Original Article

Beware the serpent: the advantage of ecologically-relevant stimuli in accessing visual awareness

Nuno Gomes [a,b], Samuel Silva [c], Carlos F. Silva [d], Sandra C. Soares [b,d,e,*]

[a] Portuguese Catholic University, Institute of Health Siences, Lisbon, Portugal
[b] William James Center for Research, ISPA-Instituto Universitário, Lisbon, Portugal
[c] Department of Electronics, Telecommunication and Informatics (DETI)/Institute of Electronics and Informatics Engineering (IEETA), University of Aveiro, Portugal
[d] CINTESIS.UA, Department of Education and Psychology, University of Aveiro, Aveiro, Portugal
[e] Department of Clinical Neuroscience, Division for Psychology, Karolinska Institutet, Sweden

ARTICLE INFO

ABSTRACT

Snakes and spiders constitute fear-relevant stimuli for humans, as many species have deleterious and even fatal effects. However, snakes provoked an older and thus stronger evolutionary pressure than spiders, shaping the vision of earliest primates toward preferential visual processing, mainly in the most complex perceptual conditions. To the best of our knowledge, no study has yet directly assessed the role of ecologically-relevant stimuli in preferentially accessing visual awareness. Using continuous flash suppression (CFS), the present study assessed the role of evolutionary pressure in gaining a preferential access to visual awareness. For this purpose, we measured the time needed for three types of stimuli - snakes, spiders (matched with snakes for rated fear levels, but for which an influence on humans but not other primates is well grounded) and birds - to break the suppression and enter visual awareness in two different suppression intensity conditions. The results showed that in the less demanding awareness access condition (stimuli presented to the participants' dominant eye) both evolutionarily relevant stimuli (snakes and spiders) showed a faster entry into visual awareness than birds, whereas in the most demanding awareness access condition (stimuli presented to the participants' non-dominant eye) only snakes showed this privileged access. Our data suggest that the privileged unconscious processing of snakes in the most complex perceptual conditions extends to visual awareness, corroborating the proposed influence of snakes in primate visual evolution.

© 2016 Elsevier Inc. All rights reserved.

1. Introduction

Evolution has equipped humans with a readiness to associate fear with situations that threatened the survival of their ancestors, with potentially deadly predators being a prime example. According to the Snake Detection Theory (SDT; Isbell, 2009) snakes may represent an archetypal fear stimulus. The SDT posits that primates (including humans) have been shaped, by evolutionary arms races, to fear and avoid snakes over evolutionary time (starting about 90–80 million years ago). Isbell (2006, 2009, for in-depth reviews) argues that the selection pressures posed by snakes, as well as the common fear of snakes in humans (Agras, Sylvester, & Oliveau, 1969) and in other primates (Mineka, Keir, & Price, 1980), have favored the origin of primates via changes in the visual system that enabled them to detect and avoid dangerous snakes. Accordingly, several recent studies have provided neurobehavioral evidence for a preferential snake processing in primates. Le et al. (2013), for instance, have shown that neurons in the medial and dorsolateral pulvinar of Japanese monkeys (Macaca fuscata) exhibit faster and stronger responses to snake images (compared with images of faces, hands of monkeys, or simple geometric shapes). In a further study with macaques, Le et al. (2016) found that snakes, again compared with images of faces and hands of monkeys, elicited earlier gamma oscillations (involved in feedforward visual information processing), in macaque pulvinar neurons, confirming that primates can detect snakes very rapidly. Preferential processing of snakes, compared to other stimuli, such as flowers, mushrooms, and other animal stimuli, has also been shown in several visual search tasks in rhesus monkeys (Shibasaki & Kawai, 2009), human children (LoBue & DeLoache, 2008; LoBue, Rakison, & DeLoache, 2010; Penkunas & Coss, 2013a, 2013b; Yorzinski, Penkunas, Platt, & Coss, 2014) and human adults (Öhman, Flykt, & Esteves, 2001; Soares & Esteves, 2013; Soares, Lindström, Esteves & Öhman, 2014; Soares, Esteves, Lundqvist & Öhman, 2009; Soares, 2012).

This neurobehavioral evidence with humans and monkeys has provided support for the notion that the undeniable need for an effective predatory defense system tailored a fear module – an independent behavioral, psychophysiological and neural system – that is relatively encapsulated from more advanced human cognition in order to foster

* Corresponding author. University of Aveiro, Department of Education and Psychology, Campus Universitário de Santiago, 3810-193, Aveiro, Portugal.
E-mail address: sandra.soares@ua.pt (S.C. Soares).

a successful development of the defense systems (see Öhman & Mineka, 2001). Although there is evidence that the fear module is selectively sensitive and automatically activated by evolutionary-relevant fear stimuli, the results from most of these studies preclude a direct test of the SDT, since no equivalent animal fear stimuli with distinct evolutionary baggage have been considered for comparison. More recently, however, Soares and her colleagues (Soares, 2012; Soares, Esteves, Lundqvist and Öhman, 2009; Soares & Esteves, 2013; Soares, Lindström, Esteves and Öhman, 2014) proposed spiders as the ideal candidate for humans, based on the premise, derived from the SDT, that selection has favored perceptual abilities to detect snakes more strongly than spiders (Isbell, 2009). Spiders attack other spiders and insects (Nyffeler, 1999) and, unlike poisonous snakes, spiders' poison did not evolve to be effective against mammals (Gerdes, Uhl, & Alpers, 2009). Moreover, unlike snakes, that continue to pose a threat to human life even today (Kasturiratne et al., 2008), only a small amount of spiders have a direct contact with humans and only a few are considered as a cause of morbidity or mortality (e.g., Steen, Carbonaro, & Schwartz, 2004). Hence, the perceptual abilities to detect camouflaged snakes have been more consistently selected for among serpents than among arachnids, making the genes promoting defense against snakes more prominent among the former than the latter (Isbell, 2009). Therefore, spiders are the ideal comparison stimuli to test the SDT, because they are also fear-relevant for humans, compared to snakes, but have a distinct evolutionary baggage. Moreover, snake and spider stimuli are matched for fear levels in humans (Lang, Bradley, & Cuthbert, 2005) and are both highly frequent objects of phobias (e.g., Agras et al., 1969). Following this premise, a growing body of behavioral (e.g., faster detection in visual search settings) and electrophysiological data (maximal amplitudes in specific early attention-related brain potentials; P1 and EPN) has now provided more direct evidence in favor of snakes' preferential processing, compared to spiders and innocuous animal stimuli (other reptiles, insects, birds, and slugs) (Hongshen, Kenta, & Nobuyuki, 2014; Soares, Kessel, Hernández-Lorca, García-Rubio, Rodrigues, Gomes, Carretié, submitted; Van Strien, Eijlers, Franken, & Huijding, 2014; Van Strien, Franken, & Huijding, 2014). More importantly, and conforming to the predictions of the SDT (Isbell, 2009), snake preferential processing has been observed particularly under conditions that may have been critical for survival, such as those involved in taxing visual conditions, such as peripheral visual field (Soares, Lindström, Esteves and Öhman, 2014), brief exposure durations (Soares & Esteves, 2013; Soares, Lindström, Esteves and Öhman, 2014), and a more cluttered environment (Soares, 2012; Soares & Esteves, 2013; Soares, Esteves, Lundqvist and Öhman, 2009; Soares, Lindström, Esteves and Öhman, 2014).

As proposed by Öhman and Mineka (2001), the rapid and efficient processing of evolutionary-relevant stimuli by the fear module may occur without the need for conscious processing before a response is elicited, most likely due to a dedicated neural circuitry, centered in the amygdala, that bypasses the visual cortex (e.g., Phelps & LeDoux, 2005; but see Pessoa & Adolphs, 2010). Although some studies have shown that such stimuli are processed preferentially outside of awareness, researchers were targeting the neurobehavioral responses of phobic participants, with no interest in showing dissociations between snake and spider stimuli (Carlsson et al., 2004; Öhman & Soares, 1994). Moreover, the authors have mainly used the backward masking (BM) paradigm to render the stimuli under unconscious awareness for a limited time frame (<40 ms) (see Wiens, 2006), and without examining whether the fear stimuli hold an advantage in entering into visual awareness.

