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Visual input signaling threat gains preferential access to awareness in a breaking continuous flash suppression paradigm

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ABSTRACT

Visual input that signals threat is inherently relevant for survival. Accordingly, it has been demonstrated that threatening visual input elicits faster behavioral responses than non-threatening visual input. Considering that awareness is a prerequisite for performing demanding tasks and guiding novel behavior, we hypothesized that threatening visual input would gain faster access to awareness than non-threatening visual input. In the present study, we associated one of two basic visual stimuli, that were devoid of intrinsic relevance (colored annuli), with aversive stimulation (i.e., electric shocks) following a classical fear conditioning procedure. In the subsequent test phase no more electric shocks were delivered, and a breaking continuous flash suppression task was used to measure how fast these stimuli would access awareness. The results reveal that stimuli that were previously paired with an electric shock break through suppression faster than comparable stimuli that were not paired with an electric shock.

1. General introduction

Detecting threatening visual input in the environment is crucial for adaptive functioning. Given that we are continuously presented with vast amounts of sensory input, any part of it that signals threat is pre-eminently relevant to the observer. Accordingly, it has been demonstrated that threatening visual stimuli, such as angry faces and spiders can be reported faster and are more difficult to ignore than non-threatening visual stimuli (e.g., Öhman, Flykt, & Esteves, 2001; for reviews, see Mather & Sutherland, 2011; Yiend, 2010). Visual awareness has been associated with such functional properties as performing demanding tasks (Dehaene, Kerszberg, & Changeux, 1998) and guiding novel behavior (Gayet, Van der Stigchel, & Paffen, 2014a; Kunde, Kiesel, & Hoffmann, 2003) and is therefore valuable for selecting the appropriate set of behaviors in response to imminent threat. Accordingly, we set out to investigate whether visual stimuli that signal threat would gain faster access to awareness than stimuli that are not associated with threat.

Access to awareness was measured by means of a breaking continuous flash suppression task (b-CFS; Jiang, Costello, & He, 2007; for a review, see Gayet, Van der Stigchel, & Paffen, 2014b). In this method, a stimulus is initially interocularly suppressed by continuous flash suppression (CFS; Tsuchiya & Koch, 2005). The time it takes for this stimulus to overcome interocular suppression, so that it can be reported by an observer, provides a measure of access to awareness (Gayet et al., 2014b; Stein, Hebart, & Sterzer, 2011). The experimental manipulation of threat was obtained by associating one of two colored annuli with electric shocks (hereafter the CS+), while never pairing the other annulus color with a shock (hereafter the CS−), following a classical fear conditioning procedure (Mackintosh, 1983; Pavlov, 1927). Unlike aversive images, the usage of electric shocks has the advantage of constituting an actual threat to participants. In this context, we defined threat as a state of the world predicting an aversive event, as evidenced by prior experience. Fear conditioning allows for isolating the manipulation of threat from the visual characteristics that typically differentiate threatening from non-threatening stimuli. This is especially relevant in the present context, as differences in visual stimulus characteristics are known to affect access to awareness in a b-CFS task (Gayet et al., 2014b; Stein & Sterzer, 2012; Yang & Blake, 2012).

Recent experiments have revealed that visual input that was previously associated with an aversive event is more readily detected (Padmala & Pessoa, 2008; Phelps, Ling, & Carrasco, 2006) and attracts attention (Armony & Dolan, 2002; Schmidt, Belopolsky, & Theeuwes, 2015a) and eye movements (Mulckhuyse, Crombez, & Van der Stigchel, 2013; Schmidt, Belopolsky, & Theeuwes, 2015b) to a greater extent than comparable visual input that was never associated with an aversive event.

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These findings lead us to hypothesize that fear conditioning increases the salience of visual input. Considering that increased stimulus contrast yields reduced suppression strength under CFS (Tsuchiya & Koch, 2005), we expected reduced suppression durations for fear-conditioned stimuli. Hence, we predicted faster response times to target gratings surrounded by a CS+ compared to a CS− annulus.

