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THE ADVANTAGE OF FEAR STIMULI IN ACCESSING VISUAL AWARENESS

Dissertação apresentada à Universidade Católica Portuguesa para obtenção do grau de mestre em

Neuropsicologia

Por

Nuno Miguel de Jesus Gomes

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Abstract

Snakes and spiders constitute evolutionary relevant stimuli for primates, having a privileged access to defense mechanisms (compared to innocuous stimuli). However, throughout evolution, these stimuli appear to have represented different threat levels. Snakes, as predicted by the Snake Detection Theory (Isbell, 2009), provoked a stronger evolutionary pressure than spiders, shaping the vision of primates towards their preferential processing, mainly in the most complex perceptual conditions. Several studies indicate that emotionally relevant and/or high arousal stimuli have faster access to visual awareness than stimuli without these features. Nevertheless, to the best of our knowledge, no studies have directly investigated the role of evolutionary pressure in this privileged access. Using continuous flash suppression (CFS), the present study assessed the role of evolutionary pressure in the access to visual awareness. For this purpose, we measured the time needed for three types of stimuli – snakes and spiders (matched with snakes for rated fear levels but for which an influenced on primate evolution is less well grounded), and birds (an innocuous animal stimulus) – to break the suppression caused by the CFS and access visual awareness in two different suppression intensity conditions. The results showed that in the less demanding suppression condition (i.e., stimuli presented to participants' dominant eye) both evolutionarily relevant stimuli (snakes and spiders) had faster access to visual awareness than the bird stimulus, whereas in the most demanding suppression condition (i.e., stimuli presented to participants' non-dominant eye) condition only snakes showed this privileged access. We propose that stimuli that suffered most evolutionary pressure show advantages in accessing to visual awareness. Our data suggests that the privileged processing of snakes in the most complex perceptual conditions extends to the access to visual awareness, corroborating the unquestionable value of snakes in the primates' evolution.

Keywords: Evolution, Fear, Snake Detection Theory, Snakes, Awareness

Resumo

As cobras e as aranhas constituem estímulos evolutivamente relevantes para os primatas, apresentando um acesso privilegiado aos mecanismos de defesa (comparativamente a estímulos inócuos). Contudo, ao longo da evolução estes estímulos parecem ter representado níveis de ameaça diferentes. As cobras (como previsto pela *Snake Detection Theory;* Isbell, 2009) provocaram uma pressão evolutiva mais forte do que as aranhas e moldaram a visão dos primatas, tornando-as preferencialmente processadas, principalmente nas condições perceptivas mais complexas. Vários estudos indicam que estímulos emocionalmente relevantes e/ou que induzem maior ativação fisiológica acedem à consciência visual mais rapidamente que estímulos sem estas características mas, do nosso conhecimento, nenhum estudo investigou directamente o papel da pressão evolutiva neste acesso privilegiado. Recorrendo à *Continuous Flash Suppression* (CFS), o presente estudo teve como principal objectivo analisar o papel da pressão evolutiva no acesso à consciência visual. Para isso registou-se o tempo necessário para 3 tipos de estímulos – cobras, aranhas (equivalentes à cobras nos níveis de medo que provocam mas diferentes na influência que apresentaram ao longo da evolução dos primatas) e pássaros (estímulo animal inócuo) – quebrarem a supressão causada pela CFS e acederem à percepção visual consciente em duas condições de supressão com intensidades diferentes. Os resultados obtidos mostraram que na condição de supressão menos exigente (i.e., estímulos apresentados ao olho dominante do participante) ambos os estímulos evolutivamente relevantes (cobras e aranhas) apresentaram um acesso mais rápido que os pássaros, enquanto que na condição de supressão mais exigente (i.e., estímulos apresentados ao olho não dominante do participante) apenas as cobras evidenciaram este acesso privilegiado. Os dados apontam para que estímulos que sofreram maior pressão evolutiva apresentem um acesso facilitado à consciência visual. Sugere-se assim que o processamento privilegiado das cobras nas condições perceptuais mais complexa se estende ao acesso à consciência visual, corroborando deste modo o valor inquestionável destas na evolução dos primatas.

Palavras-Chave: Evolução, Medo, Snake Detection Theory, Cobras, Consciência

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1. Introduction

The theory of evolution, proposed by Charles Darwin (1859), revolutionized the view of the scientific community about the origin and evolution of all species until the present. Based on his observations, Darwin (1859) suggested that the existing biological diversity originated from gradual modification processes in which organisms have been adapting to their habitats (or to changes in those habitats) from one generation to the next. The Darwin's evolutionism proposed that, starting from a common ancestor, species were branching out into new species, hence creating the different branches of the phylogenetic tree (for a review, see Darwin, 1859). According to Darwin's premises, natural selection worked as a filter, with individuals better adapted to the environment being more likely to survive and reproduce and perpetuating their genes along the succeeding generations. On the contrary, the less adapted individuals were less likely to survive. Therefore, the competitive relationship between prey and predator, called evolutionary arms-race (Dawkins & Krebs, 1979), was an important selection factor, since individuals unable to detect and avoid predators were more likely to die, thus not transmitting their genes to the next generation. The predator-prey arms race probably created the conditions of natural selection for the development of perceptual (to effectively detect threat) and motor skills (to successfully avoid threat) found in the current mammals (for a review, see Öhman & Mineka, 2001). Fear comes as an important emotion that mediates the relationship between perception and motor responses, by motivating the execution of defense strategies, in order to effectively detect and avoid threat (Epstein, 1972).

Öhman and Mineka (2001) have introduced the concept of "fear module", a mechanism that has evolved for the purpose of coping with threatening situations (with the prime example being predators). The fear module is a behavioral, psychophysiological and independent neuronal system that is automatically and selectively activated, being relatively encapsulated from the most advanced human cognition. Due to the contingencies of evolution, stimuli relevant to our phylogenetic ancestors are preferred targets for the action of this module, making us more prepared to detect and react more efficiently to these stimuli (see Seligman, 1971). Consistently, a large bulk of data has shown that some stimuli, such as those through which evolution have exerted stronger pressures (e.g., snakes; see Öhman & Mineka, 2003), have a privileged access to the fear module. These stimuli are processed automatically (even without requiring conscious processing), capture attention and activate the response defense mechanisms more effectively (for a review, see Öhman & Mineka, 2001). However, no studies have yet directly investigated the role of evolutionary value in the access to visual awareness (a subject of growing interest in the scientific community; see Yang, Brascamp, Kang, & Blake, 2014), which is the research focus of this thesis.

The study of the fear module can be extremely enlightening for many scientific fields. Fear regulation disturbances are at the center of various psychopathological conditions, including mood disorders, anxiety, panic, phobias and post-traumatic stress disorder (American Psychiatric Association, 2013; LeDoux, 1996, 2015; Öhman & Mineka, 2001). Considering that evolutionarily relevant stimuli have a privileged access (e.g., automatic) to the "fear module", understanding the mechanisms underlying the processing of these stimuli may have interest at a clinical level, particularly in the understanding and treatment of the disorders mentioned above. Specifically for neuropsychology, this study reveals its importance in understanding the neural mechanisms underlying the processing of evolutionary relevant stimuli, consequently aiding in the comprehension of the neural mechanisms implicated in the fear regulation disturbances. Moreover, the present study also provides important insights to the field of evolutionary psychology while adding more relevant knowledge on the brain's evolutionary path, in particular on the threat detection mechanisms.