Recently, interest in how emotional (fear) stimuli are processed under unawareness has grown, partly due to the emergence of interocular suppression techniques, such as the continuous flash suppression (CFS; Tsuchiya & Koch, 2005). This technique allows stronger and more time enduring states of unawareness (around ten times longer than BM) due to the suppression of static images by dynamic noise. Several studies have demonstrated that threatening stimuli, such as fearful faces (Stein, Seymour, Hebart, & Sterzer, 2014; Sterzer, Hilgenfeldt, Freudenberg, Bermpohl, & Adli, 2011; Tsuchiya, Moradi, Felsen, & Yamazaki, 2009; Yang, Zald, & Blake, 2007), faces with a direct gaze (Stein, Senju, Peelen, & Sterzer, 2011), angry body postures (Zhan, Hortensius, & De Gelder, 2015), and spiders (Schmack, Burk, Haynes, & Sterzer, 2015), emerge faster into awareness (breaking-CFS; Jiang, Costello, & He, 2007) than neutral stimuli. In this context, it is worth noting that these previous studies with CFS showing that threat-related stimuli gain a preferential access to visual awareness, have mostly considered social stimuli, i.e., differences in facial expression and bodily posture. However, as we have discussed above, ecological stimuli are also important. To the best of our knowledge no study has yet directly investigated the role of ecologically relevant fear stimuli in accessing awareness, comparing stimuli with and without such relevance. Although Schmack et al. (2015) have used spiders, the authors were only interested in studying the phobic characteristics of the stimulus, thus not attending to their evolutionary relevance. Accordingly, studies using other methodologies aiming at testing the access to visual awareness, such as change blindness and intentional blindness (for a review see Jensen, Yao, Street, & Simons, 2011), have evidenced that spiders are detected, located, and identified by a higher percentage of observers, both by participants with a specific phobia to the stimulus (Peira, Golkar, Larsson, & Wiens, 2010), and by participants with no such phobia (Mayer, Muris, Vogel, Nojoredjo, & Merckelbach, 2006; New & German, 2015;)). However, and as in the study by Schmack et al. (2015), none of these studies were interested in studying the role of the evolutionary relevance of the stimulus in entering visual awareness.

In the present study, we used CFS to investigate whether snakes overcame suppression and entered into awareness faster than spiders (compared to birds, an innocuous animal stimulus) in humans. Based on previous results showing preferential processing of evolutionarily relevant stimuli by the fear module, the first prediction of this study was that both snakes and spiders (when compared with birds) would have an advantage in entering into visual awareness (reflected in faster reaction times, RTs). Furthermore, and since no study has yet directly investigated the role of ecological stimuli in gaining preferential access to visual awareness, as mentioned earlier, we directly compared two stimuli with distinctly different evolutionary relevance for primates - snakes and spiders. Inspired by the SDT, (Isbell, 2009) and based on previous findings showing a facilitated processing of snakes (compared to spiders and neutral stimulus) under the most perceptually demanding conditions (e.g., Soares, Lindström, Esteves and Öhman, 2014) we considered, as our second prediction, that snakes would have an advantage in entering into awareness (reflected in faster RTs), compared to spiders (and innocuous animals, birds) in the most complex perceptual condition. In order to create two distinct perceptual complexity conditions during CFS, we divided participants based on their ocular dominance. The concept of ocular dominance (see Porac & Coren, 1976) refers to an evident monocular processing preference when the images viewed by the two eyes cannot be merged, such as in a dichotic stimulation condition (Valle-Inclán, Blanco, Soto, & Leirós, 2008). Data from studies that use binocular rivalry paradigms (also an interocular suppression technique) have shown that a stimulus presented to the dominant eye (assessed with sight dominance tests, such as Miles' test; see Miles, 1930) was visible for longer periods and was detected with higher accuracy than a stimulus presented to the non-dominant eye (e.g., Handa et al., 2004; Valle-Inclán et al., 2008). These data suggest a preference for processing stimuli when these are presented to the dominant eye over stimuli presented to the non-dominant eye. Therefore, during CFS, presenting the stimulus to the dominant eye or to the non-dominant eye of the participant may represent different conditions of suppression, with the latter being a more demanding stimulus detection condition. Thus, we predict that snakes will have an advantage in entering into visual awareness (reflected in faster RTs) in the most

demanding suppression condition (i.e., when stimuli are presented to the non-dominant eye) compared to spiders, for which evolutionary pressures were weaker (and innocuous animals, birds) (see Soares, Lindström, Esteves and Öhman, 2014). However, in the less demanding suppression condition (i.e., when stimuli are presented to the dominant eye), although we expect both snakes and spiders to have an advantage in entering into awareness (when compared with birds), no differences are expected between the two, as they are both fear-relevant stimuli for humans (e.g., Agras et al., 1969).

2. Methods

2.1. Participants

Sixty-one university students (forty-six women), aged between 17 and 42 (M = 21.64, SD = 4.16), participated voluntarily in the experiment after informed consent. Participants were screened for ocular dominance, revealing 32 participants with right dominance (23 women), aged 18 to 35 (M = 22.03; SD = 3.90), and 29 participants with left dominance (22 women), aged 17 to 42 (M = 21.21, SD = 4.45). All participants reported normal, or corrected to normal eyesight, no psychiatric medication intake, and no registered or observed symptoms of mental illness.

The study was approved by the local ethics committee. Moreover, the standards of the American Psychological Association and the guidelines of the Declaration of Helsinki were followed.

2.2. Stimuli

Stimuli encompassed 10 images of snakes, 10 images of spiders and 10 images of birds (see Fig. 1 for an illustration). For snakes and spiders, grayscale images were chosen from those used in Soares, Lindström, Esteves and Öhman (2014), Experiment 4). The bird images were selected from the Internet and converted to grayscale.

To rule out the role of the low level features of the stimuli on the results, spatial frequency energy across stimuli was computed (Soares, Lindström, Esteves and Öhman, 2014) along with the mean stimulus intensity (luminance) (Peli, 1990). Separate one-way ANOVAs for spatial frequency bands and luminance revealed no statistically significant differences (p > 0.05 in all cases) (Table 1).

Sixty-five volunteer university students (44 women), aged 18 to 48 (M = 21.20; SD = 4.09) took part in a pilot study to validate the stimuli to be used in the experimental task. These participants were asked to rate the 30 images, using the valence and arousal scales of the Self-Assessment Manikin (SAM) (Lang, Bradley, & Cuthbert, 1997). The results of the one way ANOVAs showed statistically significant effects in both valence [F(2, 128) = 129.48, p < .0001, η2p = .67] and arousal [F(2, 128) = 67.89, p < .0001, η2p = .52]. Bonferroni corrected post-hoc comparisons showed that both spiders and snakes were rated as more unpleasant and arousing than birds and that spiders were rated as more unpleasant and arousing than snakes (p < .01) (Table 1).

2.3. CFS masks

For building CFS, several Mondrian patterns were generated, composed of randomly arranged greyscale circles with diameters between 0.39° and 1.4°, and animated at 10 Hz. In order to enable CFS using "red-blue anaglyph glasses" (e.g., Almeida, Mahon, & Caramazza, 2010; Almeida, Mahon, Nakayama, & Caramazza, 2008; Almeida, Pajtas, Mahon, Nakayama, & Caramazza, 2013; Almeida et al., 2014; Kaunitz et al., 2011; Troiani, Price, & Schultz, 2012) the stimuli were presented using the blue RGB channel and the CFS masks using the red RGB channel. Therefore, even though the stimulus and masks overlapped, each eye of the participant was only able to see the part of the experiment shown in the same color as the correspondent lens of the "red-blue anaglyph glasses". In this case, the stimuli were always presented to the right eye while the mask was always shown to the left eye of the participant.

2.4. Display

Each participant was presented with an 8°×8° frame with a 0.5° border presenting a white noise pattern inside of which the mask and the stimulus overlapped. The stimuli were presented in one of the frame quadrants, centered at a horizontal and vertical distance of 1.9 degrees relative to a white fixation cross located at the center of the frame. All stimuli were presented randomly, appearing twice in each quadrant (see Fig. 2 for an illustration).

In some studies with facial stimuli (e.g., Stein et al., 2014), the authors used the mean luminance values of the images as the frame background and their procedure was meant to make the face image blend with the frame to avoid a detection by quadrant contrast. Since we included images of a different nature, we identified two main challenges: 1) while the face images in the studies with facial stimuli (e.g. Stein et al., 2014) were trimmed to occupy the whole area, our images necessarily have a distinct background; and 2) the face images have regions that stand out, for their different luminance, in the eyes and mouth, while our images are more uniform. Considering these differences, we could not set the background to the mean luminance since it would make detecting the images very difficult, as confirmed by preliminary experiments. Therefore, we followed a slightly different procedure: we empirically defined a fixed background value, set at 115, considering that it should be close to the mean luminance of the images, but slightly lower to allow better detection. This procedure was applied consistently to all stimuli.

