FEAR COMMANDS ATTENTION: SNAKES AS THE ARCHETYPAL FEAR STIMULUS?
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THE ARCHETYPAL FEAR
STIMULUS?

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To the most amazing result of my PhD journey, my daughter Joana
“My experience is what I agree to attend to.”

(William James)
ABSTRACT

Information regarding successful solutions to environmental hazards has accumulated in the gene pools of species, as a result of evolution. Therefore, from an evolutionary viewpoint, fear has played a central role in shaping mammalian genotypes. The goal of the present research was to elucidate the role of fear in the control of attention by investigating meaningful differences in the attentional processing of evolutionary-relevant animal stimuli and different categories of neutral stimuli. In study I we used a visual search task to examine attentional selectivity to a class of fear-relevant animal stimuli (snakes and spiders), compared to a different animal category, that of non-threatening animal stimuli presumably lacking evolutionarily derived fear-relevance (cats and fish). The results showed no asymmetry in reaction time and accuracy data between fear-relevant and neutral animals when they served either as targets or distractors. Instead, there was an increased distraction effect when the fear-relevant categories were presented simultaneously in the visual displays.

In studies II-IV we did not collapse snakes and spiders into the same category of evolutionarily fear-relevant stimuli, but compared these carefully matched stimuli in terms of their association with danger. The comparison was predicated on the notion that snakes carry a considerable more heavily evolutionary baggage to be feared by humans (Isbell, 2006; 2009) than do spiders (e.g., Davey, 1994). In order to avoid potential differences in variability among fear-relevant and neutral animal stimuli, we compared snakes and spiders with an ecologically valid stimulus, i.e., mushrooms, and presented these stimuli of interest against an emotionally neutral background composed by pictures of fruits. Moreover, we intended to study whether the perceptual load (e.g., increments in set size) modulated the attentional processing of such stimuli (Lavie, 1995; 2005). The results from studies II-IV consistently showed that snakes (compared to spiders and mushrooms) were preferentially processed, particularly under the most demanding perceptual conditions. Specifically, the privileged attentional processing of snake stimuli was most evident among many distractors (studies II-IV), in peripheral vision (study III – Experiment 1), at brief exposure times (< 300ms) (study IV), and when unexpectedly presented among the background stimuli (study III – Experiment 2). The evidence demonstrated that snakes are special and do not, like spiders, influence attention according to expectations from standard theory (Lavie, 2005). Rather this specificity of snake processing invites an evolutionary explanation, such as the one offered by Isbell’s (2009) Snake Detection Theory.

Finally, our set of results relating the effects of prior fear on attention showed somewhat inconsistent results. In study I, where snake and spider fearful participants were collapsed into one single group, participants were specifically sensitized to detect their feared stimulus, with the emotional ratings mirroring this effect. However, this result did not enable examination of potential differences in responses between snake and spider fearful individuals. Indeed, there are indications in the literature pointing to the relevance of such differentiation, showing that while snake fear is associated with the predatory defense system (e.g., Öhman, 2009), spider fear is more likely to be mediated by disgust (Matchett & Davey, 1991). Therefore, in studies II and IV, we examined potential differences between the two groups of participants. In study II there was a clear dissociation between the two types of animal fear, reflected in attention and emotion measures, indicating that spider fear was highly specific, whereas snake fear was associated with a more generalized enhanced evaluation of all negative stimuli. However, and given that in study IV the findings were not consistent, further research is clearly needed in order to clarify the potential moderators in the effects of prior fear on attention.
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Attention constitutes one of the most fascinating domains in psychology and has become a particular active and vigorous area of research. And what about emotion? Why are researchers so interested in the interface between attention and emotion? The likely answer is based on the reciprocal links intimately shared by emotion and attention, with both concepts having important evolutionary-driven functions. We are confronted with a myriad of competing stimuli simultaneously presented in our environment and the attentional system underlies the selection of some information at the expense of other information. Emotion interacts with attention by playing a key role in modulating the allocation of attentional resources for stimuli that are significant for an organism’s motivational state (e.g., Oatley & Jenkins, 1996). Hence, emotion and attention share theoretical conceptions, and are interconnected in the sense that they both deal with information processing priorities (Oatley & Johnson-Laird, 1987). In particular, threatening stimuli that are deeply rooted in evolution, such as snakes and faces (see Öhman, 2009), seem to have a unique status in such interactions. This interface warrants further investigation to elucidate the functions and mechanisms of the fear system as well as the implications for understanding emotional disorders, since many of these involve the fear system. Importantly, these evolutionary based stimuli may represent a valuable tool for studying the relation between emotion and evolution. Within a plausible evolutionary scenario, the goal of the project underlying this thesis was to refine the current conceptualization of the role of fear in guiding attention, combining experimental-cognitive and emotional approaches.
1 INTRODUCTION

