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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

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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' 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.

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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

E-mail address: sandra.soares@ua.pt (S.C. Soares).

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.

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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 nondominant 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

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