Using behavioral reports of visibility in suppression paradigms (e.g., backwards masking, bistable perception, inattentional blindness, etc.) as a measure of access to awareness brings about an important pitfall: Fear conditioning might not only affect how strongly a stimulus is suppressed, it might also affect how fast a stimulus can be responded to once it is no longer suppressed (i.e., reflecting so-called post-suppression effects). In the case of fear conditioning specifically, post-suppression effects could arise from a more liberal response bias in CS+ compared to CS− trials (requiring less perceptual evidence for deciding that a target is perceived) or increased sensitivity to CS+ compared to CS− stimuli (requiring less perceptual evidence for perceiving the target). Using interocular competition allows for dissociating between suppression (between-eyes) and post-suppression effects (within-eye). This is achieved by including a monocular control condition, in which the stimulus is presented to the eye that is already dominant. Considering that there is no interocular competition (and therefore no between-eye effect) in this control condition, it allows to selectively measure differences in response speed to the stimuli once they are already visible (i.e., post-suppression, or within-eye effects). Consequently, any difference in response times that emerges in the suppression condition but not in the monocular control condition reflects a difference in suppression durations (for discussion on this interpretation, see Gayet et al., 2014b; Stein et al., 2011). In addition to this crucial control, we designed our stimuli such as to minimize post-suppression effects. For this purpose, we created a response task (reporting the orientation of a grating) that was orthogonal to the experimental manipulation (which was tied to the color of the surrounding annulus; for a similar approach, see Salomon, Lim, Herbelin, Hesselmann, & Blanke, 2013). As a result of this, post-suppression effects that affect processing of the CS+ annulus are not expected to affect the orientation judgment task, as the grating has not been fear conditioned. Considering that we took precautions to minimize post-suppression effects, we did not expect an effect of fear conditioning in the monocular condition.

2. General methods

2.1. Participants

Eighteen healthy participants were selected for (corrected to) normal vision, including stereoscopic vision (tested by inducing diplopia) and color perception (Ishihara, 1917). The eventual group of participants that was included in the analyses consisted of 7 males and 9 females, with an average age of 23 years (*SD* = 3.5). The sample size was derived from comparable b-CFS studies (e.g., Stein & Sterzer, 2012) and fear conditioning studies (Schmidt et al., 2015a, 2015b). The experimental procedure was validated by the ethical board of the VU University of Amsterdam.

2.2. Stimuli

All stimuli were presented on a black (0.2 cd/m^2) screen. Using a dichoptic mirror stereoscope, each eye was presented with a square shaped Brownian noise frame, subtending an area of 5.0 by 5.0° on the outside, that encapsulated a gray presentation area of 2.2 by 2.2° with a fixation cross (0.2 by 0.2°) in the center.

The 'Mondrian' masks used to obtain CFS consisted of overlapping black, gray (41.2 cd/m^2) and white (87.0 cd/m^2) circles with diameters ranging from 0.35 to 0.70°. In each block 46 unique masks were generated. On each trial the order of the masks was shuffled, and the masks were replaced at 10 Hz.

The target stimuli were comprised of saturated red (5.3 cd/m^2, $SD = 0.8$, $x = 0.034$, $y = 0.344$), green (8.6 cd/m^2, $SD = 1.6$, $x = 0.152$, $y = 0.104$) and blue (reference color at 6.4 cd/m^2, $x = 0.281$, $y = 0.344$) annuli with an outer radius of 1.2° and an inner radius of 0.7°. Flicker photometry (Kaiser & Comerford, 1975) was used to perceptually equate the luminance of the different annulus colors with the gray background (6.7 cd/m^2, $SD = 0.8$). The annuli encapsulated a sine-wave grating with a spatial frequency of 8.4 cycles/°, a Gaussian profile ($SD = 0.35°$) and a mean luminance equal to that of the gray background. The grating could have an orientation of either plus or minus 45° from the vertical midline.

The aversive stimulation used for the fear conditioning procedure consisted of 400 V electric shocks with a mean amperage of 11.0 mA (*SD* = 7.5). A train of shocks with a duration of 50 μs each was delivered at 60 Hz, giving the sensation of a single 500 ms shock. Shocks were delivered through two electrocardiogram electrodes, connected to a Digitimer DS7A direct current stimulator, that were placed over the tibial nerve, at the medial malleolus of the right ankle.