2. Literature review

2.1 Fear: A product of evolution

As mentioned in the previous section, during primates' evolution, the rapid and efficient processing of threat signals was highly beneficial for survival. Fear is the emotional state that prepares the body to deal and react quickly to imminent threats (Öhman & Mineka, 2001). It's function is to modulate defense reactions (immobility, flight or fight, Blanchard & Blanchard, 1988), thus contributing to the survival of the species. Surviving is a prerequisite for the transmission of genes throughout the generations, so it is assumed that the mechanisms of fear have been a prime target of natural selection. Thus, fear is the most sculpted emotion by evolutionary contingencies (for a review, see Öhman, 2000).

Being fear a product of evolution, it is assumed that members of a species are more likely to fear situations and events that constituted threats to their ancestors

(Seligman, 1971). An example of this claim is the fact that human species are more likely to fear predators, social assessments and open spaces, rather than ontogenetic threats as weapons, motorcycles and damaged electrical equipment (Öhman & Mineka, 2001; Seligman, 1971). According to the categorization of behavior based on evolution (Mayr, 1974), these fear of ancestors' stimuli can be divided into two categories: *intraspecific* (associated with ancient systems of social submission), meaning stimuli that are likely to represent a threat within species, as the case of fearful faces and angry body postures; and *interspecific* (associated with predators' defense ancestors systems), meaning stimuli of other species that may represent a threat, such as predators like snakes and spiders (for a review, see Öhman & Mineka, 2001).

2.2 Interspecific evolutionarily relevant stimuli: Snakes and spiders, similar but not of equivalent.

Despite the importance of intraspecific fear stimuli (Mayr, 1974) and its relevance for the understanding of social behavior, the study of interspecific fear stimuli is the only one capable of elucidating about the critical role of competition between predators (such as snakes) and animal prey (such as primates) and their subsequent biological adaptations.

Snakes are one of the fear stimuli strongly linked to the evolution of the species, as evidenced by the intense and common fear of snakes in humans (Agras, Sylvester, & Oliveau, 1969) and in primates (Mineka, Keir, & Price, 1980). According to the *Snake Detection Theory* (SDT), proposed by Lynne Isbell (2009), the development of effective poisons in snakes (about 60 million years ago) was a source of strong threat to the survival of monkeys' ancestors. Isbell (2009) suggests that some primates overcame this challenge by developing their capabilities to detect snakes in order to avoid them effectively. Given the fatal outcome of an ineffective detection of snakes, these were a strong evolutionary pressure factor. As a result of this strong evolutionary pressure, snakes are preferentially processed and have a privileged access to the fear systems (for a review, see Öhman & Mineka, 2001), being detected more effectively than stimuli without the same evolutionary characteristics. Isbell (2009) argues that this advantage in detecting snakes is due to adaptations of the visual system, which are reflected in an improved vision and in the emergence of bidirectional links between sensory systems (such as the visual system) and the amygdala (LeDoux, 1996; Öhman, Carlsson, Lundqvist, & Ingvar, 2007), being this brain structure identified as central in fear processing, both in humans and in nonhuman primates (Adolphs & Tranel, 2000; Aggleton & Passingham, 1981; Blanchard & Blanchard, 1972; Cahill, Babinsky, Markowitsch, & McGaugh, 1995; Carlsson et al., 2004; Chudasama, Izquierdo, & Murray, 2009; Davis & Whalen, 2001; Davis, 1992; Feinstein, Adolphs, Damasio, & Tranel, 2011; Hamann, 2001; Izquierdo, Suda, & Murray, 2005; Kalin, Shelton, & Davidson, 2004; LeDoux, 2007; Liddell et al., 2005; Meunier, Bachevalier, Murray, Malkova, & Mishkin, 1999; Öhman & Mineka, 2001; Öhman et al., 2007; Öhman, 2005; Prather et al., 2001; Tamietto & de Gelder, 2010; Weiskrantz, 1956).

The number of studies aimed at understanding the preferential snake detection and their neural substrates is increasing in the literature. Van Le and colleagues (2013) have found that neurons in the medial and dorsolateral pulvinar of Japanese monkeys showed faster and stronger responses to snake images (compared with images of faces and hands of monkeys and with simple geometric shapes). In a follow-up study, the authors showed that this effect was enhanced when the snakes were in an attack position, compared with snakes shown in other positions (Van Le et al., 2014). These results were replicated in behavioral studies using models of snakes with rhesus monkeys (Etting & Isbell, 2014), as well as with children and adult humans (Masataka, Hayakawa, & Kawai, 2010). In a recent study with macaques (macaca fuscata), Van Le and colleagues (2016) found that snakes (compared with images of faces and hands of monkeys) elicit earlier gamma oscillations (which have been suggested to be 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 and mushrooms as well as other animal stimuli, also has been shown with several visual search tasks in reshus 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).

Spiders are also a highly fear relevant stimulus for humans. As snakes, they are one of the most prevalent fears in the human species (Agras et al., 1969). Indeed, several studies show its relevance for humans, also showing their preferential processing compared to neutral stimuli (Lipp & Derakshan, 2005; Öhman et al., 2001; Rinck, Reinecke, Ellwart, Heuer, & Becker, 2005). However, the vast majority of studies collapse snakes and spiders in the same category of evolutionary fear stimuli, not performing direct comparisons between the two. Nevertheless, in an evolutionary perspective, differences between them are expected. Spiders and snakes are similar in their emotional impact, both showing negative valence, high arousal and perceptual dominance (Lang, Bradley, Cuthbert, 2005). However, unlike snakes that constituted a strong predator to mammals (Isbell, 2009), this was not the case with spiders. Generally, spiders attack other spiders and insects (Nyffeler, 1999) and, unlike poisonous snakes, the poison of spiders did not evolve to be effective against mammals (Gerdes, Uhl, & Alpers, 2009). These facts suggest that snakes have been a stronger source of natural selection than spiders. 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 contact with humans and only a few are considered a cause of morbidity or mortality (e.g., Steen, Carbonaro, & Schwartz, 2004).

Several recent studies have been devoted to study the processing differences between snakes and spiders. Soares (2012) and Soares and colleagues (2009; 2013; 2014) conducted a series of behavioral experiments that evaluated the detection of snakes under conditions that may have been critical for survival. These studies demonstrated that snakes are detected more effectively than spiders (and control stimulus, mushrooms) in more challenging visual conditions, such as when the stimuli are presented for short exposure times, presented in the visual periphery, camouflaged in cluttered environments and in conditions where attention must be automatically redirected to snakes that are presented in the surrounding environment.