1.1 EMOTION

There are many definitions of emotions, although no one is accepted by a majority of investigators in the field. However, a common point in these definitions is the notion that emotions have important functional relationships with the environment (see Oatley & Jenkins, 1996). Emotions mark environment events as significant to the individual, giving them priority for cognitive processing. Indeed, many definitions of emotion involve the concept of goal-relevance (e.g., Ellsworth & Scherer, 2003). Such goals may include immediate survival pressures, such as those related to predation, as well as more complex social goals, e.g., building social relationships (Öhman, Dimberg, & Öst, 1985). These assumptions reflect an important Darwinian influence (Darwin, 1872) on the contemporary study of emotions. Being attacked by predators or by rival conspecifics constitute potentially life-ending situations that risk to nullify reproductive success for all animals. Therefore, the outcomes of predatory-prey encounters determined whether or not individuals survived and reproduced, with many systems, such as fight and flight responses, evolving from these types of selection pressures (Oatley & Jenkins, 1996). The recurrence of particular classes of evolutionary requirements thus seemed to have deeply shaped emotions.

Emotions helped individuals meet specific evolutionary pressures by shaping the organism to attend to potential threat and to get ready for urgent action. Therefore, emotions promoted action-programs that assisted our ancestors in life-regulating behaviors, thus furthering the transfer of genes across generations (Öhman, 2006). These action-programs involve both the orientation to significant events in the environment, and the consequent organization of adaptive responses to such events (e.g., Levenson, 1999), which in turn involve a set of multi-component responses. The emotional responses may include physiological reactions (e.g., heart rate and respiratory changes), behavioural changes (e.g., approach or avoidance), and verbal reports of subjectively experienced feelings (e.g., likes or dislikes) (Lang, Greenwald, Bradley, & Hamm, 1993; Levenson, 1999). These responses are particularly important for responding to the challenges that are deemed important for the motivational goals of the individuals (Oatley & Jenkins, 1996) and, in concert, offer objective dimensions that allow the scientific study of emotions (Öhman, 2006).

1.2 FEAR

The emotion of fear is an aversive emotional state that enables the organisms to cope with impending danger (Öhman, 2000a). It has been shaped by evolutionary contingencies to protect creatures from perilous environments, promoting escape and avoidance in situations where survival is at stake. Hence, from an evolutionary perspective, fear appears to be a central aspect to the mammalian evolution. Considering that staying alive is a prerequisite to the central role of biological evolution - gene transfer across generations, fear is thought to be a preferential target of natural selection, sculpted by evolutionary forces (for reviews, see Öhman, 1993; 2000b; 2008).

From a functional perspective, it is likely that for behavioral defense systems to be effective in a potentially deadly situation, perceptual systems must be biased towards efficient identification of threat (Öhman, 2000b, 2008). Undoubtedly, fear promotes a maximal benefit, as failures to effectively locate threats and elicit the
appropriate defense systems (i.e., false negatives) are evolutionarily more costly than activating a defense response to an innocuous stimulus (i.e., false positives). The latter type of bias merely spends unnecessary energy, whereas the former may be lethal, and put an end to further reproduction. Susan Mineka (1992) has defined this cautiousness of evolution in facing with potential lethal events or situations as “evolutionary conservatism”. Indeed, this “play it safe” bias is assumed to be the evolutionary foundation of anxiety disorders (Öhman & Rücker, 2007).

