discrimination accuracy, rather than response time² (Jiang et al., 2006). Attention was thus
5 measured by subtracting the probe discrimination accuracy in invalid trials from accuracy in
6 valid trials. A positive score reflects greater discrimination accuracy at the location of the
7 target stimulus (vs. the scrambled image) suggesting that attention has been allocated to the
8 target (Chica, Martin-Arevalo, Botta, & Lupiáñez, 2014).

9 Figure 3 shows substantial differences in attentional allocation between aware and
10 unaware trials. We first compared the accuracy difference scores in each condition to zero
11 (no accuracy difference between valid and invalidly cued trials). In aware trials, threatening
12 images attracted spatial attention ($M = 8.95\%$, 95% CI [1.13, 16.80], $p = .027$), but non-
13 threatening images did not: observers did not show significantly enhanced probe
14 discrimination following non-threatening images ($M = 6.03\%$, 95% CI [-2.35, 14.25], $p =$
15 $.153$). In contrast, in unaware trials, neither threatening ($M = 0.96\%$, 95% CI [-5.71, 7.74], p
16 $= .783$), nor non-threatening images ($M = 1.14\%$, 95% CI [-5.57, 7.89], $p = .748$) attracted
17 spatial attention. In other words, in the absence of awareness, there is no attentional
18 preference for intact images of either category, relative to their scrambled counterparts. Next,
19 we directly compared stimulus categories (threat vs. non-threat) in terms of attentional
20 allocation. The difference in attention to threatening and non-threatening images was not
21 significant in aware trials ($p = .640$) or unaware trials ($p = .944$). When collapsing accuracy
22 difference scores across stimulus categories, overall attentional allocation to intact vs.
23 scrambled images was significantly greater in aware than unaware trials ($p = .047$), consistent
24 with an increased attentional preference for intact / behaviourally relevant images in aware
25 trials, irrespective of stimulus type. Finally, to decompose the effect of awareness on

1 attentional orienting to intact images, we compared the accuracy difference scores for aware
 2 vs. unaware trials for each stimulus category (e.g. threat stimuli in aware trials compared to
 3 threat stimuli in unaware trials). This analysis revealed that the overall enhanced attending to
 4 intact images in aware trials, relative to unaware trials was 1.6 times greater for threatening
 5 (mean difference = 7.99, $p = .065$), than non-threatening stimuli (mean difference = 4.89, $p =$
 6 $.188$). In summary, consistent with the physiological measures, the data suggest that threat
 7 stimuli only modulate attention when they are available to awareness.



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

3

4

Discussion

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

21 Many previous demonstrations of selective responses to unconsciously presented
22 threat stimuli have primarily used backward masking to prevent briefly presented stimuli
23 from reaching awareness. However, some of these studies did not assess objective awareness
24 on an individual basis (e.g. Carlson & Reinke, 2008; Dimberg, Thunberg, & Elmehed, 2000;
25 Esteves et al., 1994; Fox et al., 2010; Morris et al., 1999; Writh & Schultheiss, 2007), or

1 extrapolated objective 2AFC data from one sample of observers to another (e.g. Carlson et
2 al., 2009; Nomura et al., 2004; Ohman & Soares, 1994; Phillips et al., 2004; Sutton &
3 Altarriba, 2011). Moreover, some objective awareness checks may have lacked sufficient
4 statistical power to establish above-chance detection performance, leaving open the
5 possibility of awareness on at least some trials (e.g. Katkin, Wiens, & Ohman, 2001; Wiens
6 et al., 2003). For these reasons, it is unclear whether these studies can unequivocally support
7 claims of unconscious perception. Here, we assessed awareness at the individual level by
8 using both subjective and objective criteria and found no evidence for physiological or
9 behavioural threat responses under unaware conditions. Our results are thus more consistent
10 with other lines of evidence that suggest that responses to threatening stimuli are strongly
11 modulated by their conscious detection (Hoffman, Lipka, Mothes-Lasch, Miltner, & Straube,
12 2012; Mayer et al., 1999; Peira, Golkar, Ohman, Anders & Wiens, 2012).