Some studies using event-related potentials (ERPs), also investigated the neural correlates of responses to snakes and spiders compared to different classes of animals stimuli. The data from these studies show that snakes, compared to birds and insects (non-evolutionary relevant stimuli), as well as to other reptiles and slugs (Van Strien, Franken, & Huijding, 2014), capture visual attention more rapidly (Hongshen, Kenta, & Nobuyuki, 2014; Van Strien, Eijlers, Franken, & Huijding, 2014). Another recent ERP study also show that snakes are more efficient in attracting early exogenous attention than spiders and birds (Soares, Kessel, Hernández-Lorca, García-Rubio, Rodrigues, Gomes, Carretié, submitted). Together, these data suggest a preferential processing of snakes, compared with spiders.

2.3 Automatic processing of evolutionarily relevant stimuli

Even when stimuli with biological relevance are presented very briefly, outside our attentional focus or even in the absence of visual awareness, they are processed in a very effective way when compared to neutral or innocuous stimuli (for a review, see Öhman & Mineka, 2001; Pessoa, 2005; Vuilleumier, 2005). Considering that these stimuli carried important cues to avoid the threat, it seems natural that throughout evolution this fast and efficient processing has been developed due to its obvious benefit for survival (Öhman, 2009). At a neural level, this type of processing is thought to be based on a rudimentary mechanism of visual perception, usually associated with the concept of a "low road", a subcortical pathway that mediates the transmission of information about the threat to the amygdala, bypassing cortical processing (LeDoux, 1996; Öhman, 2005). This has been supported by data showing amygdala activation to evolutionarily relevant stimuli, even when visual perception is suppressed, and by data showing that this access occurs through the superior colliculus and nucleus pulvinar, suggesting the existence of a retina-colliculus-pulvinar-amygdala pathway (e.g., Morris, Öhman, & Dolan, 1999; for a review, see Öhman et al., 2007).

In order to study the automatic processing in the absence of visual awareness, researchers generally use masking techniques that aim to prevent conscious visual perception. Several studies have reported data in support of such unconscious processing, for both interspecific (such as snakes and spiders) and intraspecific (such as fearful faces) relevant stimuli. One of the pioneer studies was performed at Ohman's laboratory (Öhman & Soares, 1994). Using the backward masking (BM; see Wiens, 2006), the authors showed an increase in skin conductance response in individuals with high fear level of snakes or spiders (but not both) while presented with their specific feared stimulus (but not while presented with the non-feared but evolutionarily relevant stimulus, e.g., spiders to snake fearful participants). Carlsson and colleagues (2004), in a similar study (BM with individuals with snake or spider phobia), used a PET scan with the aim of documenting the underlying neural processing and showed that in the absence of visual awareness a stronger amygdala response was shown for both phobic and relevant biological stimuli (compared with an innocuous stimulus, mushrooms). Whalen and colleagues (1998), also using the BM, showed stronger activation of the amygdala to another type of evolutionarily relevant stimuli, fearful faces (compared with happy and neutral expressions).

Using binocular rivalry (BR), another technique capable of suppressing the access to visual awareness (see Tong, Meng, & Blake, 2006)), William and colleagues (2004) in an fMRI study, also documented the increased activation of the amygdala to emotional facial expressions (compared with neutral expressions). Pasley and colleagues (2004) in a similar fMRI study (BR with fearful facial expression) also showed significant amygdala's activation for unperceived fearful faces (but not for unperceived non-face objects, such as chairs).

Using the interocular suppression technique "Continuous Flashing Suppression" (CFS; see section 2.3), capable of suppressing visual conscious perception for longer periods of time (see Lin & He, 2009), Jiang and He (2006) confirmed the activation of the amygdala for fearful faces (compared to neutral faces), presented in the absence of visual conscious perception. While also using the CFS, Troiani and colleagues (2012) reported an activation pattern similar to the study described above.

The data presented throughout this section point to a differentiate processing of evolutionary relevant stimuli (either interspecific or intraspecific), even when individuals are subjected to masking techniques, which cause the suppression of visual awareness.

2.4 CFS in the study of evolutionarily relevant stimuli: Preferential access to visual awareness

A new paradigm often used to study the processing of stimuli with biological relevance outside the visual awareness is an interocular suppression technique called Continuous Flashing Suppression (CFS; Tsuchiya & Koch, 2005). In the CFS, low-contrast stimuli presented to an eye are suppressed by dynamic high-contrast patterns (usually patterns of Mondrian, also called CFS masks) presented to the opposite eye (Tsuchiya & Koch, 2005).

At a neural level, the interocular suppression techniques appear to reduce the level of activity in the geniculostriate pathway and strongly suppress visual processing in the striate cortex (for review see Lin & He, 2009). Despite the existent discussion, CFS does not seem to be different from the other interocular suppression techniques, also suppressing the conscious visual perception in the primary levels of vision (for a review, see Sterzer, Stein, Ludwig, Rothkirch, & Hesselmann, 2014). Yuval-Greenberg and Heeger (2013) using fMRI, have shown that in the CFS, visual perception of a target stimulus is related to the BOLD activity (Blood-Oxygen Level Dependent) in V1.

The authors found that when the stimulus and the CFS mask were presented to opposite eyes (condition with suppressed visual perception) the BOLD activity in V1 was similar to trials where only the mask was presented. In contrast, in trials where the stimulus and the CFS mask were presented to both eyes (condition with conscious visual perception) the BOLD activity in V1 was significantly higher. These results led the authors to conclude that the CFS suppresses visual awareness by shaping the gain of neuronal responses in the primary visual cortex (Yuval-Greenberg & Heeger, 2013). Because CFS is capable of suppressing visual awareness of a stimulus for long periods of time, thus providing a stronger suppression than more classical techniques (Tsuchiya & Koch, 2005) such as BM and BR, this has been assumed as an ideal technique for studying the unconscious mechanisms (Yang, Zald, & Blake, 2007).

An increasingly popular way to use CFS in behavioral studies is to record the time required for a stimulus, after an initial suppression period, to access visual awareness. This variant of CFS, called "breaking - CFS" (Jiang, Costello, & He, 2007), has proved extremely useful and sensible in the study of conscious detention thresholds for different stimuli classes. The breaking-CFS is based on a property of binocular rivalry which states that emotional stimuli remain suppressed for shorter periods of time (Jiang et al., 2007; Levelt, 1965; Yang et al., 2007). However, whether this technique constitutes a preferred unconscious processing measure continues to be a subject of debate in the literature (Gayet, Van Der Stigchel, & Paffen, 2014; Stein, Hebart, & Sterzer, 2011a; Stein & Sterzer, 2014; Yang et al., 2014). Nevertheless, it is consensual that b-CFS represents a powerful and highly sensitive tool in the study of the visual consciousness access thresholds for different groups of stimuli (Stein et al., 2011a).

Results from several studies, using the breaking-CFS, have been showing contributions of emotion, arousal and, ultimately, evolutionary significance in reducing suppression times, providing evidence that relevant stimuli are prioritized during visual processing and have a privileged access to visual awareness. Stein and colleagues (2011b) showed that faces with direct gaze (which seems to be more arousing than averted gaze faces; Gale, Spratt, Chapman, & Smallbone, 1975; Nichols & Champness, 1971) had lower detection thresholds than faces with averted gaze. Studies using fearful faces also show that these stimuli break the suppression caused by the technique more efficiently, accessing visual awareness faster than neutral or happy faces (Stein, Seymour, Hebart, & Sterzer, 2014; Sterzer, Hilgenfeldt, Freudenberg, Bermpohl, & Adli, 2011; Tsuchiya, Moradi, Felsen, & Yamazaki, 2009; Yang et al., 2007). Zhan, Hortensius, and Gelder (2015), in a study using body postures, also showed that anger postures had lower suppression times than fear or neutral postures. Finally, Schmack, Burk, Haynes, and Strezer (2015) in a study investigating the mechanisms underlying the affective salience in breaking-CFS, showed an advantage of spiders (compared with flowers) in accessing visual awareness. However, Schmack and colleagues (2015) were only interested in studying the phobic characteristics of spiders, not attending to their evolutionary relevance.