Stimuli presentation and data collection were performed on computer with a Dell Professional P2212H monitor 21.5-inch LED VGA (1920x1080) using a custom software developed for this experiment.

2.5. Procedure

After evaluating ocular dominance using the Miles's test (Miles, 1930), the participant's position was adjusted to ensure that the head was 50 cm away from the screen center. Each trial (see Fig. 3 for an
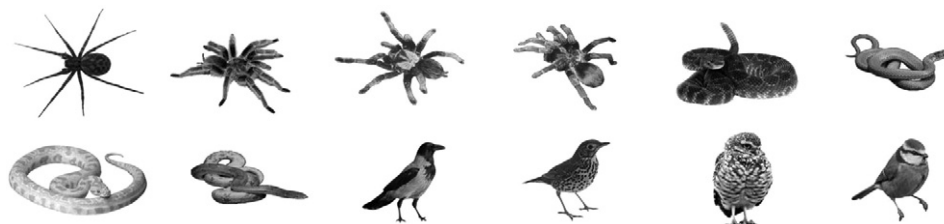

Fig. 1. Four examples of each stimuli category (snakes, spiders, birds) used in the experiment.

Table 1
Means and standard deviations (in parenthesis) of: (i) spatial frequency bands (ii) luminosity, and (iii) subjective ratings of the stimuli.

	Spider		Bird		Snake	
Spatial frequency bands						
768–384 (cpp)	$9.36*10^1$	$(3.41*10^1)$	$9.72*10^1$	$(5.44*10^1)$	$9.64*10^1$	$(4.26*10^1)$
384–192 (cpp)	$9.03*10^2$	$(1.43*10^2)$	$7.46*10^2$	$(3.12*10^2)$	$8.12*10^2$	$(2.19*10^2)$
192–96 (cpp)	$6.65*10^3$	$(1.34*10^3)$	$5.15*10^3$	$(1.83*10^3)$	$5.22*10^3$	$(1.36*10^3)$
96–48 (cpp)	$4.33*10^4$	$(1.17*10^4)$	$3.50*10^4$	$(0.98*10^4)$	$3.42*10^4$	$(0.95*10^4)$
48–24 (cpp)	$2.73*10^5$	$(0.58*10^5)$	$2.24*10^5$	$(0.54*10^5)$	$2.27*10^5$	$(0.75*10^5)$
24–12 (cpp)	$1.32*10^6$	$(0.28*10^6)$	$1.40*10^6$	$(0.36*10^6)$	$1.46*10^6$	$(0.59*10^6)$
12–6 (cpp)	$6.29*10^6$	$(1.55*10^6)$	$7.28*10^6$	$(2.60*10^6)$	$8.38*10^6$	$(3.33*10^6)$
6–3 (cpp)	$2.52*10^7$	$(0.95*10^7)$	$4.66*10^7$	$(1.05*10^7)$	$3.25*10^7$	$(3.33*10^7)$
Residuals (cpp)	$3.70*10^9$	$(0.09*10^9)$	$3.67*10^9$	$(0.08*10^9)$	$3.58*10^9$	$(2.37*10^9)$
Luminosity						
(0 = black to 255 = white)	235	(4)	234	(4)	231	(9)
Subjective ratings of stimuli						
Valence (1 = negative to 9 = positive)	2.87	(1.40)	6.57	(1.45)	3.48	(1.53)
Arousal (1 = calming to 9 = arousing)	5.34	(2.24)	2.74	(1.62)	5.21	(2.12)

Note: Luminosity corresponds to the average luminosity of each picture.
Spatial frequency was measured as the energy in eight frequency bands, expressed in cycles per picture (cpp), plus residuals (size of images was 1024×768 pixels in all cases).

illustration) started with a 1 s presentation of a blank frame with the white fixation cross only; next, the stimulus was introduced, in one of the four quadrants, by ramping up its contrast over 1.1 s; during this ramping, CFS masks were shown at 10 Hz. After 1.1 s, CFS mask contrast was ramped down over a period of 4 s. Trials ended with the participant's response or after 7 s.

To achieve an objective measure of perceptual awareness, we considered a forced choice paradigm (e.g., Stein et al., 2014; Yang et al., 2007). Participants were instructed to identify, as quickly and accurately as possible, in which quadrant a stimulus or any part of a stimulus became visible. This was accomplished by pressing one of four keys on a QWERTY keyboard corresponding to the four quadrants ("keys 'F' and 'V', with their left hand, for the 2nd and 3rd quadrants, and keys 'J' and 'N', with their right hand, for the 1st and 4th), and the response times were recorded.

The experiment started with a training session consisting of 30 trials randomly selected from the full trial set for the experiment, followed by the main experiment, consisting of 240 trials (30 stimuli × 4 quadrants × 2 repetitions), with three mandatory breaks (one every 60 trials). The average total duration of the experimental procedure was 45 min.

2.6. Statistical analysis

Trials with no response or incorrect responses (<10%) were excluded from the data analyses. The mean reaction times were
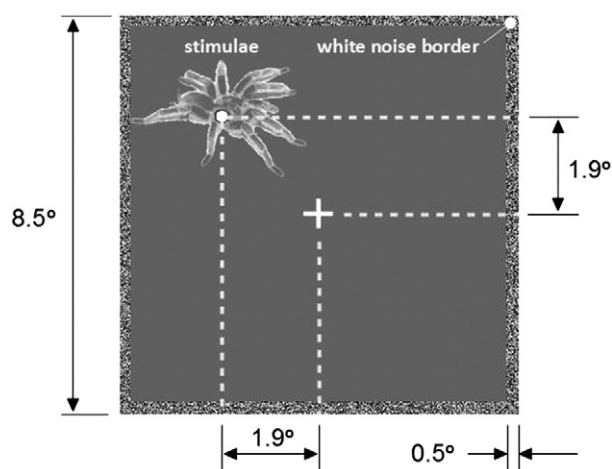

Fig. 2. Schematic example of the stimuli presentation. Participants were presented with an 8°×8° frame with a 0.5° border presenting a white noise pattern. The stimuli were presented in one of the frame quadrants, centered at a horizontal and vertical distance of 1.9 degrees relative to a white fixation cross located at the center of the frame.

compared in a mixed 3×2 ANOVA factorial design with the animal category (spider, snake, bird) as a within-participants factor and the ocular dominance (right dominance corresponding the less demanding suppression condition and left dominance corresponding to the most demanding suppression condition) as a between-participants factor.

For the repeated measures effect we used the Greenhouse–Geisser correction to correct the degrees of freedom. We performed post-hoc comparisons, using the Bonferroni correction procedure, to determine the significance of pairwise contrasts.

As a measure of effect size of ANOVAs, we reported the partial eta square ($\eta 2p$).

3. Results

Conforming to our first prediction, the results showed a significant main effect of animal stimuli [$F(2, 118) = 24.43$, $p < 0.001$, $\eta 2p = 0.29$], with snakes and spiders ($M = 3927.50$ ms; $SD = 982.70$, and $M = 3918.58$ ms; $SD = 1022.98$, respectively) showing faster access to visual awareness than birds ($M = 4099.46$ ms; $SD = 1006.65$), as confirmed by Bonferroni post-hoc comparisons ($p < 0.001$). No statistically significant differences were found between snakes and spiders ($p = 1.000$).

The results also showed a significant interaction between the animal stimuli and ocular dominance [$F(2, 118) = 4.48$, $p < 0.05$, $\eta 2p = 0.07$]. Again conforming to our prediction, the results showed that when participants were presented with the stimuli in their dominant eye, snakes and spiders ($M = 3750.14$ ms; $SD = 983.22$, and $M = 3706.01$ ms; $SD = 994.76$, respectively) accessed visual awareness faster than birds ($M = 3968.11$ ms $SD = 1027.69$), as confirmed by Bonferroni post-hoc comparisons ($p < 0.001$). As predicted, no significant differences were found between snakes and spiders in this condition ($p = 0.816$). Importantly, however, in the non-dominant eye group, snakes ($M = 4123.21$ ms; $SD = 960.94$) showed faster access to visual awareness than birds ($M = 4244.40$ ms $SD = 980.14$), as shown by Bonferroni post-hoc comparisons ($p < 0.01$). No statistically significant differences were found between snakes and spiders ($p = 1.000$) or between spiders and birds ($p = 0.181$) for this condition (see Fig. 4).