13 It is important to note that two recent studies with stringent awareness measures have
14 reported SCR's to conditioned (Raio, Carmel, Carasco, & Phelps, 2012) and unconditioned
15 fearful faces presented under CFS (Lapate, Bokers, Li, & Davidson, 2013). It is possible
16 therefore, that fearful faces, but not animals in attack postures, are able to modulate
17 autonomic responses independently of awareness (notably, Lapate and colleagues also
18 observed that physiological responses to threatening animal stimuli were dependent on
19 awareness). However, to maximise ecological benefit, an effective threat-detection system
20 should mediate adaptive responses to a wide range of threat stimuli in a variety of viewing
21 conditions. For instance, the fear expression is only an *indicator* of threat in the environment,
22 rather than being a *direct* threat to survival and wellbeing. It seems unlikely that humans
23 would have evolved unconscious sensitivity to an indicator of unspecified threat in the
24 environment (fear), without sensitivity to the classes of directly threatening stimuli (e.g.
25 animal attack). Indeed, single cell recordings indicate that the amygdala contains large

1 populations of neurons that are highly selective to both face (Rutishauser et al., 2011) and
2 animal stimuli (Mormann et al., 2011). Moreover, human neuroevolutionary models claim
3 that unconscious vision remains particularly sensitive to snakes, due to the deadly threat they
4 posed to early mammals (Cook & Mineka, 1991; Ohman & Mineka, 2001). Future studies
5 should therefore directly compare autonomic and behavioural responses to a broader range of
6 threat stimuli to investigate the source of this discrepancy.

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

23 Recently, concerns have been raised regarding the measurement of awareness in
24 binocular rivalry paradigms (including CFS). The boundary between aware and unaware
25 states in rivalry may be graded rather than discrete (Pessoa, 2005), and involve “mixed”

1 states of “piecemeal” rivalry (Alais & Blake, 2005). For this reason, an observer’s perceptual
2 report of awareness is likely to be influenced by their response criteria. These concerns apply
3 to bCFS studies that use suppression duration (indexed by response time) as a measure of
4 differential unconscious processing (as in Gray et al., 2013; Sylvers, Brennan, & Lilienfeld,
5 2011; Yang et al., 2007). This response time comprises both an unconscious component that
6 reflects “pure” suppression duration, but is also confounded by the time observers take to use
7 visible information to report a stimulus (Stein et al., 2011). It may therefore be inappropriate
8 to conceptualise differential response times in these studies as genuine differences in
9 unconscious processing. We obviated these issues by using fixed presentation durations and
10 a more conservative forced choice task to evaluate awareness and found no advantage for
11 threatening images in breaking suppression. In addition, work from our lab shows that the
12 widely reported “fear advantage” in which fear faces emerge quickly from CFS (Yang et al.,
13 2007) can be explained entirely by the low-level characteristics of fear faces; stimuli with the
14 same low-level properties (i.e. spatial frequency content) but whose emotional expressions
15 are unrecognizable are similarly detected faster following CFS (Gray et al., 2013; Hedger,
16 Adams, & Garner, 2013). Critically, this finding is explained without reference to a sub-
17 cortical pathway that prioritises threat during the suppression phase of CFS and is thus
18 consistent with the present data.