1.3 DISTINGUISHING FEAR FROM ANXIETY

Fear and anxiety are closely related and overlapping emotional aversive states with threat as the central component. They share a similar response signature involving intensive negative feelings and strong mobilization of bodily responses. Such conflation between fear and anxiety is still evident in current clinical classifications, with the Diagnostic and Statistical Manual of Mental Disorders (DSM-IV-TR; American Psychiatric Association [APA], 2000), for instance, still including phobias and generalized anxiety disorder into the single nosological category of “anxiety disorders”. However, there are several factors known to differentiate these overlapping concepts. The critical distinction, according to Gray and McNaughton (2000), rests on the so called “defensive reaction” (McNaughton & Corr, 2004). Fear evokes a dire need to escape from a harmful situation (active avoidance behavior). Anxiety, on the other hand, may occur either when entering a dangerous situation (by a cautious “risk assessment”) or when passively avoiding it. Therefore, as argued by Epstein (1972), fear can be regarded as a coping emotion, while anxiety is elicited when the coping attempts fail, since there is an inappropriate activation of the defensive systems (Öhman, 2000b, 2008). This is tied to a further distinction involving the notion that fear, but not anxiety, is stimulus-driven, i.e., is elicited by an identifiable stimulus or situation. Finally, fear and anxiety can also be neuroanatomically distinct (see Davis, 1998). Although the amygdala complex, a collection of nuclei in the medial temporal lobe, plays a central role in both fear and anxiety, fear responses are mediated via the central nucleus of the amygdala (more acute and stimulus-driven responses), whereas the bed nucleus of the stria terminalis mediates anxiety (more lasting and not specifically associated with an eliciting stimulus).

Although fear and anxiety are functional and adaptive emotions, they can become a central component in many psychopathologies. Pathological fear and anxiety supervenes when the emotions are more recurrent and persistent, with an unreasonable intensity, and when the individuals are unable to cope with the objective danger or threat (e.g., Öhman, 2008). In particular, phobias are intense, uncontrollable, irrational and malfunctioning fears associated with specific stimuli.

1.4 FEAR-RELEVANT AND PHOBIC STIMULI

One of the theoretical attempts to explain the prominence of fears and phobias is predicated on Seligman’s (1971) preparedness account, which hypothesizes that human fears and phobias reflect an evolutionary prepared learning to fear events or situations that may have had fatal consequences to our ancestors. According to Seligman (1971), this could elucidate why intense fears and phobias tend to cluster around objects and situations that are fear-relevant in a phylogenetic rather than an ontogenetic perspective. Thus, we are more prone to fear, for instance, deadly predators, social evaluations, and wide-open spaces, rather than more contemporary threats, such as handguns, motorcycles, and broken electrical equipment (Seligman, 1971; Öhman & Mineka, 2001). Hence, Seligman (1971) states that evolution has prepared humans with a tendency to relate fear with situations that threatened the
survival of their ancestors. As a result, only minimal input is required to elicit fear responses toward such evolutionary-related stimuli. In addition, these prepared fears are highly resistant to extinction, and less affected by cognitive factors, compared to fears of more modern hazards (see e.g., Öhman & Mineka, 2001).

According to Mayr (1974), behavior can either be “intra-specific” or “inter-specific”. While the former is directed towards one’s own species thus involving social behaviors, the latter is directed at members of other species, with a critical role on the constant competition between predators and prey animals, the designated predator-prey arms races. This arms-race involves mutual adaptations by both predators and preys towards the development of more advanced systems to face the competitive relationships (e.g., Öhman, 2009). As noted by Öhman et al. (1985), this classification outlines prominent types of phobias (APA, 2000), namely animal phobia (e.g., snake and spider phobia) and social phobia (excessive fear of events and situations where the individual is the target of social attention and evaluation). These categories were also represented as dimensions in factor analyses data regarding self-reported fear questionnaires (A rrindel, Pickersgill, M erckelbach, Ardon, & Cornel, 1991). Additional factors also emerged in the self-reported questionnaires, such as the fear of bodily ailment, illness and death (blood phobia), as well as agoraphobic fears, which involve fear of, e.g., entering crowded or public places (agoraphobia).

1.5 PRINCIPLES OF FEAR

In a recent review by Öhman and Rück (2007), four principles of fear were suggested based on extensive empirical research. The authors also discussed the potential implications of these principles of fears for phobias.