3. The present research

Several studies using breaking-CFS show an advantage of evolutionarily relevant stimuli in accessing visual awareness. However, to our knowledge, the vast majority of those studies used evolutionarily relevant intra-specific stimuli (i.e., faces). To date, only one study showed evidence of a privileged access to visual awareness by evolutionarily relevant interspecific stimuli (i.e., spiders) (Schmack et al., 2015). Although intra-specific behavior is highly relevant for understanding social behavior, it does not allow the study of inter-specific behavior (as previously mentioned in section 2.2). Indeed, only the study of interspecific behavior allows the understanding of the critical role of the constant competition between predators (snakes) and prey animals (primates) and the subsequent biological adaptions of the later. Moreover, data from other research fields point to the possibility of a differential processing between intraspecific and interspecific ancestors' stimuli (Öhman, Soares, Juth, Lindström, & Esteves, 2012). Thus, it becomes important to ascertain whether the privilege in accessing visual awareness extends to other evolutionarily relevant stimuli categories. The first goal of this study was to investigate whether the evolutionarily relevant stimuli - snakes and spiders, access conscious visual processing faster than neutral stimuli, during the CFS. Based on previous results showing a preferential processing of evolutionarily relevant stimuli in accessing the fear module, this study presents as the first hypothesis an advantage of both snakes and spiders (compared with innocuous animal stimuli, birds) in accessing conscious visual perception.

Furthermore, and since no study has directly investigated the role of evolutionary pressure in accessing visual awareness, in the present study direct comparisons between two stimuli with distinct evolutionary relevance for primates - snakes and spiders, will be performed. Attending to the differences in evolutionary significance between snakes and spiders and taking into account the behavioral and electrophysiological data described above (see section 2.2), we expect differences in the access to awareness between these two stimuli, particularly in the more complex perceptual conditions (Soares et al., 2014). In order to create two distinct perceptual complexity conditions during the CFS, we divided participants based on their ocular dominance. The concept of ocular dominance (Porac & Coren, 1976) refers to an evident monocular processing preference when the images viewed by the two eye cannot be merged, such as in a dichotic stimulation condition (Valle-Inclán, Blanco, Soto, & Leirós, 2008). Data from studies that use binocular rivalry paradigms have shown that when participants perceive the stimuli presented to one of the eyes with lower reaction times and higher accuracy, such eye is appointed as their dominant eye. Importantly, this measure is usually related with the results obtained by more classical tests (such as Miles' test; Miles, 1930) (e.g., Valle-Inclán, Blanco, Soto, & Leirós, 2008). During the CFS, presenting the stimulus to the dominant eye or to the non-dominant eye of participant may represent different conditions of suppression, with the latter being a stronger and more complex stimulus detection condition. 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 (Soares et al., 2014), we also predict that snakes will access visual awareness faster (reflected in lower times of suppression) in the most demanding suppression condition (i.e., when stimuli are presented to non-dominant eye) than spiders, for which evolutionary pressures were weaker (and innocuous animals, birds). However, in the less demanding suppression condition (i.e., when stimuli are presented to the dominant eye), no differences are expected between snakes and spiders (compared to birds), as they are both fear stimulus to humans. It is also important to note that, unlike other studies in the literature which compare snakes and spiders to non-animal stimuli, the present study uses birds as a control stimulus, i.e., an animal stimulus that did not represent any threat to primates. We use an animal control stimulus given that previous data point to the fact that more efficient detection of snakes and spiders, compared to non-animal control stimuli (flowers and mushrooms) may reflect an attentional bias to animals instead of a bias to threatening animals (New, Cosmides, & Tooby, 2007).

4. Methods

4.1. Participants

Sixty-one university students (forty-six women), aged between 17 and 42 (M=21.64, SD = 0.53), 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 = 0.69), and 29 participants with left dominance (22 women), aged 17 to 42 (M = 21.21, SD = 0.83). All participants reported normal, or corrected to normal, eyesight, no psychiatric medication intake, and no registered or observed symptoms of mental illness.

4.2. Stimuli

Stimuli encompassed 10 images of snakes, 10 images of spiders and 10 images of birds. For snakes and spiders, grayscale images were chosen from those used in Soares et al. (2014, Experiment 4). The bird images were selected from the internet and converted to grayscale. Image luminance was automatically tuned to result in brighter images with equal mean luminance.

To rule out the role of the low level features of the stimuli on the results, spatial frequency energy across stimuli was computed (Soares et al. 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) rated 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 [$F(2, 128) = 129.48$, $p < .0001$, $\eta 2p = .67$] and arousal [$F(2, 128) = 67.89$, $p < .0001$, $\eta 2p = .52$]. 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).

Table 1: Means and standard deviations (in parenthesis) of: (i) spatial frequency bands (ii) luminosity, and (iii) subjective ratings of 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 effect of 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 x 768 pixels in all cases).

4.3. CFS mask

For building the CFS, several Mondrian patterns were generated, composed of randomly arranged greyscale circles with diameters between 0.39º and 1.4º, and animated at 10Hz. In order to enable the CFS technique using "red-blue anaglyph glasses" (e.g., Almeida, Mahon, Nakayama, & Caramazza, 2008; Almeida et al., 2014; Almeida, Mahon, & Caramazza, 2010; Almeida, Pajtas, Mahon, Nakayama, & Caramazza, 2013; Kaunitz et al., 2011; Troiani et al., 2012) the stimuli were presented using the blue RGB channel and the CFS masks using the red RGB channel. By overlapping the stimulus and the CFS masks, 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.

4.4. Display

The participant was presented with a 8º x 8º frames with a 0.5º border presenting a white noise pattern inside of which the mask and the stimulus overlapped. 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.

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.

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

4.5. Procedure

After evaluating ocular dominance using the Miles's test (Miles, 1930), the participant's position was adjusted to ensure that the head was 50cm away from the screen center. Participants were not informed about the nature of the stimuli they would be shown. Each trial started with a 1s presentation of a blank frame with the white fixation cross only; next, the stimuli was introduced, in one of the four quadrants, by ramping up its contrast over 1.1s; during this ramping, CFS masks were shown at 10Hz. After 1.1s the CFS mask contrast was ramped down over a period of 4s. Trials ended with the participant's response or after 7s (see Figure 1).

To achieve an objective measure of perceptual awareness we considered a forced choice paradigm (Jäkel & Wichmann, 2006; 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, followed by the main experiment, consisting of 240 trials (30 stimuli x 4 quadrants x 2 repetitions), with three mandatory breaks (one every 60 trials). The average total duration of the experimental procedure was 45 minutes.