2.3. Experimental design

The experimental design comprised the within-subject factors Conditioning (CS+ or CS− annulus), Suppression (suppression or monocular condition) as factors of interest, and the factors Eye (target presented to the left or right eye), and Orientation (grating tilted leftwards or rightwards) as factors of no interest. This resulted in 16 unique combinations of within-subject conditions, which were presented twice within the first 32 trials of the experiment, and twice within the last 32 trials of the experiment. Trial order was randomized within these two experimental halves. Eventually, the experiment was divided into four experimental blocks. The factor Color (CS+ annulus is blue or red) was a between-subject factor and was counterbalanced between participants. Taken together, each of the four Suppression × Conditioning conditions contained 16 trials. We limited the test phase of the experiment to this relatively small number of trials, as we expected that the effect of fear conditioning would extinguish after repeatedly presenting a CS+ stimulus unaccompanied by a shock.

2.4. Procedure

The experiment started with 32 practice trials, in which participants were instructed to report the orientation of the grating as fast and accurately as possible (see Fig. 1). Each trial started with a fixation cross (500 ms), and between 300 and 600 ms after onset of the Mondrian masks the annulus and grating were presented either to the same eye as the mask (monocular condition), or to the other eye (suppression condition). These stimuli were ramped up to full intensity in either one second (suppression condition) or three seconds (monocular condition). These durations were chosen such as to elicit comparable RT distributions in the two Suppression conditions (for other studies using this approach, see Gayet, Paffen, & van der Stigchel, 2013; Stein et al., 2011). After a response was given, or 4000 ms had elapsed, the masks were removed from the screen, and the target was presented binocularly for 500 ms.

Next, the electrodes were attached to the ankle of the participants, and electric shocks of increasing intensity were administered following a shock workup procedure (adapted from Heitland, Groenink, Bijlsma, Oosting, & Baas, 2013). This procedure

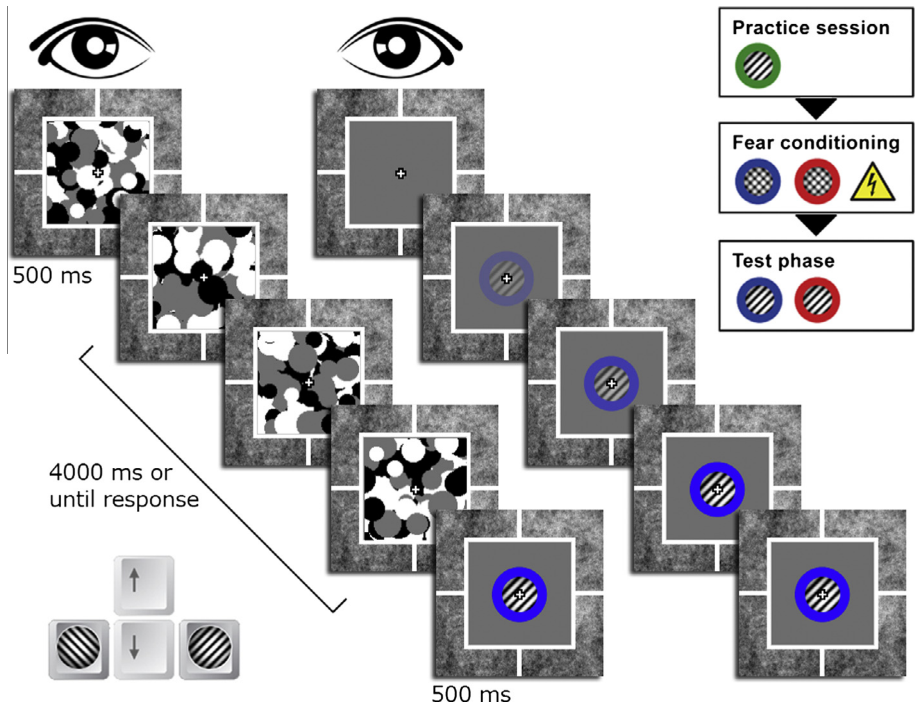

Fig. 1. Schematic depiction of an experimental trial in the suppression condition. Participants were instructed to report the orientation of the grating. The same stimulus chronology was used throughout every phase of the experiment. The panel in the upper right indicates the stimuli that were used in these different phases.

was aborted once participants rated the aversiveness of the shock as a 4 out of 5.

During the subsequent 16 trials acquisition block, six out of eight trials with one annulus color (hereafter CS+) were paired with an electric shock, whereas none of the trials with the other annulus color (hereafter CS−) were paired with an electric shock. The two grating orientations (left and right tilt) were superimposed during acquisition, to avoid that participants would incidentally couple the occurrence of an electric shock to a particular orientation, rather than to a particular color.