1.5.1 Mobilize the Body for Defense

The emotion of fear prompts the mobilization of defensive responses, which are mediated by the sympathetic branch of the autonomic nervous system to enable metabolic resources for vigorous action. Functionally, information concerning threat should be prioritized in order to promote escape or avoidance when the threat is imminent (Fanselow, 1994). In the absence or at a low level of threat, fear stimuli, as well as novel and other relevant stimuli, elicit orienting responses. Typically, these responses involve scanning of the environment to assess the risk involved, as well as behaviorally passive responses (e.g., heart rate and skin conductance deceleration; Öhman, Hamm, & Hugdahl, 2000) that primes a readiness to act (e.g., Öhman & Wiens, 2004). When the threat imminence increases, such as when a predator comes near, there is a shift to active defense responses (e.g., fight or flight; Lang, Davis, & Öhman, 2000b), associated with a gradual mobilization of the autonomic nervous system activity (e.g., heart rate and skin conductance increase), and potentiated defensive reflexes (e.g., startle reflex) (e.g., Lang, Bradley, & Cuthbert, 1997).

Studies have shown distinct and enhanced psychophysiological responses in phobic participants. When exposed to their feared stimulus (e.g., snakes for snake fearful individuals), these participants show an activation of the fight-or-flight behavior, as reflected in an elevated skin conductance, a potentiation of the startle responses, and a stronger heart rate acceleration. In contrast, non-fearful participants exhibit orienting responses towards animal fear stimuli (e.g., snakes and spiders), compared to neutral stimuli (e.g., household objects, cute animals) (Globisch, Hamm, Esteves, & Öhman, 1999). The activation of autonomic responses in fearful individuals is also evident in mental imagery of fear relevant scenes (e.g., Cuthbert, Lang, Strauss, Drobes, Patrick, & Bradley, 2003).
1.5.2 Fear Can Be Conditioned and Extinguished

Potentially threatening events may be announced by subtle cues (smells and noises), which through Pavlovian fear conditioning can become learned warning signals of the imminent predator (see Öhman & Mineka, 2001, for a review). Hence, by learning to anticipate the threatening event, organisms can activate defense early, thus improving their odds to cope with the predator and survive the encounter. This type of learning is a case of classical (or Pavlovian) conditioning, in which organisms learn that an innocuous or non-aversive stimulus signals the occurrence of an aversive event allowing the fear responses towards the aversive stimuli to transfer to the signal stimulus (see Öhman & Wiens, 2003, for a review). Although Pavlov assumed that any stimulus paired with an unconditioned stimulus (e.g., aversive stimulus) could result in similar degrees of learning, Seligman (1971) has challenged this premise of equipotentiality. According to the evolutionary preparedness account, the adaptive function of learning might have been shaped by natural selection to potentiate survival-relevant relationships between cues and consequences (e.g., Seligman, 1971), such that evolutionary-relevant stimuli become more easily associated with aversiveness than cues that have not been associated with threat (e.g., food). Therefore, learning to associate subtle cues (e.g., smells or sounds) to a lurking predator seems to be highly evolutionarily prepared in the sense that minimal input (e.g., training) is required for connecting the cues to the predator.

There is strong evidence suggesting that fear learning, through Pavlovian conditioning, is more effective to evolutionary relevant stimuli (snakes, spiders, and angry faces) than to stimuli without such relevance (e.g., flowers) (see Öhman & Wiens, 2004, for a review). The most remarkable evidence comes from studies with lab-reared rhesus monkeys with no previous contact with snakes and no initial signs of fear when exposed to a snake or to snake-related stimuli. However, when the monkeys watched manipulated videos of a conspecific exhibit strong fear responses to snake stimuli, the monkeys rapidly acquired strong fear reactions to such stimuli, thus showing the effectiveness of snakes for observational fear conditioning (e.g. Mineka & Cook, 1993). Such fear conditioning to snakes was not evidenced when the monkeys observed a “model” monkey showing identical fear responses towards a neutral stimulus (e.g., flowers) (e.g., Cook & Mineka, 1990). These findings provide good support in favor of the preparedness postulate (Seligman, 1971).

Psychophysiology studies with human participants have also been conducted in order to test the preparedness account. By using differential conditioning tasks, Öhman and colleagues have shown more robust conditioning to fear-relevant (e.g., snakes and spiders), rather than to fear-irrelevant stimuli (e.g., flowers and mushrooms) (see Öhman, 1993; 2000; 2008; Öhman & Mineka, 2001, Öhman & Wiens, 2003, for reviews). Furthermore, results have shown enhanced resistance to extinction (repeatedly presentation of the signal stimulus in the absence of the aversive stimulus) to fear-relevant conditioned stimuli than to the neutral stimuli. Interestingly, these effects were not extended to other unconditioned stimulus types, such as non-aversive stimuli (Öhman, Frederikson, & Hugdahl, 1978), or contemporary relevant stimuli, such as broken electric equipment (Hugdahl & Kräker, 1981) or guns (Cook, Hodes, & Lang, 1986). In fact, the elevated resistance to extinction in humans is more evident than the rapid acquisition, which makes the persistence of the conditioned fear a central explanation for why phobias are pathological.