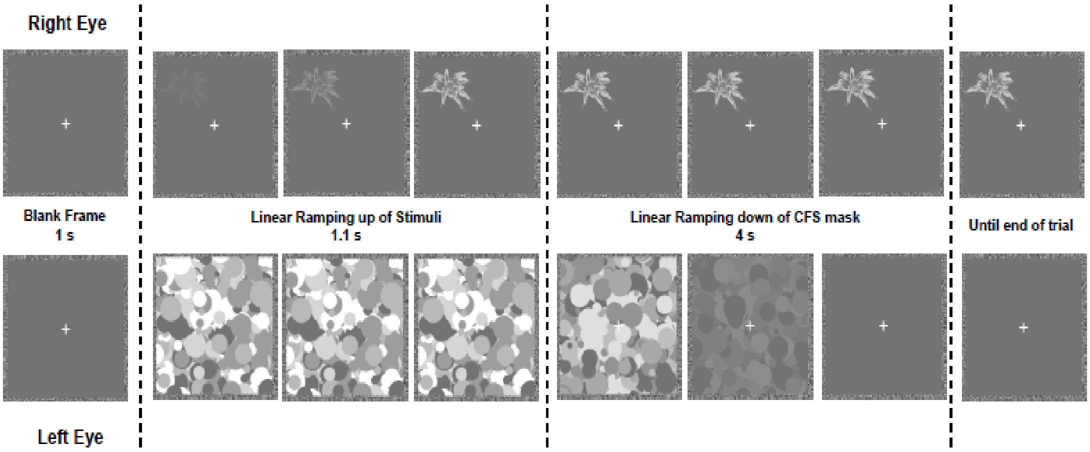

Figure 1: Schematic example of a trial. The stimuli were gradually introduced to the right eye, while CFS masks (Mondrian-like pattern blinking at 10 Hz) were presented to the left eye. Participants localized as quickly as possible the quadrant in which the stimulus became visible.

4.6. Statistical analysis

Trials with no response or incorrect responses (< 10%) were excluded from the data analyses. The mean reaction times were compared in a mixed 3x2 ANOVA factorial design with the *animal category* (spider, snake, bird) as a within-participants factor and the *ocular dominance* (right dominance, or the dominant eye group, corresponding to the less demanding suppression condition and left dominance, or the non-dominant eye group, 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 contracts.
As a measure of effect size of ANOVAs, we reported the partial eta square (η2p).

5. Results

Conforming to our first hypothesis, the results showed a significant main effect of animal stimuli [$F(2, 118) = 24.43$, $p < 0.001$, $\eta2p = 0.29$], with snakes and spiders ($M = 3936.68$ms; $SD = 124.69$, and $M = 3929.57$ms; $SD = 129.00$, respectively) showing a faster access to visual awareness than birds ($M = 4106.26$ms; $SD = 128.89$), as confirmed by Bonferroni post-hoc comparisons ($p < 0.001$). No statistical significant differences were found between snakes and spiders ($p > 0.05$).

The results also showed a significant interaction between the animal stimuli and ocular dominance [$F(2, 118) = 4.48$, $p < 0.05$, $\eta2p = 0.07$]. Again conforming to our hypothesis, the results showed that when participants were presented with the stimuli in their dominant eye, snakes and spiders ($M = 3750.14$ms; $SD = 171.95$, and $M = 3706.01$ ms; SD = 177.89, respectively) accessed visual awareness faster than birds ($M = 3968.11$ ms $SD = 177.73$), as shown by Bonferroni post-hoc comparisons ($p< 0.001$). As predicted, no significant differences were found between snakes and spiders in this condition ($p > 0.05$). Importantly, however, in the non-dominant eye group, snakes ($M = 4123.21$ms; SD = 180.63) showed a faster access to visual awareness faster than birds ($M = 4244.40$ ms $SD = 186.70$), as shown by Bonferroni post-hoc comparisons ($p < 0.01$). No statistically significant differences were found between snakes and spiders ($p > 0.05$) or between spiders and birds ($p > 0.05$) (see Figure 2).

No significant main effect of ocular dominance was revealed [$F(1, 59) = 2.09$, $p > 0.05$, $\eta2p = 0.03$].

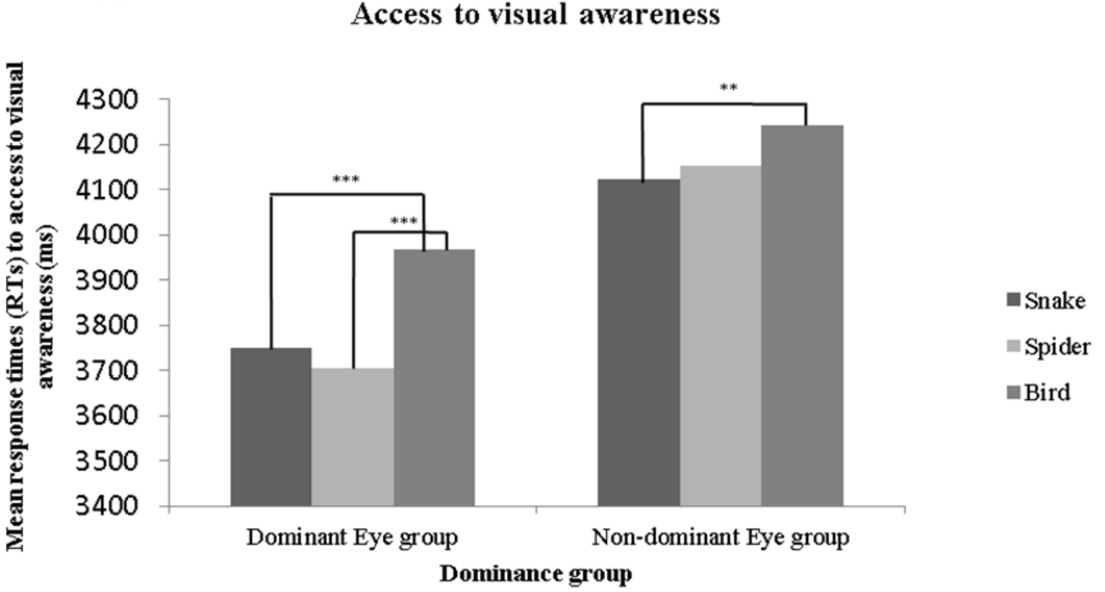

Figure 2: Mean response times (RTs) to access visual awareness in milliseconds (ms) for the three animal stimuli in the two suppression conditions; ** indicates p<0.01; *** indicates p < 0.001.

6. Discussion

6.1 The influence of threat in accessing awareness

The present thesis examined the access to visual awareness by evolutionarily relevant interspecific stimuli, snakes and spiders. Confirming our first hypothesis, the results showed that, overall, snakes and spiders accessed awareness faster than birds, thus corroborating the evidence showing that emotional stimuli with high arousal and/or evolutionary charge gain preferential access to visual awareness during the CFS (Schmack et al., 2015; Stein et al., 2011, 2014; Sterzer et al., 2011; Tsuchiya et al., 2009; Yang et al., 2007; Zhan et al., 2015). This study also confirms that this advantage in the access to visual awareness extends to interspecific evolutionarily relevant stimuli, which is essential to understand the critical role of competition between predator (snakes) and prey (primates) in the evolution of species.