After the acquisition phase, the participants were presented with 64 experimental trials. Participants were told that no more shocks would be delivered and they were instructed to report the orientation of the gratings as fast and accurately as possible.

2.5. Data analysis

For the analysis of response times, only trials with correct responses (93.3%, *SD* = 6.1) were included. One participant was at chance level in reporting the orientation of the target grating and was therefore excluded from all analyses. Median response times were computed for each participant's Conditioning and Suppression conditions. Truncating two response time distributions at the same numerical value (i.e., at the response time deadline of 4000 ms) would cause the analysis to include more data (from the slower end of the distribution) in the condition that yielded the fastest response times, thereby compromising a fair statistical comparison between the two conditions. To circumvent this problem, we included trials in which no response was given within the 4000 ms time limit (8.3% of the trials, *SD* = 9.3) in the analysis as well, as they reflect long suppression durations. On these trials, response times were registered as "infinitely long". This approach allowed for computing median response times that include all trials, and therefore reflect the entire response time distribution, rather than the average of the response times that were within the arbitrary deadline of 4000 ms. In four participants, at least 50% of the trials in either the CS+ or the CS− condition yielded an infinitely long response (i.e., no response). As a consequence, the median response time for these participants was infinitely long as well, in at least one condition, and was therefore deemed uninformative. For these participants, we computed the median response times by including only the trials in which the target was presented to the dominant eye (i.e., the Eye condition that yielded the shortest response times). This allowed for preserving the equal prevalence of experimental conditions within these participants. One participant was excluded from further analyses as trials in neither Eye condition retained more than 50% of responses within the 4000 ms time limit. As such, the analyses in the Results section are based on 16 participants, for eight of which the shocks were associated with the red annulus color. For these participants, 7.8% (*SD* = 2.4) of the trials yielded either no response or an incorrect response. Additional analyses with alternative inclusion criteria are provided in Supplementary materials S1 and S2.

3. Results Experiment 1

We conducted a 2 × 2 repeated-measures ANOVA with the within-subject factors Conditioning and Suppression, and the between-subject factor Color. This revealed a main effect of Conditioning, $F(1,14) = 8.97$, $p = .010$, $\eta^2 = .39$, showing that, irrespective of the Suppression condition, trials in which a CS+ annulus was presented (*M* = 1557 ms, *SD* = 284) yielded faster response times than trials in which a CS− annulus was presented (*M* = 1718, *SD* = 432). The absence of a main effect of Suppression, $F(1,14) = .20$, $p = .659$, $\eta^2 = .01$, indicated that we successfully matched the response times of trials in which the targets were interocularly suppressed (*M* = 1660 ms, *SD* = 524), and trials in which they were not (*M* = 1615 ms, *SD* = 248). This is an important requirement for making a fair comparison between effects in the suppression condition and the monocular control condition (Stein et al., 2011). The between-subject factor Color did not interact with either Suppression ($p = 0.175$) or Conditioning ($p = 0.623$). Finally, there was an interaction between Suppression and Conditioning on response times, $F(1,14) = 13.98$, $p = .002$, $\eta^2 = .50$, but no three-way interaction with the between-subject factor Color, $F(1,14) = .08$, $p = .780$, $\eta^2 = .01$. This shows that the interaction between Conditioning and Suppression did not depend on the specific color that was paired with electric shocks.

Subsequent paired-samples *t*-tests revealed that when targets were interocularly suppressed, discrimination of the oriented gratings was faster when they were surrounded by a CS+ annulus ($M = 1498$ ms, $SD = 416$) than a CS− annulus ($M = 1822$ ms, $SD = 646$), $t(15) = 3.72$, $p = .002$, Cohen's $d = 1.92$. When the grating and annulus were not interocularly suppressed (i.e., in the monocular condition), however, response times did not differ between CS+ trials ($M = 1615$ ms, $SD = 252$) and CS− trials ($M = 1614$ ms, $SD = 271$), $t(15) = .04$, $p = .968$, Cohen's $d = .02$. There was no correlation between the influence of conditioning on response times in the monocular condition and the suppression condition, $R(14) = .29$, $p = .276$. To assert that the absence of an effect of conditioning in the monocular condition reflected a null effect rather than experimental insensitivity we computed a Bayes factor (Dienes, 2014). The alternative hypothesis was modelled as a uniform distribution with a lower bound of zero and an upper bound equaling the effect of conditioning in the suppression condition. This revealed that the data was over seven times more likely to reflect a null effect than the alternative hypothesis ($B_{01} = 7.14$). Together, these findings demonstrate that stimuli that were previously paired with aversive stimulation, and therefore signal threat, are released from interocular suppression (322 ms) faster than stimuli that were not paired with a shock. The effect of conditioning on response times as a function of Suppression condition is depicted in Fig. 2A (group results) and 2B (individual results).