No significant main effect of ocular dominance was revealed [$F(1, 59) = 2.09$, $p = 0.154$, $\eta 2p = 0.03$].

4. Discussion

In the present study we assessed the average reaction times for snakes and spiders (stimuli with different histories as dangerous stimuli to primates) in entering into awareness (compared to an innocuous animal stimulus, birds), across two different suppression conditions. Confirming our first prediction, the results showed an advantage of
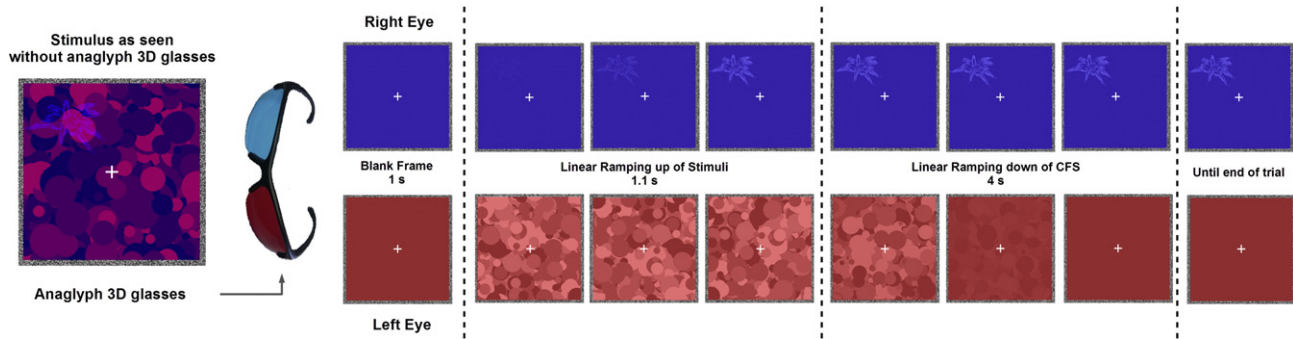
Fig. 3. Schematic example of a trial. The stimuli were gradually introduced to the right eye, while CFS masks (Mondrian-like pattern blinking at 10 Hz) were presented to the left eye. Participants identified, as quickly as possible, the quadrant in which the stimulus became visible.

emotional stimuli in general (snakes and spiders vs birds), corroborating the evidence that emotional stimuli (e.g., fearful faces) gain preferential access to visual awareness during CFS (Stein et al., 2011, 2014; Sterzer et al., 2011; Tsuchiya et al., 2009; Yang et al., 2007; Zhan et al., 2015). Our results also extend recent data obtained by Schmack et al. (2015), showing that the advantage of emotional stimuli in entering into awareness is also observed for ecological stimuli, such as spiders. However, in contrast to the aim of the current study, Schmack et al. (2015) were only interested in studying individual differences in spider fear, as previously mentioned, thus neglecting the role of other evolutionary-relevant selective pressures in this advantage.

Our results also confirmed the second prediction, while showing differences between snakes and spiders (compared to birds) in gained preferential access to awareness depending on the level of suppression. More specifically, when the stimulus was presented to the participant's dominant eye (the less demanding suppression condition), the two evolutionarily fear-relevant stimuli (snakes and spiders) showed faster access to awareness than birds. However, when the stimulus was presented to the participant's non-dominant eye (the more demanding suppression condition), only snakes gained preferential access to visual awareness (compared to birds). These data constitute the first direct evidence for the role of ecological stimuli in gaining preferential access to visual awareness, consistent with the proposed privileged role of snakes in primate visual evolution (Isbell, 2009). Following the SDT (Isbell, 2009), the pressure exerted by snakes resulted in adjustments to the mammalian visual system, thus resulting in the evolution of primates with a specialized vision that would enable a better detection of this stimulus (as an anti-predator measure), even in highly taxing perceptual conditions, in which the detection of other classes of stimuli is difficult. Confirming this notion, the results of the present study showed that the snake advantage in entering into awareness was particularly evident under the more demanding awareness access condition (i.e., when the stimulus was present to the participant's non-dominant eye). Although the results did not show a significant main effect of ocular dominance, we did obtain a significant interaction between the animal stimuli and ocular dominance showing a different pattern of response depending on the type of stimulus. These results are in agreement with the results obtained by Soares, Esteves, Lundqvist and Öhman (2009), Soares (2012), Soares & Esteves (2013), Soares, Lindström, Esteves and Öhman (2014)), that showed consistent snake preferential processing in taxing visual conditions (peripheral visual field, brief exposure durations, and a more cluttered environment). These behavioral studies have also been complemented with event-related potential (ERP) data, which suggest that snakes are better attention grabbers than spiders, being more efficient in attracting early visual attention, as reflected in larger early posterior negativity (EPN) amplitudes (Hongshen et al., 2014; Van Strien, Franken and Huijding, 2014; Van Strien et al., 2014). More recent ERP data also showed that snakes are better (compared with spiders and birds) at capturing early exogenous attention (evidenced by significantly larger amplitudes in P1) under high perceptual load conditions, indicating more dependence on bottom-up processes (Soares et al., submitted).

The more efficient capture of attention by snakes and its reliance on bottom-up processing, consistently shown in previous studies (e.g., Van Strien et al., 2014), may help explain the results of the present study. Some behavioral studies have shown that certain classes of stimuli (e.g., high arousal images or emotional facial expressions), suppressed by CFS, attract visual attention for their physical location (Jiang, Costello, Fang, Huang, & He, 2006; Rothkirch, Stein, Sekutowicz, & Sterzer, 2012; Xu, Zhang, & Geng, 2011; Yang et al., 2011). Moreover, voluntary allocation of attention to the localization of a suppressed stimulus seems to enhance the degree to which it is processed unconsciously, as confirmed by stronger visual aftereffects (Kanai, Tsuchiya, & Verstraten, 2006; Shin, Stolte, & Chong, 2009; Yang, Hong, & Blake, 2010), while the deliberate removal of attention leads to the disappearance of these visual aftereffects (Bahrami, Carmel, Walsh, Rees, & Lavie, 2008; Kaunitz, Fracasso, & Melcher, 2011; Shin et al., 2009). These data suggest that attention can modulate the degree of unconscious visual processing during CFS (for a review, see Yang, Brascamp, Kang, & Blake, 2014). In fact, fMRI studies confirm this effect in the processing of suppressed stimuli, showing that the allocation of attention modulates BOLD responses in V1 to the suppressed stimuli (Bahrami, Lavie, & Rees, 2007; Watanabe et al., 2011; Yuval-Greenberg & Heeger, 2013). We suggest that, in our more demanding awareness access condition, snakes captured attention to a larger degree. Therefore, its processing occurred with a stronger intensity (compared with the processing of spiders and birds), thus reducing the time needed to access visual awareness. Worthy of note is the fact that spiders were rated as more negatively valenced and arousing than snakes and low-level perceptual features (luminance and spatial frequency) were controlled for. Therefore, the effects observed in entering into awareness cannot be attributed to the conscious ratings nor to the low level features of the stimuli,
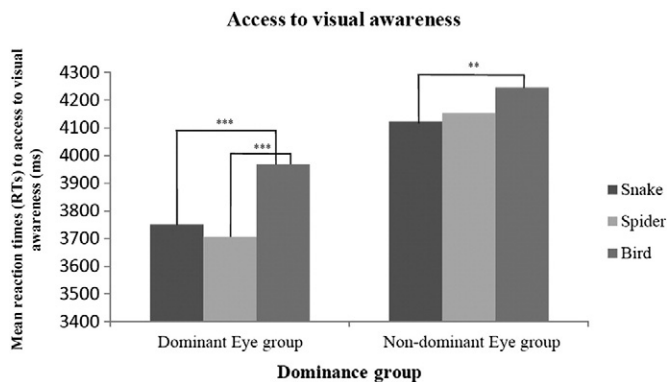

Fig. 4. Mean response times (RTs) to access visual awareness in milliseconds (ms) for the three animal stimuli in the two suppression conditions. ** indicates p < 0.01; *** indicates p < 0.001.

hence arguing in favor of an advantage of snakes in grabbing attention as the result of an evolutionary adaptation.