19 One other important issue in the measurement of awareness is whether an observer’s
20 attempts to monitor their detection of a target may interfere with any unconscious processing
21 that may have otherwise taken place. As Koudier, de Gardelle, Sackur and Dupoux (2010)
22 note, this is conceptually similar to an “observer effect”, in which an observer’s attempt to
23 monitor the state of a system may alter the processes of that system. For instance, in the
24 masked priming literature, Carr and Dagenbach (1990) found that asking observers to make
25 semantic judgements about a masked stimulus could disrupt priming effects. Is it possible

1 that, in the current study, unconscious processing was similarly disrupted by observers'
2 concurrent monitoring of target visibility? We think this is unlikely for several reasons.
3 Firstly, our awareness check required a simple, low-level perceptual judgement (i.e. “was
4 anything other than the mask visible?”), which contrasts with the more demanding, semantic
5 judgement employed by Carr and Dagenbach. Our dynamic mask was a uniform hue, which
6 was easily differentiated from the target stimulus: observers were not required to identify the
7 target and could detect it purely on the basis of hue. The cognitive and attentional resources
8 required to monitor target visibility were thus minimised, making it unlikely that our
9 concurrent awareness measures muted any unconscious processing. In fact, one recent eye
10 tracking study has shown that, despite observers actively trying (and failing) to detect a
11 suppressed Gabor patch, attention was nonetheless driven to its location (Rothkirch et al.,
12 2012). Furthermore, in our study, effects in unaware trials were not simply reduced in
13 magnitude, but were in the opposite direction predicted by the unconscious prioritisation of
14 threat: in unaware trials SCRs and attentional cueing effects were greater to *non-threatening*
15 images (this is also opposite to the pattern found in aware trials, where effects were
16 consistent with enhanced threat processing). Lastly, in our study, CFS was used in all trials
17 and thus observers monitored target visibility in all trials. Trials were classified as ‘aware’ or
18 ‘unaware’ post hoc on the basis of target detection. Thus, the process of monitoring
19 awareness would equally affect both aware and unaware trials.

20 Finally, on a cautionary note, we must consider the limitations of CFS and other
21 paradigms used to manipulate awareness. To assess the role of awareness in threat
22 processing, an optimal paradigm would modulate only awareness, and not any other aspect of
23 visual processing. However, current methods for rendering sensory inputs invisible create
24 stimulus conditions that may not be commonly encountered during everyday visual
25 experience (Kim & Blake, 2005), or require conclusions to be generalized from small

1 samples of individuals with brain damage (e.g. Tamietto et al., 2009). Indeed, neuroimaging
2 data suggest that suppression via both backward masking and CFS disrupts neural activity
3 representing the suppressed stimulus at early stages of visual processing (Rolls, Tovee &
4 Panzeri, 1999; Tong, 2003; Yuval-Greenberg & Heeger, 2013) and differentially affects
5 activity in the ventral and dorsal processing stream (Almeida, Mahon, Nakayama, &
6 Caramazza, 2008; Fang & He, 2005). It remains possible, therefore, that suppression
7 paradigms with different underlying mechanisms, such as motion induced blindness (Bonneh,
8 Cooperman, & Sagi, 2001), or visual crowding (Koudier, Berthet, & Faivre, 2011) may
9 eliminate awareness but spare visual processing to the extent that threat-responses remain
10 effective.

11 To summarise, using a CFS paradigm, we found no evidence for physiological or
12 behavioural responses to threat when awareness is eliminated according to stringent
13 subjective and objective criteria. Our data compliment other lines of evidence (see Pessoa,
14 2005; Pessoa & Adolphs, 2010) that challenge current claims that threat is identified
15 unconsciously to direct processing resources.

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

7 ² Enhanced probe discrimination in aware trials was not the product of a speed
8 accuracy trade-off; probe validity did not modulate reaction times in any condition ($p > .18$).
9 Raw accuracy scores for each of the eight conditions were also statistically above chance
10 (binomial limit = 68%), suggesting null effects were not due to floor effects. In aware trials:
11 (threatening valid: 82%, threatening invalid: 73% non-threatening valid: 74%, non-
12 threatening invalid: 68%) and in unaware trials: (threatening valid: 76%, threatening invalid:
13 75%, non-threatening valid: 77%, non-threatening invalid: 76%).

14