Finally, there are results showing that human participants tend to perceive illusory correlations between the occurrence of fear-relevant stimuli and other aversive stimuli, such as shocks, even thought the latter was as likely to occur after the presentation of either the fear-relevant or the fear-irrelevant stimuli (e.g., Tomarken, Cook, & Mineka, 1989). Moreover, even though the immediate illusory correlations did
not differ between aversive events (likelihood of shock) and between evolutionary versus contemporary threats, the retrospective illusory correlation was confined to the former stimulus (e.g., Tomarken, Sutton, & Mineka, 1995).

1.5.3 Fear is Nonconsciously and Automatically Activated

It is reasonable to assume that stimuli that have served as signals to important survival threats over the course of evolution are processed very rapidly and efficiently, and with restricted conscious access, as this carry obvious benefit for survival (Öhman, 2009). Ancient sensory mechanisms with an origin in organisms with primitive brains evolved for rapid detection of what could turn out life-threatening events, on the basis of a “quick and dirty” analysis, calling on an attentional shift in order to monitor the environment for potential hazardous stimuli. Such mechanism evolved in brains with limited capacity for advanced cognitive elaboration to promote early defense recruitment, which carried an obvious survival benefit. There are data implying that evolutionary-relevant stimuli contain features that can activate relatively early structures in the visual pathways even prior to recognition of the stimulus (Öhman & Wiens, 2004). This rudimentary perceptual analysis is predicated on the concept of a “low road”, which mediates the information about threat through the amygdala and without involving the cortex (LeDoux, 1996; Öhman, 2005).

Evidence to date strongly supports the notion that fear-relevant stimuli are quickly and non-consciously detected by a subcortical circuit that is centered in the amygdala (LeDoux, 1996; Öhman, 1993). This structure has downstream connections to structures (hypothalamic, midbrain and brainstem nuclei) that control both psychophysiological (e.g., cardiovascular changes) and behavioral responses (e.g., escape), which are central in fear activation.

To exclude conscious recognition of stimuli as a mediating factor of fear activation, researchers typically use backward masking techniques, i.e., they present the target stimulus very briefly and immediately followed by the presentation of a masking stimulus so that participants only are able to report that they have seen the masking picture (e.g., Wiens, 2006). There is a bulk of data showing that fear stimuli activates the amygdala even when conscious recognition is prevented by masking techniques, with evidence showing that this access occurs via the superior colliculus of the midbrain and the pulvinar nucleus of the dorsal thalamus (e.g., Morris, Öhman, & Dolan, 1999). The results from studies using imaging techniques show non-conscious activation of responses to fear stimuli (snakes, spiders, and emotional faces), evidenced in specific activation of the central structure of the fear circuit (amygdala) to masked, compared to non-masked fear stimuli (e.g., Whalen et al., 1998, for facial stimuli). A further study showed that the activation of the amygdala was not affected by whether the emotional face (fearful) was spatially attended or not (Vuilleumier, Armony, Driver, & Dolan, 2001).

The specific brain responses to masked stimuli have also been shown to be specifically enhanced in participants with specific fear of either snakes or spiders (but not both) (Carlsson, Petersson, Lundqvist, Karlsson, Ingvar & Öhman, 2004). Moreover, Öhman and his co-workers showed elevated skin conductance responses to masked presentations of the feared stimuli (snakes and spiders) by using a similar recruitment criterion as that used by Carlsson et al. (2004) (Öhman & Soares, 1994). This psychophysiological effect was not shown when the participants were exposed to masked pictures of fear-relevant but non-feared stimuli (i.e., snakes for spider fearful participants and spiders for snake fearful participants). The results also showed that the shorter the interval between the onsets of the target and masked stimulus (the stimulus-onset asynchrony, SOA), the lower the confidence of the participants in the recognition of the target pictures (snakes, spiders, mushrooms, and
flowers), supporting the effectiveness of the manipulation (see Esteves & Öhman, 1993, for similar results with emotional facial stimuli). Moreover, this pattern of results have also been shown in non-fearful participants who have been exposed and masked fear-relevant stimuli (snakes, spider, and angry faces) after Pavlovian conditioning to unmasked presentation of the stimuli (e.g., Öhman & Soares, 1993; Esteves, Dimberg, & Öhman, 1994).