The effectiveness of snakes in grabbing early attention (Hongshen et al., 2014; Soares et al., submitted; Van Strien et al., 2014a, 2014b), regardless of available resources (Soares, Esteves, Lundqvist and Öhman, 2009; Soares, 2012; Soares & Esteves, 2013; Soares, Lindström, Esteves and Öhman, 2014), and the faster access to awareness shown in the current study, are probably associated with the existence of a subcortical pathway to the amygdala (LeDoux, 1996; Öhman, Carlsson, Lundqvist, & Ingvar, 2007; although this has been disputed, see Pessoa & Adolphs, 2010). This pathway is thought to include the superior colliculus and the pulvinar (Liddell et al., 2005; Morris, Öhman, & Dolan, 1999; Öhman et al., 2007). Its role is to perform a "quick and dirty" analysis (linked to magnocellular pathways; Vuilleumier, Armony, Driver, & Dolan, 2003) with the aim of identifying the threat (by orienting attention through the superior colliculus and the pulvinar; Arend et al., 2008; Knudsen, 2007), and quickly activating the defense mechanisms (via the superior colliculus and the amygdala; see Isbell, 2006; Tamietto & de Gelder, 2010) to avoid it (LeDoux, 1996; Öhman, 2005; Öhman et al., 2007). The action of this pathway also appears to interfere with perception. The efferent cortical connections (Emery & Amaral, 2000) between the amygdala and the ventral visual stream (responsible for visual awareness; (Goodale & Milner, 1992, 2004; Milner & Goodale, 1993, 2008) seem to enhance the visual processing for emotional stimuli in the ventral visual stream (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). This highlights the role of the amygdala (and probably the subcortical pathway to such stimuli, via the superior colliculus and pulvinar) in perceptual performance (for a review, see Öhman et al., 2007). Indeed, the superior colliculus and pulvinar have been associated with the processing of snakes in primates. Capuchin monkeys with bilateral lesions of the superior colliculus (compared to healthy monkeys) seem to lose the ability to process snakes as a threatening stimulus (Maior et al., 2011). Moreover, snakes appear to modulate pulvinar activity in monkeys (Le et al., 2013, 2016) and, in addition, monkeys with lesions in the amygdala (compared to healthy monkeys) show a reduced aversion to snakes (Kalin, Shelton, Davidson, & Anonymous, 2004; Kluver & Bucy, 1939; Machado, Kazama, & Bachevalier, 2009; Prather et al., 2001). Also, in humans, fMRI data show the activation of the superior colliculus, the pulvinar and the amygdala for true snake stimuli (vs. stimuli with snake shapes, such as cables) (Almeida, Soares, & Castelo-Branco, 2015). Finally, a study with a patient with a bilateral lesion of the amygdala evidenced that, after the lesion, the aversion to snakes was extinguished (Feinstein, Adolphs, Damasio, & Tranel, 2011). Together, these data argue in favor of the important role of these subcortical structures in processing snakes.

Several studies have shown that, during CFS, the superior colliculus, the pulvinar, and the amygdala are implicated in the processing of suppressed relevant stimuli (for a review, see Sterzer, Stein, Ludwig, Rothkirch, & Hesselmann, 2014). Interocular suppression techniques are known to reduce the processing throughout the geniculostriate pathway and to strongly suppress the activity in visual striate cortex (Lin & He, 2009). Thus, the action of a subcortical pathway and the amygdala are proposed as the explanation for the differentiated processing of these relevant stimuli during suppression (for a review, see Lin & He, 2009; but see Stein et al., 2014; Willenbockel, Lepore, Nguyen, Bouthillier, & Gosselin, 2012). The action of these structures most likely involve the allocation of attentional resources of the suppressed stimulus (see above), thus modulating the activity of V1 (e.g., Bahrami et al., 2007; Watanabe et al., 2011), as well as other parts in the ventral visual stream; Vuilleumier et al., 2004), and therefore gaining a preferential access to awareness. Indeed, neuroimaging studies (using interocular suppression techniques) have shown the activation of the amygdala for relevant stimuli (i.e., emotional faces) suppressed from awareness (Jiang & He, 2006; Pasley, Mayes, & Schultz, 2004; Troiani et al., 2012; Williams, Morris, McGlone, Abbott, & Mattingley, 2004; but see Schmack et al., 2015; Tsuchiya et al., 2009). Neuroimaging data have

also presented indirect evidence for the role of superior colliculus (Pasley et al., 2004) and the pulvinar (Troiani & Schultz, 2013; Troiani et al., 2012) in driving this information to the amygdala. However, a recent fMRI study found that the advantage in entering into visual awareness during CFS by spiders (compared to flowers), could be predicted by the activation of the orbitofrontal and the occipitotemporal cortex but not by the activation of the amygdala (Schmack et al., 2015), arguing against the role of this structure in the access to awareness during CFS. To our understanding, this is in agreement with our interpretation. Although this seems counter-intuitive, previous data have shown that spider processing, unlike snakes (which probably relies on magnocellular pathways, related with faster visual information with low acuity; see Leventhal, Rodieck, & Dreher, 1985; Schiller & Malpeli, 1978), appears to rely on high visual acuity information (see Soares, Lindström, Esteves and Öhman, 2014), which is linked to parvocellular pathways (Livingstone & Hubel, 1988). These pathways (unlike magnocellular pathways, which are associated with subcortical visual structures; see Schiller, Malpeli, & Schein, 1979) are known to primarily project to cortical areas (Merigan & Maunsell, 1993). Therefore, it is likely that the subcortical pathways are more involved in the processing of snakes than spiders, probably because snakes represented a more rooted evolutionary stimulus for primates. However, additional neuroimaging data using stimuli that represented different evolutionary pressures (as it is the case with snakes and spiders) are needed in order disentangle this question.

In addition to the previously argued, it is also important to mention the possible role of the koniocellular pathway in the privileged processing of snakes. According to Isbell (2006, 2009), the involvement of koniocellular pathways could be associated with the advantage of primates to process and detect snakes. Unlike the magnocellular pathways, which remain preserved throughout the different primate species, the koniocellular pathways seem to increase consistently throughout evolution depending on the coexistence with poisonous snakes. Actually, these visual pathways appear to strongly contribute to the fear system. These pathways constitute the largest retinal input for the superior colliculus and they are the only visual pathway known to connect this structure with the lateral geniculate nucleus (Casagrande, 1994), thus being strongly related to the superior colliculus–pulvinar connection, which has been deeply involved in the privileged processing snakes (see above). The koniocellular pathways, due to their connection with the superior colliculus, have also been implicated in attentional processes, arousal and eye movements (e.g., Casagrande & Xu, 2004). In addition, they appear to be involved in unconscious visual stimuli processing (e.g., in blindsight phenomena; see Vakalopoulos, 2005). The action of this type of visual pathways, during the CFS, could then provide an explanation for the results of the present study. A possible issue for future research would be to evaluate the role of this kind of pathways in the advantage of fear stimuli in the access to awareness.

Taken together, our findings show evidence that the evolutionary value of ecological stimuli (snakes and spiders) is associated with an advantage in entering into visual awareness in humans during CFS. While showing that an advantage of snakes (unlike spiders) remains throughout suppression conditions with different intensities, the results corroborate the assumptions derived from the SDT (Isbell, 2009), supporting the importance of snakes in the evolution of primate vision and showing the relevance of snakes in understanding threat detection mechanisms. Future studies should aim at replicating the findings of the present study using a within-subjects design, since in the present study, and in order to prevent fatigue, participants were only exposed to one condition of ocular dominance.

References

Agras, S., Sylvester, D., & Oliveau, D. (1969). The epidemiology of common fears and phobia. *Comprehensive Psychiatry*, *10*(2), 151–156. http://dx.doi.org/10.1016/0010-440X(69)90022-4.

Almeida, J., Mahon, B. Z., & Caramazza, A. (2010). The role of the dorsal visual processing stream in tool identification. *Psychological Science: A Journal of the American Psychological Society/APS*, 21(6), 772–778. http://dx.doi.org/10.1177/0956797610371343.

Almeida, J., Mahon, B. Z., Nakayama, K., & Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. *Proceedings of the National Academy of Sciences of the United States of America*, 105(39), 15214–15218. http://dx.doi.org/10.1073/pnas.0805867105.