A separate 2 × 2 repeated-measures ANOVA, revealed no interaction effect between the factors Suppression and Conditioning on accuracy, $F(1,15) = .23$, $p = .638$. Consequently, the larger response time difference in the suppression condition compared to the monocular condition is not potentiated by a larger uncertainty in the suppression condition. Finally, Supplementary analyses (S1 and S2) underline the robustness of the effect of fear conditioning on suppression durations.

4. Discussion Experiment 1

The data demonstrate that fear-conditioned stimuli are released from interocular suppression faster than equivalent stimuli that were never paired with an aversive stimulus. This speed-up was not caused by an increased response speed after the annuli were released from suppression. The correlational analysis provides further evidence that response times in the suppression condition reflect suppression durations. The absence of a correlation between the effect of fear conditioning in the suppression condition and the monocular control condition shows that participants that were faster on CS+ trials in the suppression condition were not necessarily faster on CS+ trials in the monocular control condition. This confirms that two different processes are operating in these two conditions. Additionally, the Bayesian analysis confirms that we obtained a reliable null-effect in the monocular control condition. That is, fear conditioning did not affect response times after the stimuli were released from suppression. Taken together, our experimental paradigm was successful in measuring differences in suppression durations elicited by fear conditioning, which were not contaminated by effects of fear conditioning on response times after the stimuli were released from suppression.

5. Experiment 2

5.1. Introduction Experiment 2

We hypothesized that the advantage of threatening visual input to access awareness could be accounted for by an increase in salience of these stimuli. In Experiment 2, we set out to investigate the possibility that an increase in salience could indeed shorten suppression durations while leaving response times unaffected by post-suppression effects. For this purpose we manipulated the bottom-up salience of the annuli (i.e., the luminance contrast). We expected that, under conditions of interocular competition, an increase in the luminance contrast of an annulus would shorten suppression durations and thereby lead to faster response times to the target grating. Again, in the monocular condition no such difference was expected, as the eye to which annulus and grating were presented was already dominant.

5.2. Methods Experiment 2

In Experiment 2, the stimuli and presentation were identical to that of Experiment 1, except for one difference. Whereas the blue and green target colors and the gray background color were matched for perceptual equiluminance, as in Experiment 1, the red target color was set to its maximal luminance (27.7 cd/m^2, $x = 0.639$, $y = 0.344$). As a result of this, the red annulus had an average Michelson luminance contrast of 61% with the gray background.