The advantage in accessing awareness by fear relevant stimuli has been linked to the activity of the amygdala (for review see Lin & He, 2009; Sterzer et al., 2014), which appears to be involved in unconscious processing of threatening stimuli (for a review, see (Öhman, 2005; Öhman et al., 2007). As evidenced along section 2.3, several studies confirm the activation of this structure towards fear relevant stimuli processed in the absence of awareness, during BM, BR and CFS (Carlsson et al., 2004; Jiang & He, 2006; Öhman & Soares, 1994; Pasley et al., 2004; Troiani et al., 2012; Whalen et al., 1998; Williams et al., 2004; but see Schmack et al., 2015; Tsuchiya et al., 2009). These data are in accordance with the literature advocating the automatic activation of the amygdala when threatening are presented, even before its conscious processing (Öhman, 2005; Öhman et al., 2007; Zald, 2003) and with the ultimate adaptive goal of triggering defensive responses (Tamietto & de Gelder, 2010). Several studies also indicate that the activation of the amygdala result in an improvement of perceptual performance (Öhman et al., 2007). The conscious visual perception is associated with the activity of the ventral stream of vision (Goodale & Milner, 1992, 2004; Milner & Goodale, 1993, 2006, 2008), with the amygdala having efferent cortical connections to multiple levels of this pathway (Emery & Amaral, 2000). Vuilleumier and colleagues (2004), using individuals with focal lesions in the amygdala or the hippocampus, tested whether the rapid activation of the amygdala modulated visual processing. They demonstrated an emotional reinforcement in cortical areas of vision (fusiform gyrus) to fearful faces, both for patients with damage to the hippocampus and for control individuals. However, in patients with lesions in the amygdala, this emotional reinforcement was not observed, arguing in favor of the influence of this structure in visual perception (see also Phelps, Ling, & Carrasco, 2006).

Despite the role attributed to the amygdala in threat processing, as well as its role in enhancing perceptual performance, the neural substrates of the amygdala’s automatic activation remains under discussion in the literature (for a in-depth review, see de Gelder, van Honk, & Tamietto, 2011; Pessoa & Adolphs, 2010; see section 4.3). The interocular suppression techniques, such as CFS, may be enlightening in this discussion. These techniques are known to reduce the activity along the geniculostriate pathway, and to strongly suppress the processing in the primary visual cortex (Lin & He, 2009). Therefore, a possible explanation for the activation of the amygdala, and consequently for a differentiated processing of evolutionarily relevant stimuli during the CFS, are subcortical visual pathways that bypass the cortical processing (Lin & He, 2009). This explanation is in accordance with the model of the fear mechanisms activation proposed by LeDoux (1996). In this theoretical construct, based on animal models, the author proposes that the amygdala is rapidly activated by a "low road", without requiring cortical processing (LeDoux, 1996). Indeed, studies in patients with lesions in the primary visual cortex (Morris, DeGelder, Weiskrantz, & Dolan, 2001), as well as in patients with extensive lesions of the occipital cortex associated with total blindness without any residual vision (Pegna, Khateb, Lazeyras, & Seghier, 2005), and in individuals with visual hemineglect (Vuilleumier et al., 2002), have confirmed this activation of the amygdala in the absence of cortical visual processing. The role of this “low road” is to perform a “quick and dirty” analyses (linked to magnocellular pathways; Vuilleumier, Armony, Driver, & Dolan, 2003) with the aim of efficiently identifying the threat, and quickly activating the defense mechanisms (via amygdala; Tamietto & de Gelder, 2010) in order to avoid its potentially deadly outcome (LeDoux, 2000; LeDoux, 1996; Öhman, 2005; Öhman et al., 2007).

In an attempt to reveal which structures were associated with this subcortical route, Morris and colleagues (1999) found that activation of the amygdala to masked stimuli could be reliably predicted by the activation of subcortical structures (but not by cortical structures) related with vision, as the superior colliculus and the pulvinar. Indeed, this pattern of activation was also confirmed by Liddell and colleagues (2005) for masked fearful faces (compared to neutral faces). Moreover, Paisley and collaborators (Pasley et al., 2004), using BR, showed that the amygdala activity for suppressed fearful faces co-varied with the superior colliculus activity. In similar studies, using CFS, Troiani and colleagues (2012), and Troiani and Schultz (2013), showed covariance in activity between the amygdala and the pulvinar. These results provide indirect evidence for the existence of a retina-colliculus-pulvinar-amygdala pathway, possibly responsible for the activation of the amygdala in the absence of conscious visual processing which, consequently, play an important role in the advantage of emotional stimuli in accessing awareness (even during the CFS).

6.2 The influence of evolutionary pressure in accessing awareness: Snakes vs. spiders

In the second hypothesis of the present study, we predicted that snake's detection would reveal its unquestionable evolutionary value (Isbell, 2009) mainly in the most challenging visual conditions (see Soares et al., 2014). For this purpose, we assessed the average response time for snakes and spiders (stimuli with different evolutionary charge) in accessing awareness (compared to an innocuous animal stimulus, i.e., a bird), across two suppression conditions with different intensities. In fact, the data showed differences between snakes and spiders as a function of the level of suppression. When the stimulus was presented to the participant's dominant eye (the less demanding suppression condition), the two evolutionarily relevant stimuli (both snakes and spiders) showed a faster access to awareness than birds. However, when the stimulus was presented to the participant's non-dominant eye (the most demanding suppression condition), only snakes (but not spiders) gained preferential access to visual awareness (compared to birds), thus confirming our hypothesis.

This data constitutes the first direct assertion about the role of evolutionary charge in accessing awareness. Comparing the accessing thresholds for snakes and spiders (two stimuli with different evolutionary values; see section 2.2), our study presents the first behavioral results that demonstrate that the unquestionable value of snakes (Isbell, 2009) also extend to the access to visual awareness. The present results, interpreted in the light of the Snake Detection Theory (SDT; Isbell, 2009), reinforce the value of snakes in the evolution of primates. The pressure exerted by this predator resulted in adjustments to the visual system (an anti-predator measure developed by primates), such as a more efficient detection of this stimulus, even in perceptual conditions which difficult the detection of other classes of stimuli. As demonstrated in this study, the advantage in snake detection was particularly evident under the most demanding suppression condition (i.e. when the stimulus was present to the participants' non-dominant eye).