Almeida, J., Mahon, B. Z., Zapater-Raberov, V., Dziuba, A., Cabaço, T., Marques, J. F., & Caramazza, A. (2014). Grasping with the eyes: The role of elongation in visual recognition of manipulable objects. *Cognitive, Affective & Behavioral Neuroscience*, 14(1), 319–335. http://dx.doi.org/10.3758/s13415-013-0208-0.

Almeida, J., Pajtas, P. E., Mahon, B. Z., Nakayama, K., & Caramazza, A. (2013). Affect of the unconscious: visually suppressed angry faces modulate our decisions. *Cognitive, Affective & Behavioral Neuroscience*, 13(1), 94–101. http://dx.doi.org/10.3758/s13415-012-0133-7.

Almeida, I., Soares, S. C., & Castelo-Branco, M. (2015). The distinct role of the amygdala, superior colliculus and pulvinar in processing of central and peripheral snakes. *PloS One*, 10(6), 1–21. http://dx.doi.org/10.1371/journal.pone.0129949.

Arend, I., Machado, L., Ward, R., McGrath, M., Ro, T., & Rafal, R. D. (2008). The role of the human pulvinar in visual attention and action: Evidence from temporal-order judgment, saccade decision, and antisaccade tasks. *Progress in Brain Research*. http://dx.doi.org/10.1016/S0079-6123(08)00669-9.

Bahrami, B., Carmel, D., Walsh, V., Rees, G., & Lavie, N. (2008). Unconscious orientation processing depends on perceptual load. *Journal of Vision*, 8(3), 12.1–1210. http://dx.doi.org/10.1167/8.3.12.

Bahrami, B., Lavie, N., & Rees, G. (2007). Attentional load modulates responses of human primary visual cortex to invisible stimuli. *Current Biology*, 17(6), 509–513. http://dx.doi.org/10.1016/j.cub.2007.01.070.

Carlsson, K., Petersson, K. M., Lundqvist, D., Karlsson, A., Ingvar, M., & Öhman, A. (2004). Fear and the amygdala: Manipulation of awareness generates differential cerebral responses to phobic and fear-relevant (but nonfeared) stimuli. *Emotion (Washington, D.C.)*, 4(4), 340–353. http://dx.doi.org/10.1037/1528–3542.4.4.340.

Casagrande, V. A. (1994). A third parallel visual pathway to primate area V1. *Trends in Neurosciences*. http://dx.doi.org/10.1016/0166-2236(94)90065-5.

Casagrande, V. A., & Xu, X. (2004). Parallel visual pathways: A comparative perspective. In L. Chalupa, & J. S. Werner (Eds.), *The visual neurosciences* (pp. 494–506). Cambridge, Massachusetts: MIT Press.

Emery, N. J., & Amaral, D. G. (2000). The role of the amygdala in primate social cognition. In R. D. Lane, & L. NAdel (Eds.), *Cognitive neuroscience of emotion* (pp. 156–191). New York: Oxford University Press.

Feinstein, J. S., Adolphs, R., Damasio, A., & Tranel, D. (2011). The human amygdala and the induction and experience of fear. *Current Biology*, 21(1), 34–38. http://dx.doi.org/10.1016/j.cub.2010.11.042.

Gerdes, A. B. M., Uhl, G., & Alpers, G. W. (2009). Spiders are special: Fear and disgust evoked by pictures of arthropods. *Evolution and Human Behavior*, 30(1), 66–73. http://dx.doi.org/10.1016/j.evolhumbehav.2008.08.005.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20–25. http://dx.doi.org/10.1016/0166-2236(92)90344-8.

Goodale, M. A., & Milner, A. D. (2004). *Sight unseen: an exploration of conscious and unconscious vision.* Oxford: Oxford University Press.

Handa, T., Mukuno, K., Uozato, H., Niida, T., Shoji, N., & Shimizu, K. (2004). Effects of dominant and nondominant eyes in binocular rivalry. *Optometry and Vision Science.*, 81(5), 377–383. http://dx.doi.org/10.1097/01.opx.0000135085.54136.65.

Hongshen, H., Kenta, K., & Nobuyuki, K. (2014). Spiders do not evoke greater early posterior negativity in the event-related potential as snakes. *Neuroreport*, 25(13), 1049–1053. http://dx.doi.org/10.1097/WNR.0000000000000227.

Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, 51, 1–35. http://dx.doi.org/10.1016/j.jhevol.2005.12.012.

Isbell, L. A. (2009). *The fruit, the tree, and the serpent.* Harvard University Press.

Jensen, M. S., Yao, R., Street, W. N., & Simons, D. J. (2011). Change blindness and inattentional blindness. *Wiley Interdisciplinary Reviews: Cognitive Science*, 2(5), 529–546. http://dx.doi.org/10.1002/wcs.130.

Jiang, Y., & He, S. (2006). Cortical responses to invisible faces: Dissociating subsystems for facial-information processing. *Current Biology*, 16(20), 2023–2029. http://dx.doi.org/10.1016/j.cub.2006.08.084.

Jiang, Y., Costello, P., Fang, F., Huang, M., & He, S. (2006). A gender- and sexual orientation-dependent spatial attentional effect of invisible images. *Proceedings of the National Academy of Sciences of the United States of America*, 103(45), 17048–17052. http://dx.doi.org/10.1073/pnas.0605678103.

Jiang, Y., Costello, P., & He, S. (2007). Processing of invisible stimuli. *Psychological Science : A Journal of the American Psychological Society / APS*, 18(4), 349–355. http://dx.doi.org/10.1111/j.1467-9280.2007.01902.x.

Kalin, N. H., Shelton, S. E., Davidson, R. J., & Anonymous (2004). The role of the central nucleus of the amygdala in mediating fear and anxiety in the primate. *Journal of Neuroscience*, 24(24), 5506–5515. http://dx.doi.org/10.1523/JNEUROSCI.0292-04.2004.

Kanai, R., Tsuchiya, N., & Verstraten, F. A. J. (2006). The scope and limits of top-down attention in unconscious visual processing. *Current Biology*, 16(23), 2332–2336. http://dx.doi.org/10.1016/j.cub.2006.10.001.

Kasturiratne, A., Wickremasinghe, A. R., de Silva, N., Gunawardena, N. K., Pathmeswaran, A., Premaratna, R., ... de Silva, H. J. (2008). The global burden of snakebite: a literature analysis and modelling based on regional estimates of envenoming and deaths. *PLoS Medicine*, 5(11), e218.

Kaunitz, L., Fracasso, A., & Melcher, D. (2011a). Unseen complex motion is modulated by attention and generates a visible aftereffect. *Journal of Vision*, 11(13), 10. http://dx.doi.org/10.1167/11.13.10.

Kaunitz, L. N., Kamienkowski, J. E., Olivetti, E., Murphy, B., Avesani, P., & Melcher, D. P. (2011b). Intercepting the first pass: Rapid categorization is suppressed for unseen stimuli. *Frontiers in Psychology*, 2(AUG). http://dx.doi.org/10.3389/fpsyg.2011.00198.

Kluver, H., & Bucy, P. (1939). Preliminary analysis of functions of the temporal lobes in monkeys. *Archives of Neurology & Psychiatry*, 42(6), 979–1000. http://dx.doi.org/10.3171/2013.4.JNS121829.

Knudsen, E. I. (2007). Fundamental components of attention. *Annual Review of Neuroscience*, 30, 57–78. http://dx.doi.org/10.1146/annurev.neuro.30.051606.094256.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). *International affective picture system (IAPS): Technical manual and affective ratings.* NIMH: Center for the Study of emotion and attention.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2005). *International affective picture system (IAPS): Instructions manual and affective ratings.* Technical report A-6, the center for research in psychophysiology, University of Florida.

Le, Q., Isbell, L. A., Matsumoto, J., Le, V. Q., Nishimaru, H., Hori, E., ... Nishijo, H. (2016). Snakes elicit earlier, and monkey faces, later, gamma oscillations in macaque pulvinar neurons. *Scientific Reports*, 6(February), 20595. http://dx.doi.org/10.1038/srep20595.

Le, Q., Isbell, L. A., Matsumoto, J., Nguyen, M., Hori, E., Maior, R. S., ... Nishijo, H. (2013). Pulvinar neurons reveal neurobiological evidence of past selection for rapid detection of snakes. *Proceedings of the National Academy of Sciences of the United States of America*, 110(47), 19000–19005. http://dx.doi.org/10.1073/pnas.1312648110.

LeDoux, J. (1996). *The emotional brain: the mysterious underpinnings of emotional life.* New York: Shuster Sa.