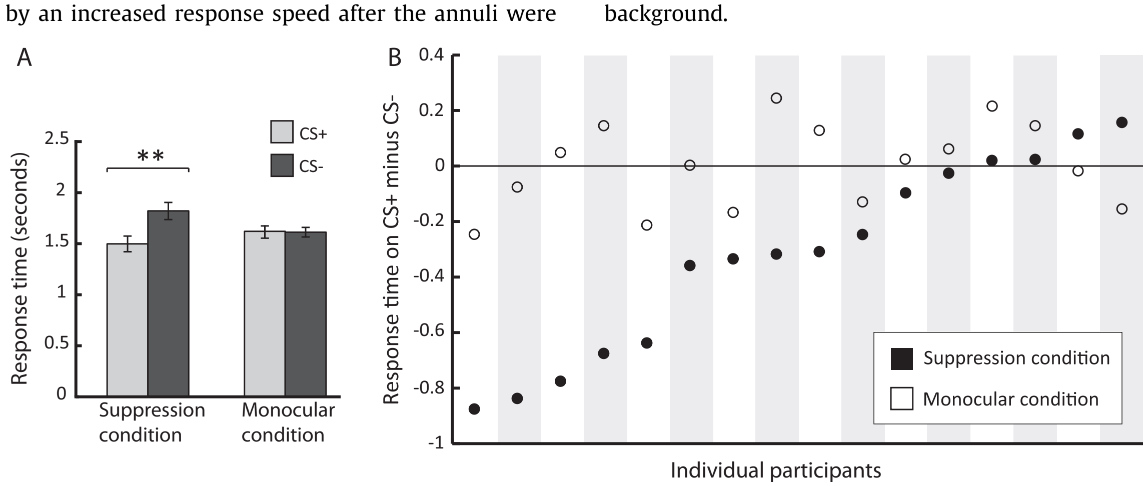

Fig. 2. Group results (A) and individual results (B) for all 16 participants. In panel A, the *y*-axis represents the response time as a function of presentation condition (labeled on the *x*-axis) and fear conditioning (shades of gray). In panel B, the *y*-axis represents the difference in response time between CS+ trials and CS− trials for each participant (depicted along the *x*-axis). ** $p < .005$.

To ensure that there were no a priori differences in suppression durations of the blue and red annuli, we ran an additional control experiment (Experiment 3), which comprised 15 of the 16 participants that were included in Experiment 2. In this control experiment, the blue and red annuli were perceptually equiluminant. Here, no difference in response times was observed between trials with blue ($M = 1689$ ms, $SD = 754$) and red annuli ($M = 1661$ ms, $SD = 702$), $t(14) = 0.26$, $p = 0.798$, in the suppression condition. This shows that, at least for these participants, perceptual equiluminance matching ensures equal suppression durations in a b-CFS paradigm.

Eighteen healthy students, to which all same inclusion criteria applied as to that of the main experiment, participated in this supplemental experiment. One participant was excluded from further analyses because none of his responses were registered within the 4000 ms time limit. Another participant was excluded because he reported having repeatedly experienced diplopia throughout the experiment. The eventual group of participants consisted of 6 males and 10 females, with an average age of 22 years ($SD = 3.3$).

5.3. Results Experiment 2

The results of this experiment are presented in Fig. 3. A 2 × 2 repeated-measures ANOVA with the within-subject factors Contrast (high or low) and Suppression (interocular suppression or monocular presentation) revealed a main effect of Contrast, $F(1,15) = 4.65$, $p = .048$, $\eta^2 = .24$, no main effect of Suppression, $F(1,15) = 1.39$, $p = .257$, $\eta^2 = .09$, and an interaction between Suppression and Contrast, $F(1,15) = 7.32$, $p = .016$, $\eta^2 = .33$. Subsequent paired-samples *t*-tests (see Fig. 2B) revealed that when targets were interocularly suppressed, discrimination of the orientated gratings was faster when they were surrounded by high contrast annuli ($M = 1477$ ms, $SD = 605$) than low contrast annuli ($M = 1650$ ms, $SD = 712$), $t(15) = 2.47$, $p = .026$, Cohen's $d = 0.67$. When the gratings and annuli were not interocularly suppressed, however, response times did not differ between trials in which gratings were surrounded with high contrast annuli ($M = 1398$ ms, $SD = 266$) and low contrast annuli ($M = 1399$ ms, $SD = 258$), $t(15) = .03$, $p = 0.979$, Cohen's $d = .01$). These findings demonstrate that increasing the luminance contrast of an annulus yields the same pattern of results as associating that annulus with a threat (main experiment).

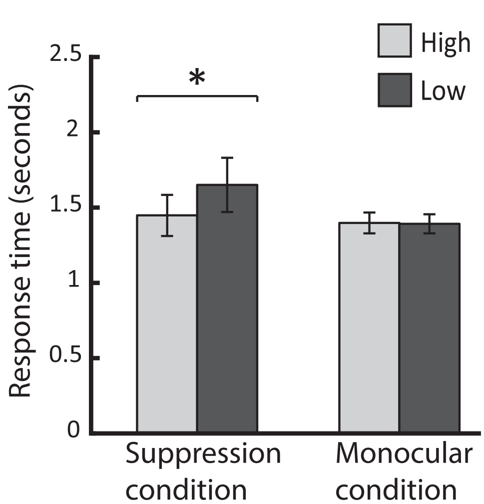

Fig. 3. Group results for all 16 participants. The *y*-axis represents the response time as a function of presentation condition (labeled on the *x*-axis) and annulus contrast (shades of gray). * $p < .05$.