The results from the present study are in agreement with the data presented by Soares (2012) and Soares and colleagues (2009; 2013; 2014). In these set of studies, the authors showed consistent evidence that snakes are detected more effectively than spiders (and than innocuous control stimulus) especially in most challenging visual conditions, such as short exposure times, stimuli presented in visual peripheral areas and stimuli camouflaged in cluttered environments. These behavioral studies are complemented with ERP data, which suggest that snakes are better attention grabbers than spiders, being more efficient in attracting early visual attention, reflected in larger early posterior negativity (EPN) amplitudes (Hongshen et al., 2014 Van Strien et al., 2014a; Van Strien et al., 2014b). More recent ERP data also showed that snakes are also better (compared with spiders and birds) at capturing early exogenous attention (evidenced by a significantly larger amplitudes in P1) under high perceptual load conditions, indicating more dependence on bottom-up processes (Soares et al., submitted). Given that stimuli processed by magnocellular pathways seem to capture attention more strongly (e.g., constitute more effective distracters in a demanding attention task) than stimuli processed in the parvocellular systems, and the magnocellular-based attentional capture seems to be less susceptive to top-down control (Leonard & Luck, 2011), these evidences are in accordance with the results showed by Soares and colleagues (2014). Based on their data, the authors suggest that the snake detection probably relies in magnocellular pathways, which process fast visual information with low acuity (Knudsen, 2007). On the other hand, spider detection is most likely linked to parvocellular pathways, which are related with high visual acuity information (Knudsen, 2007).

The discussion about the relation between attention and awareness is extensive. However, the notion that the attention can be dissociated from awareness has gained considerable importance in the literature (for a review, see Koch & Tsuchiya, 2007; Van Boxtel, Tsuchiya, & Koch, 2010; but see Cohen, Cavanagh, Chun, & Nakayama, 2012). More specifically, the role of attention in processing stimuli in the absence of awareness and, consequently, the role of attention during CFS, is currently a matter of interest in several studies. Certain classes of stimuli, such as images that induce high arousal (Jiang, Costello, Fang, Huang, & He, 2006), as well as emotional facial expressions (Yang et al., 2011), when suppressed by CFS, seem to attract the observers' attention to its location. Rothkirch and colleagues (2012), using a visual search task, demonstrated that the participants fixed their eyes during a longer period at the location of a suppressed stimuli (by CFS) (in comparison with other locations), even if the stimuli remained imperceptible. Moreover, in a study with averted gaze faces suppressed from awareness (by CFS), Xu and colleagues (2011) found that these stimuli could act as cues to the allocation of observer's endogenous spacial attention. Additionally, voluntary allocation of attention to the localization of a suppressed stimulus seemed to enhance the degree to which it was processed unconsciously, shown in stronger visual aftereffects (Kanai, Tsuchiya, & Verstraten, 2006; Shin, Stolte, & Chong, 2009; Yang, Hong, & Blake, 2010). One the other hand, 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 the CFS (for a review, see Yang et al., 2014). Actually, fMRI studies confirm this effect in the processing of suppressed stimuli, showing that the allocation of attention modulates BOLD responses to the suppressed stimuli (Bahrami, Lavie, & Rees, 2007; Watanabe et al., 2011; Yuval-Greenberg & Heeger, 2013). Following the reasoning of Lin and He (2009), probably the role of attention in processing stimuli outside awareness would be temporarily connected to the coded features of a stimulus, in order to create high-level representations that would enable perceptual and behavioral processes in the absence of awareness. Thus, snakes' effectiveness in grabbing attention under taxing perceptual conditions can justify the data obtained in our study. We suggest that, in our most demanding suppression condition, only snakes were able to elicit attention, with its processing occurring with a stronger intensity (compared with the other stimuli), thus reducing the time needed to access visual awareness (see Levelt, 1965; Jiang et al., 2007).

As in Soares and colleagues' ERP study (submitted), spiders were rated as more negatively valenced and arousing than snakes. We also controlled for low-level perceptual features (luminance and spatial frequency). Therefore, the effects observed in accessing awareness cannot be attributed to the conscious ratings or to the psychical properties of the stimuli, hence arguing in favor of an advantage of snakes in grabbing attention as being the result of an evolutionary adaptation.

Snakes' capacity to be processed regardless of available resources (Soares et al., 2009; 2012; 2013; 2014), and their efficiency in grabbing early visual attention

(Hongshen et al., 2014; Van Strien et al., 2014a; 2014b; Soares et al., submitted), are compatible with the existence of a superior colliculus-pulvinar “low road” to the amygdala (see section 6.1) (LeDoux, 1996; Öhman et al., 2007; but see Pessoa & Adolphs, 2010). The superior colliculus (implicated in the processing of threat stimuli, such as fearful faces; Tamietto & de Gelder, 2010) is identified as the neuronal locus for reflexive shifts of attention, associated with bottom-up processes (Knudsen, 2007). Moreover, it predominantly receives magnocellular inputs which, as mentioned above, are associated with snake processing (see Lovejoy & Krauzlis, 2010; Soares et al., 2014). The pulvinar, connected to the superior colliculus for the orientation of attention (Arend et al., 2008; Pessoa & Adolphs, 2010; Shipp, 2003), is known to play a key role in regulating the transfer of information during automatic processing of relevant information (Tamietto & de Gelder, 2010; Ward, Calder, Parker, & Arend, 2007). Thus, the “low road” activity is capable of eliciting the reorienting of attention (characteristic in the processing of snakes) via the superior colliculus and the pulvinar and, consequently, in improving perceptual performance (see Öhman et al., 2007) and activating defensive responses (see Tamietto & de Gelder, 2010) through the amygdala.

Indeed, the “low road” structures to the amygdala 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). Snakes appear to elicit rapid and strong responses in neurons of the medial and dorsolateral portions of the pulvinar in Japanese macaques (Van Le et al., 2013). Van Le and colleagues (2016) found that snakes elicit earlier gamma oscillations (which have been suggested to be involved in feedforward visual information processing) in macaque (macaca fuscata) pulvinar neurons. Monkeys with lesions in the amygdala (compared to healthy monkeys) presented a reduced aversion to snakes (Kalin et al., 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, as cables) (Almeida, Soares, & Castelo-Branco, 2015). Moreover, a study with a patient with a bilateral lesion of the amygdala evidenced an absence of aversion to snakes (Feinstein et al., 2011). Together, these data argue in favor of the importance of these subcortical structures in processing snakes.

6.3 Subcortical structures and the processing of threat: A subject under discussion

Although the vast majority of the literature (above mentioned in section 6.1) argue in favor of the role of the amygdala in the rapid processing of relevant stimuli and their consequent advantage in accessing visual awareness, some recent studies have questioned the role of this structure, attributing a greater importance to the neocortex (Pessoa & Adolph, 2010). Tsuchiya and colleagues (2009), in a set of experiments with a patient who had a bilateral lesion of the amygdala, showed that this structure was not essential neither for the first fear processing steps, nor to the advantage in accessing visual awareness (during CFS) by emotional faces. Based on their results, the authors suggested that the role of the amygdala relates only to the modulation of recognition and social judgments. In addition, a recent fMRI study found that the advantage in accessing 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.

Even though the idea of a subcortical pathway to amygdala is commonly applied to the primates' visual system, some authors argue that there is no evidence of any anatomical feed-forward connection between the superior colliculus, the pulvinar and the amygdala in the primates' brain. Instead, they argue that the existence of a "low road" to the amygdala is inferred indirectly from the functional properties attributed to this route (for a review, see Pessoa & Adolphs, 2010). In addition to its high speed processing (for a review, see Öhman et al., 2007), another property assigned to the "low road" to the amygdala is the preference of this pathway for processing visual low acuity information (or low spatial frequency information; LSF), rather than high visual acuity information (or high spatial frequency information; HSF) (Vuilleumier et al., 2003). In a study using deep electrodes implanted in the amygdala, Willenbockel and colleagues (2012) showed that the responses of the amygdala to fearful faces, suppressed from visual awareness (by CFS), occurred relatively late, about 140 ms after the presentation, and were mediated by both HSF and LSF information. Moreover, in a study with breaking-CFS, Stein and colleagues (2014) suggest that the advantage of fearful faces in accessing visual awareness, was based on HSF information. None of these studies support the properties attributed to the "low road", contributing to the growing discussion about the threat detection mechanisms.