Leventhal, A. G., Rodieck, R. W., & Dreher, B. (1985). Central projections of cat retinal ganglion cells. *The Journal of Comparative Neurology*, 237(1985), 216–226. http://dx.doi.org/10.1002/cne.902370206.

Liddell, B. J., Brown, K. J., Kemp, A. H., Barton, M. J., Das, P., Peduto, A., ... Williams, L. M. (2005). A direct brainstem-amygdala-cortical "alarm" system for subliminal signals of fear. *NeuroImage*, 24(2005), 235–243. http://dx.doi.org/10.1016/j.neuroimage.2004.08.016.

Lin, Z., & He, S. (2009). Seeing the invisible: The scope and limits of unconscious processing in binocular rivalry. *Progress in Neurobiology*, 87(4), 195–211. http://dx.doi.org/10.1016/j.pneurobio.2008.09.002.

Livingstone, M., & Hubel, D. (1988). Segregation of depth: Form, anatomy, color, physiology, and movement, and perception. *Science. New Series*, 240(4853), 740–749. http://dx.doi.org/10.1126/science.3283936.

LoBue, V., & DeLoache, J. S. (2008). Detecting the snake in the grass. *Psychological Science*, 19(3), 284. http://dx.doi.org/10.1111/j.1467-9280.2008.02081.x.

LoBue, V., Rakison, D. H., & DeLoache, J. S. (2010). Threat perception across the life span: evidence for multiple converging pathways. *Current Directions in Psychological Science*, 19(6), 375–379. http://dx.doi.org/10.1177/0963721410388801.

Machado, C. J., Kazama, A. M., & Bachevalier, J. (2009). Impact of amygdala, orbital frontal, or hippocampal lesions on threat avoidance and emotional reactivity in nonhuman primates. *Emotion*, 9(2), 147–163. http://dx.doi.org/10.1037/a0014539.

Maior, R. S., Hori, E., Barros, M., Teixeira, D. S., Tavares, M. C. H., Ono, T., ... Tomaz, C. (2011). Superior colliculus lesions impair threat responsiveness in infant capuchin monkeys. *Neuroscience Letters*, 504(3), 257–260. http://dx.doi.org/10.1016/j.neulet.2011.09.042.

Mayer, B., Muris, P., Vogel, L., Nojoredjo, I., & Merckelbach, H. (2006). Fear-relevant change detection in spider-fearful and non-fearful participants. *Journal of Anxiety Disorders*, 20(4), 510–519. http://dx.doi.org/10.1016/j.janxdis.2005.05.001.

Merigan, W. H., & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, 16, 369–402. http://dx.doi.org/10.1146/annurev.ne.16.030193.002101.

Miles, W. R. (1930). Ocular dominance in human adults. *Journal of General Psychology*, 3, 412–430.

Milner, A. D., & Goodale, M. A. (1993). Visual pathways to perception and action. *Progress in Brain Research*, 95, 317–337.

Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, 46(3), 774–785. http://dx.doi.org/10.1016/j.neuropsychologia.2007.10.005.

Mineka, S., Keir, R., & Price, V. (1980). Fear of snakes in wild- and laboratory-reared rhesus monkeys (*Macaca mulatta*). *Animal Learning & Behavior*. http://dx.doi.org/10.3758/BF03197783.

Morris, J. S., Öhman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating "unseen" fear. *Proceedings of the National Academy of Sciences of the United States of America*, 96(February), 1680–1685. http://dx.doi.org/10.1073/pnas.96.4.1680.

New, J. J., & German, T. C. (2015). Spiders at the cocktail party: An ancestral threat that surmounts inattentional blindness. *Evolution and Human Behavior*, 36(3), 165–173. http://dx.doi.org/10.1016/j.evolhumbehav.2014.08.004.

Nyffeler, M. (1999). Prey selection of spiders in the field. *The Journal of Arachnology*, 27, 317–324. http://dx.doi.org/10.2307/3706003 (Table 4).

Öhman, A. (2005). The role of the amygdala in human fear: Automatic detection of threat. *Psychoneuroendocrinology*, 30, 953–958. http://dx.doi.org/10.1016/j.psyneuen.2005.03.019.

Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, 108(3), 483–522. http://dx.doi.org/10.1037/0033-295X.108.3.483.

Öhman, A., & Soares, J. J. F. (1994). "unconscious anxiety": Phobic responses to masked stimuli. *Journal of Abnormal Psychology*, 103(2), 231–240. http://dx.doi.org/10.1037/0021-843X.103.2.231.

Öhman, A., Carlsson, K., Lundqvist, D., & Ingvar, M. (2007). On the unconscious subcortical origin of human fear. *Physiology and Behavior*, 92, 180–185. http://dx.doi.org/10.1016/j.physbeh.2007.05.057.

Öhman, A., Flykt, A., & Esteves, F. (2001). Emotion drives attention: Detecting the snake in the grass. *Journal of Experimental Psychology. General*, *130*, 466–478. http://dx.doi.org/10.1037/0096-3445.130.3.466.

Pasley, B. N., Mayes, L. C., & Schultz, R. T. (2004). Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron*, *42*(1), 163–172. http://dx.doi.org/10.1016/S0896-6273(04)00155-2.

Peira, N., Golkar, A., Larsson, M., & Wiens, S. (2010). What you fear will appear: Detection of schematic spiders in spider fear. *Experimental Psychology*, *57*(6), 470–475. http://dx.doi.org/10.1027/1618-3169/a000058.

Peli, E. (1990). Contrast in complex images. *Journal of the Optical Society of America. A, Optics and Image Science*, *7*(10), 2032–2040 (Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/2231113).

Penkunas, M. J., & Coss, R. G. (2013a). A comparison of rural and urban Indian children's visual detection of threatening and nonthreatening animals. *Developmental Science*, *16*, 463–475. http://dx.doi.org/10.1111/desc.12043.

Penkunas, M. J., & Coss, R. G. (2013b). Rapid detection of visually provocative animals by preschool children and adults. *Journal of Experimental Child Psychology*, *114*(4), 522–536. http://dx.doi.org/10.1016/j.jecp.2012.10.001.

Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: From a "low road" to "many roads" of evaluating biological significance. *Nature Reviews Neuroscience*, *11*(11), 773–783. http://dx.doi.org/10.1038/nrn2920.

Phelps, E. A., & LeDoux, J. E. (2005). Contributions of the amygdala to emotion processing: From animal models to human behavior. *Neuron*. http://dx.doi.org/10.1016/j.neuron.2005.09.025.

Porac, C., & Coren, S. (1976). The dominant eye. *Psychological Bulletin*, *83*(5), 880–897. http://dx.doi.org/10.1097/00006324-192910000-00018.

Prather, M. D., Lavenex, P., Mauldin-Jourdain, M. L., Mason, W. A., Capitanio, J. P., Mendoza, S. P., & Amaral, D. G. (2001). Increased social fear and decreased fear of objects in monkeys with neonatal amygdala lesions. *Neuroscience*, *106*(4), 653–658. http://dx.doi.org/10.1016/S0306-4522(01)00445-6.

Rothkirch, M., Stein, T., Sekutowicz, M., & Sterzer, P. (2012). A direct oculomotor correlate of unconscious visual processing. *Current Biology*, *22*(13). http://dx.doi.org/10.1016/j.cub.2012.04.046.

Schiller, P. H., & Malpeli, J. G. (1978). Functional specificity of lateral geniculate nucleus laminae of the rhesus monkey. *Journal of Neurophysiology*, *41*(3), 788–797.

Schiller, P. H., Malpeli, J. G., & Schein, S. J. (1979). Composition of geniculostriate input ot superior colliculus of the rhesus monkey. *Journal of Neurophysiology*, *42*(4), 1124–1133 (Retrieved from http://jn.physiology.org/content/42/4/1124).

Schmack, K., Burk, J., Haynes, J. -D., & Sterzer, P. (2015). Predicting subjective affective salience from cortical responses to invisible object stimuli. *Cerebral Cortex*, 1–8. http://dx.doi.org/10.1093/cercor/bhv174.

Shibasaki, M., & Kawai, N. (2009). Rapid detection of snakes by Japanese monkeys (*Macaca fuscata*): an evolutionarily predisposed visual system. *Journal of Comparative Psychology*, *123*, 131–135. http://dx.doi.org/10.1037/a0015095.