Participants' average percentage correct over all conditions was 91.7% ($SD = 8.6$). A separate repeated measures analysis, revealed no interaction effect between the factors Suppression and Conditioning on accuracy, $F(1,15) = 0.15$, $p = .708$. Again, the effect of contrast manipulation on response times mentioned above, is not accounted for by a greater uncertainty in the suppression condition compared to the monocular condition.

5.4. Discussion Experiment 2

Here, we demonstrated that an increase in bottom-up salience (i.e., luminance contrast of the annuli) yielded a similar pattern of results as was obtained with fear conditioning. That is, we found shorter suppression durations for higher contrast stimuli compared to lower contrast stimuli, while the response speed to higher contrast stimuli remained unaffected. From this we conclude that (1) the combined use of an orthogonal response mapping and a monocular control condition allows for selectively measuring differences in suppression durations elicited by modulating stimulus salience and (2) increases in bottom-up stimulus salience elicit patterns of results that are similar to those engendered by fear conditioning.

6. General discussion

The present study reveals that a priori neutral visual stimuli gain faster access to awareness when they have been associated with electric shocks, following a classical fear conditioning procedure. We cannot ascertain whether the fear conditioning procedure successfully elicited a fear response to CS+ stimuli, as we did not include physiological response measurements. But, considering that CS+ trials and CS− trials only differed by virtue of the preceding fear conditioning procedure, it is implied that the fear conditioning procedure potentiated the faster access to awareness of CS+ compared to CS− stimuli. Based on the history of occurrence, the CS+ therefore constituted a threat, as it signaled an aversive event. Importantly, the visual stimuli were manipulated experimentally to be either threatening to the observer or not. By this, we successfully isolated the effect of threat from the visual characteristics that typically constitute the threatening stimuli. As the association of a stimulus with threat co-determined the time at which this stimulus entered awareness, it can be inferred that the perceptual system was able to differentiate threatening stimuli from non-threatening stimuli before they entered awareness. It is argued that the b-CFS method is suitable to measure access to awareness, but cannot unequivocally measure non-conscious processing (Gayet et al., 2014b; Stein et al., 2011; Stein & Sterzer, 2014). In line with our interpretation, however, earlier studies have demonstrated that threatening versus non-threatening stimulus categories (Jiang & He, 2006; Lipp, Kempnich, Jee, & Arnold, 2014; Morris, Öhman, & Dolan, 1998; Schmack, Burk, Haynes, & Sterzer, 2015; Whalen et al., 1998; Williams, Morris, McGlone, Abbott, & Mattingley, 2004; for a review, see Pessoa, 2005) as well as CS+ versus CS− stimuli (Raio, Carmel, Carrasco, & Phelps, 2012) can indeed be segregated non-consciously. The present study shows that the visual system can use this non-conscious segregation between threatening and non-threatening visual input to determine the contents of awareness.

In line with our findings, Alpers and colleagues observed increased predominance of fear conditioned stimuli in a binocular rivalry task (Alpers, Ruhleder, Walz, Mühlberger, & Pauli, 2006). While their findings are in line with the present study, they do not address the question of whether threatening information gains faster access to awareness. In binocular rivalry, it is impossible to discern whether the experimental manipulation alters dominance durations by impacting the visual processing of the perceived stimulus or that of the suppressed stimulus. As CS+ stimuli attract attention (Armony & Dolan, 2002; Schmidt et al., 2015a), it might take more time to disengage from a CS+ stimulus than from a CS− stimulus, and it might take less time to initiate report of a CS+ stimulus than a CS− stimulus, both leading to longer reported percept durations. In the present study this was not an issue, as observers initially only perceived the mask, and response speeds were therefore necessarily dependent on the suppressed stimulus rather than the dominant stimulus. Additionally, in our experiment, we were able to assert that the differences in response times were not accounted for by differences in response speed after the interocular conflict was resolved (i.e., post-suppression), by the inclusion of a monocular control condition.