Taken together, the studies cited throughout this section provide evidence against the role of amygdala and the existence of a "low road" in the advantage of relevant stimuli in accessing visual awareness. However, as evidenced throughout this discussion, stimuli with distinct evolutionary charges, may present a distinct processing. Thus, studies using different classes of stimuli (e.g., snakes) could prove enlightening in disentangling this heated debate about the threat detection mechanisms (see section 6.4).

6.4 Future research directions

As previously mentioned, several studies suggest that snakes have a different processing, even when compared to fear relevant stimuli such as spiders. Indeed, the data of this thesis argue in favor of this tendency and extend it to the access to awareness. Studies that provide arguments against the role of the amygdala and the "low road" in the differential processing of relevant stimuli, and their consequent advantage in the access to awareness, did not yet use snakes as stimulus. For instance, as mentioned above, Schmack and collegues (2015) found that advantage in accessing visual awareness, during CFS, by spiders does not seem to be related with the amygdala's activity. However, although this seems counter-intuitive, previous data has shown that spider processing, unlike snakes, appear to rely in high visual acuity information (see Soares et al., 2014), which is linked to parvocellular pathways (Knudsen, 2007). These pathways are known to primarily project to cortical areas (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993). Therefore, it is likely that the subcortical pathways are less associated with processing spiders than processing snakes, because snakes constitute a more rooted evolutionary stimulus for primates, but more data is need. Neuroimaging studies with stimuli that represented different evolutionary pressure, such as the ones used in the current study, could help to solve this important question.

Following this reasoning, another approach that could be followed to study the visual pathways responsible for processing threat would involve the manipulation of spatial frequency, exploiting the selective response properties of the cells in the different structures of visual systems. Studies using CFS and manipulating spatial frequency have also presented evidence against the role of the "low road" and the amygdala in the access to awareness (see Willenbockel et al., 2012; Stein et al., 2014 cited above). However, these studies only used fearful faces. Thus, a suggested direction for future research in this area would be to introduce this manipulation of spatial frequency for different classes of stimuli as those used in the present study in order to understand whether the use of these stimuli would lead to different observations regarding the threat detection mechanisms.

6.5 Limitations

The main limitation of the present study is related to the differences between the various ocular dominance measures and the definition of stronger suppression condition here operationalized. Data with BR indicate that introducing the stimulus to the participant’s dominant eye or to the non-dominant eye may represent different suppression conditions, with the last proving to be stronger and to represent a more complex stimulus detection condition (regardless of the dominance measure type used) (Valle-Inclán, Blanco, Soto, & Leirós, 2008). However, one study with CFS have pointed to differences between the more traditional measures of "sighting dominance" (as the case of Miles’ test used in this study) and ocular dominance measures using binocular rivalry techniques, known as "sensory dominance" (Yang, Blake, & McDonald, 2010). The data obtained by Yang and colleagues (2010), although confirming that the stimuli presented to one of the participant's eyes are processed more easily (i.e., with lower reaction times) than the stimuli presented to the other eye, also show that in some cases the eye with preferred processing does not corresponds to the dominant eye evaluated with the classical "sighting dominance" tests. Indeed, several authors pointed out that the "sighting dominance" and "sensory dominance" measures represent different processes (Mapp, Ono, & Barbeito, 2003; Seijas et al., 2007; Suttle et al., 2009). Thus, as a consequence, the data from the present study needs to be interpreted with caution. Nevertheless, the results from this study are highly relevant and represent a valuable contribution to the field, as previously highlighted. So the data of the present study show evidence for a differentiated access to visual awareness when different classes of stimuli are presented to the dominant or no dominant eye, when the dominance is evaluated using measures of "sighting dominance". However, further studies using other forms of measuring ocular dominance are needed.

The use of "red-blue anaglyph glasses" can also be seen as a limitation to this study. Due to the fact that it is difficult to match exactly the color of the stimuli and the CFS mask with the color of the corresponding lenses, it is possible that certain wavelengths of the suppressed stimulus could also have accessed the eye receiving the mask CFS, invalidating the dichotic view condition, necessary to CFS (Troiani & Schultz, 2013). However, several studies in the literature use "red-blue anaglyph glasses" in other to cause CFS and the obtained data has been consistent (e.g., Almeida et al., 2008; Almeida et al., 2014, 2010, 2013; Kaunitz et al., 2011; Troiani et al., 2012). So, although this is a limitation, this factor should not be a cause for invalidation of the data obtained in the study. To reinforce our data, further studies with other dichotic view tools (e.g., mirror stereoscope) are needed.

Another issue to highlight as a possible limitation is the role of perceptual low level features in our data. Despite the careful control of the luminance and spatial frequency to ensure that there were no differences between the different stimuli, we cannot rule out the possibility that these characteristics might have somehow influenced the results. Studies with faces, which controlled the luminance and spatial frequency, have shown that the advantage of emotional faces in accessing awareness can sometimes be explained by perceptual low level features (such as the contrast around the eyes), instead of the classical explanation that points to the face emotional value (see Gray, Adams, Hedger, Newton, & Garner, 2013). Thus, there is the need to perform further studies with different control tasks. For example, compare the detection of snakes and spiders with different shapes or compare the detection of snakes and spiders with innocuous stimuli with snake-like (or spider-like) shapes. It can be the case that this kind of task may be informative about which the characteristics of these stimuli that lead to the advantage in access to awareness. However, even we find that this advantage depends on perceptual low level features this does not appear to invalidate the role of evolutionary charge in the advantage in accessing to visual awareness. Following the reasoning presented by Capitão and colleagues (2014), if the privileged access is based on perceptual low level features, this mechanism may correspond to an adaptive response of our visual system. Given that, from an evolutionary perspective, the visual system of primates, shaped by predator-prey relationships, may have evolved by prioritizing certain low level features, indicative of threat. According to Öhman and Mineka (2003), *"Delineating these features would allow the construction of a super fear stimulus. It could be argued that such a stimulus would depict "the archetypical evil" as represented in the human brain"* (p. 8).

7. Conclusion

Taken together, our findings show evidence that the evolutionary value of interspecific relevant stimuli is associated with an advantage in accessing visual awareness during the CFS. While showing that an advantage of snakes (unlike spiders) remains throughout suppression conditions with different intensities, the results corroborate the assumptions predicted by SDT, testifying in favor of the unquestionable value of snakes in the evolution of vision in primates and showing the relevance of this stimulus for understanding the threat detection mechanisms.

Along with the important contribution on evolution, our results also provide further insights in the understanding of the mechanisms and functions of the fear systems, which could even prove useful in understanding of the emotional disorders involving these systems.

8. References

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