Shin, K., Stolte, M., & Chong, S. C. (2009). The effect of spatial attention on invisible stimuli. *Attention, Perception, & Psychophysics*, *71*(7), 1507–1513. http://dx.doi.org/10.3758/App.71.7.1507.

Soares, S. C. (2012). The lurking snake in the grass: Interference of snake stimuli in visually taxing conditions. *Evolutionary Psychology*, *10*(2), 187–197.

Soares, S. C., & Esteves, F. (2013). A glimpse of fear: Fast detection of threatening targets in visual search with brief stimulus durations. *PsyCh Journal*, *2*(1), 11–16. http://dx.doi.org/10.1002/pchj.18.

Soares, S. C., Esteves, F., Lundqvist, D., & Öhman, A. (2009). Some animal specific fears are more specific than others: Evidence from attention and emotion measures. *Behaviour Research and Therapy*, *47*(12), 1032–1042. http://dx.doi.org/10.1016/j.brat.2009.07.022.

Soares, S. C., Kessel, D., Hernández-Lorca, M., García-Rubio, M. J., Rodrigues, P., Gomes, N., & Carretié, L. Deconstructing exogenous attention to fear: behavioral and electrophysiological correlates. (submitted).

Soares, S. C., Lindström, B., Esteves, F., & Öhman, A. (2014). The hidden snake in the grass: Superior detection of snakes in challenging attentional conditions. *PloS One*, *9*(12), e114724. http://dx.doi.org/10.1371/journal.pone.0114724.

Steen, C. J., Carbonaro, P. A., & Schwartz, R. A. (2004). Arthropods in dermatology. *Journal of the American Academy of Dermatology*, *50*(6), 819–842 l. http://dx.doi.org/10.1016/j.jaad.2003.12.019.

Stein, T., Senju, A., Peelen, M. V., & Sterzer, P. (2011). Eye contact facilitates awareness of faces during interocular suppression. *Cognition*, *119*(2), 307–311. http://dx.doi.org/10.1016/j.cognition.2011.01.008.

Stein, T., Seymour, K., Hebart, M. N., & Sterzer, P. (2014). Rapid fear detection relies on high spatial frequencies. *Psychological Science*, *25*, 566–574. http://dx.doi.org/10.1177/0956797613512509.

Sterzer, P., Hilgenfeldt, T., Freudenberg, P., Bermpohl, F., & Adli, M. (2011). Access of emotional information to visual awareness in patients with major depressive disorder. *Psychological Medicine*, *41*(8), 1615–1624. http://dx.doi.org/10.1017/S0033291710002540.

Sterzer, P., Stein, T., Ludwig, K., Rothkirch, M., & Hesselmann, G. (2014). Neural processing of visual information under interocular suppression: A critical review. *Frontiers in Psychology*, *5*(MAY), 1–12. http://dx.doi.org/10.3389/fpsyg.2014.00453.

Tamietto, M., & de Gelder, B. (2010). Neural bases of the non-conscious perception of emotional signals. *Nature Reviews. Neuroscience*, *11*(10), 697–709. http://dx.doi.org/10.1038/nrn2889.

Troiani, V., & Schultz, R. T. (2013). Amygdala, pulvinar, and inferior parietal cortex contribute to early processing of faces without awareness. *Frontiers in Human Neuroscience*, *7*(June), 241. http://dx.doi.org/10.3389/fnhum.2013.00241.

Troiani, V., Price, E. T., & Schultz, R. T. (2012). Unseen fearful faces promote amygdala guidance of attention. *Social Cognitive and Affective Neuroscience*, *9*(2), 133–140. http://dx.doi.org/10.1093/scan/nss116.

Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, *8*(8), 1096–1101 (Retrieved from http://dx.doi.org/10.1038/nn1500).

Tsuchiya, N., Moradi, F., Felsen, C., & Yamazaki, M. (2009). Intact rapid detection of fearful faces, *12*(10), 1224–1225. doi:10.1038/nn.2380.Intact

Vakalopoulos, C. (2005). A theory of blindsight - The anatomy of the unconscious: a proposal for the koniocellular projections and intralaminar thalamus. *Medical Hypotheses*, *65*(6), 1183–1190. http://dx.doi.org/10.1016/j.mehy.2005.05.039.

Valle-Inclán, F., Blanco, M. J., Soto, D., & Leirós, L. (2008). A new method to assess eye dominance. *Psicologica*, *29*(1), 55–64.

Van Strien, J. W., Eijlers, R., Franken, I. H. A., & Huijding, J. (2014a). Snake pictures draw more early attention than spider pictures in non-phobic women: Evidence from event-related brain potentials. *Biological Psychology*, *96*, 150–157. http://dx.doi.org/10.1016/j.biopsycho.2013.12.014.

Van Strien, J. W., Franken, I. H. A., & Huijding, J. (2014b). Testing the snake-detection hypothesis: Larger early posterior negativity in humans to pictures of snakes than to pictures of other reptiles, spiders and slugs. *Frontiers in Human Neuroscience*, *8*(September), 1–9. http://dx.doi.org/10.3389/fnhum.2014.00691.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience*, *6*(6), 624–631. http://dx.doi.org/10.1038/nn1057.

Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience*, *7*(11), 1271–1278. http://dx.doi.org/10.1038/nn1341.

Watanabe, M., Cheng, K., Murayama, Y., Ueno, K., Asamizuya, T., Tanaka, K., & Logothetis, N. (2011). Attention but not awareness modulates the BOLD signal in the human V1 during binocular suppression. *Science*, *334*(6057), 829–831. http://dx.doi.org/10.1126/science.1203161.

Wiens, S. (2006). Current concerns in visual masking. *Emotion (Washington, D.C.)*, *6*(4), 675–680. http://dx.doi.org/10.1037/1528–3542.6.4.675.

Willenbockel, V., Lepore, F., Nguyen, D. K., Bouthillier, A., & Gosselin, F. (2012). Spatial frequency tuning during the conscious and non-conscious perception of emotional facial expressions - An intracranial ERP study. *Frontiers in Psychology*, *3*(JUL), 1–12. http://dx.doi.org/10.3389/fpsyg.2012.00237.

Williams, M. A., Morris, A. P., McGlone, F., Abbott, D. F., & Mattingley, J. B. (2004). Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. *Journal of Neuroscience*, *24*(12), 2898–2904. http://dx.doi.org/10.1523/JNEUROSCI.4977-03.2004.

Xu, S., Zhang, S., & Geng, H. (2011). Gaze-induced joint attention persists under high perceptual load and does not depend on awareness. *Vision Research*, *51*(18), 2048–2056. http://dx.doi.org/10.1016/j.visres.2011.07.023.

Yang, E., Brascamp, J., Kang, M. S., & Blake, R. (2014). On the use of continuous flash suppression for the study of visual processing outside of awareness. *Frontiers in Psychology*, *5*(July), 1–17. http://dx.doi.org/10.3389/fpsyg.2014.00724.

Yang, E., Hong, S. -W., & Blake, R. (2010). Adaptation aftereffects to facial expressions suppressed from visual awareness. *Journal of Vision*, *10*, 24. http://dx.doi.org/10.1167/10.12.24.

Yang, E., Zald, D. H., & Blake, R. (2007). Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion (Washington, D.C.)*, *7*, 882–886. http://dx.doi.org/10.1037/1528–3542.7.4.882.

Yang, Z., Zhao, J., Jiang, Y., Li, C, Wang, J., Weng, X., & Northoff, G. (2011). Altered negative unconscious processing in major depressive disorder: An exploratory neuropsychological study. *PloS One*, *6*(7). http://dx.doi.org/10.1371/journal.pone.0021881.

Yorzinski, J. L., Penkunas, M. J., Platt, M. L., & Coss, R. G. (2014). Dangerous animals capture and maintain attention in humans. *Evolutionary Psychology : An International Journal of Evolutionary Approaches to Psychology and Behavior*, *12*(3), 534–548 (Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/25299991).

Yuval-Greenberg, S., & Heeger, D. J. (2013). Continuous flash suppression modulates cortical activity in early visual cortex. *Journal of Neuroscience*, *33*(23), 9635–9643. http://dx.doi.org/10.1523/JNEUROSCI.4612-12.2013.

Zhan, M., Hortensius, R., & De Gelder, B. (2015). The body as a tool for anger awareness-differential effects of angry facial and bodily expressions on suppression from awareness. *PloS One*, *10*(10), 1–13. http://dx.doi.org/10.1371/journal.pone.0139768.