In order to minimize post-suppression effects of fear conditioning on response times, we segregated the stimulus part that dictated the suppression duration (the CS+ or CS− annulus) from the stimulus part to which observers respond (the neutral grating). Chromatic annuli are more perceptually salient than low contrast sine gratings. As a result of this difference in saliency, the time point at which a switch in ocular dominance occurred was primarily driven by the time point at which the chromatic annuli broke through suppression. This is crucial, since the experimental manipulation was tied to the color of the annulus. Switches in ocular dominance likely initiated at the location of the salient stimulus (Paffen, Naber, & Verstraten, 2008; Stuit, Verstraten, & Paffen, 2010) and then spread over the initially suppressed stimulus (Kaufman, 1963) throughout the rest of the ipsi-ocular percept (Ooi & He, 1999; Zhang, Jiang, & He, 2012). As such, faster breakthrough of the chromatic annulus resulted in faster breakthrough of the sine grating, eventually allowing observers to report its orientation. Considering that, in the present case, there was no difference in post-suppression effects (Experiment 1, monocular control condition), the difference in response times between CS+ and CS− trials reflected a difference in suppression durations.

Recent studies using a binocular rivalry task showed that monetary reward engenders an increase in dominance duration for the rewarded percept (Marx & Einhäuser, 2015; Wilbertz, van Slooten, & Sterzer, 2014) whereas monetary punishment engenders a decrease in dominance durations for the punished percept (Wilbertz et al., 2014). This latter finding seems at odds with the present data. In their paradigm, the act of perceiving the punished percept itself resulted in a monetary loss for the participant. In the present study, however, the CS+ stimulus signaled a potential threat. Its detection is therefore beneficial from a behavioral point of view, as detecting threat allows for selecting appropriate behavior. Taken together, our findings and those of Wilbertz and colleagues show that negative valence does not necessarily lead to faster switches in ocular dominance. Rather, visual input associated with negative valence selectively gains preferential access to awareness when it serves an adaptive function.

One possible account for the present findings is that the association of visual input with threat increases its salience, which leads to faster release from suppression. Considering that interocular competition is biased towards stimuli of higher contrast (Brascamp, Van Ee, Noest, Jacobs, & van den Berg, 2006; Levelt, 1965), a stimulus that is of higher salience, although equal in contrast, is likely to be favored in interocular competition as well (e.g., Gayet, Brascamp, Van der Stigchel, & Paffen, 2015). This idea finds some substantiation in the strikingly similar results elicited by fear conditioning (Experiment 1) and by manipulation of the luminance contrast (Experiment 2) in the present study. An increase in salience could also explain the related findings that CS+ stimuli attract attention (Armony & Dolan, 2002; Schmidt et al., 2015a) and eye movements (Mulckhuyse et al., 2013; Schmidt et al., 2015b), as well as the finding that CS+ stimuli can be more readily detected than CS− stimuli (Padmala & Pessoa, 2008). Accordingly, imaging studies have reported stronger BOLD activity in the visual cortex for CS+ compared to CS− stimuli (Lim, Padmala, & Pessoa, 2009; Padmala & Pessoa, 2008).

The amygdala might play a role in modulating the cortical response to hitherto invisible threatening stimuli. A number of studies successfully detected amygdala activation of interocularly suppressed emotional stimuli (Jiang & He, 2006; Pasley, Mayes, & Schultz, 2004; Williams et al., 2004). Back-projections from the amygdala to the visual cortex, which have been directly observed in primates (Amaral, Behniea, & Kelly, 2003; Amaral & Price, 1984), could then allow for mediating the cortical response to threat stimuli (Pessoa & Adolphs, 2010). In line with this idea, amygdala activation has been shown to mediate the differential response to CS+ compared to CS− stimuli in the visual cortex (Lim et al., 2009). Framing our findings within this literature leads us to tentatively suggest that visual input signaling threat is initially detected non-consciously, as a result of which the cortical activation elicited by this visual input is enhanced. This enhanced cortical activation could potentiate the preferential access to awareness of that part of the visual world that signals threat.

7. Conclusion

Our results demonstrate for the first time that visual input that signals threat is not only privileged by the visual system such as to elicit stronger behavioral and neural effects, but that the very content of our consciousness is more likely to be comprised of visual information that signals threat. Considering that our experimental manipulation of threat affected the time taken to breach the threshold of awareness, we propose that threat signals were extracted from visual input *before* they reached awareness.

Author contributions

All authors developed the study concept and contributed to the study design. Programming, testing, data collection and data analyses were performed by S. Gayet. Data interpretation and writing of the manuscript were performed by S. Gayet and critical revisions were provided by all co-authors. All authors approved the final version of the manuscript.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2016.01.009.

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