### 1.5.4 Fear Guides Attention

To allow for effective defensive responses, the perceptual system must be biased towards early and reliable recognition of threat-related stimulus, such as predators (e.g., Calvo & Lang, 2005). Based on the distinction between “automatic” and “controlled” processing of information (e.g., Schneider, Dumais, & Shiffrin, 1984), it is argued that both processing mechanisms interact to monitor for the presence of potential threat in the environment (see section 1.7). Studies have shown that fear-relevant stimuli serve as a guide to attention by providing a switch from automatic to controlled processing (e.g., Öhman, 2008, for a review), with the amygdala playing a crucial role in prioritizing emotional stimuli for focal attention.

In a pioneering study by Öhman and his co-workers (Öhman, Flykt, & Esteves 2001a), the authors set out to examine whether perceptual processes would be biased towards fear-relevant stimuli at an automatic, rather than controlled, level of processing. Using a visual search task, they presented arrays of pictures of snakes, spiders, mushrooms and flowers, in two conditions: without a target picture (all pictures of the same category) and with a target picture (one picture from a different category). In participants non-selected to fear either snakes or spiders the results showed a general bias for a faster (shorter response times) and more efficient detection (more correct responses) when the deviant target was fear-relevant (snake or spider), compared to non-fear-relevant pictures (mushrooms and flowers). In a separate experiment in which the set size of the stimulus display was manipulated, the results showed that this fear-relevance advantage was independent of the number of distractors in the display. Moreover, in a further experiment, the attentional bias was further enhanced when the target stimulus actually elicited fear in groups of spider or snake fearful participants.

The results showing that threatening animals are more quickly and efficiently detected in visual search settings have been replicated by several research groups (e.g., Lipp, 2006; Lipp, Derakshan, Waters, & Logies, 2004; Rinck, Reinecke, Ellwart, Heuer, & Becker, 2005) and have been extended to visual search studies with emotional facial stimuli (e.g., Eastwood, Smilek, & Merikle, 2001; Öhman, Lundqvist, & Esteves, 2001b). Further research using visual search tasks have also showed that when the fear stimuli are presented as unexpected distractors while the participants are actively looking for a neutral target picture, they interfere more with the central search task, compared to neutral stimuli (Lipp & Waters, 2007; Miltner, Krichef, Hecht, Trippe, & Wiss, 2004). In addition, it has also been shown that when fear stimuli are presented as a class of background stimuli to be ignored, they interfere with the task to a larger extent than classes of neutral background stimuli.

These results show that when fear stimuli are presented as targets they facilitate attention and, on the other hand, when they are presented as distractors, they interfere with attention. Hence, the results suggest that fear stimuli are effective in shifting and engaging attention (e.g., Öhman et al., 2001a; Miltner et al., 2004), and in impeding the disengagement of attention from the fear stimuli (e.g., Rinck, et al., 2005) (see Posner & Peterson, 1990).
1.6 THE FEAR MODULE

Based on the extensive literature reviewed above, Öhman and Mineka (2001) introduced the concept of an evolved Fear Module in order to facilitate an overall characterization of the fear system. This module is thought to be an independent behavioral, psychophysiological and neural system that has evolved in order to solve adaptive problems related to potentially life-threatening situations such as encounters with hunting predators. The module is automatically and selectively activated by such stimuli, relying on a dedicated neural circuitry and being relatively encapsulated from more advanced human cognition (Öhman & Mineka, 2001).

1.6.1 Snakes as the Prototypical Fear Stimulus

As alluded to in the earlier sections, there are commonalities across humans in the type of events or situations that are deemed emotionally significant because they were related to powerful evolutionary forces (e.g., Arrindel et al., 1991; Öhman, 1986). Snakes are part of such hard-wired fear stimuli that are deeply grounded in evolution. The high prevalence of an intense fear of snakes in humans (e.g., Agras, Sylvester, & Oliveau, 1969) and in other primates (Mineka, Keir, & Price, 1980) has been taken to suggest that the fear of snakes is a result of an ancient evolutionary history. In fact, snakes remain a major threat to humans, because global mortality attributed to envenoming from snakebites worldwide was recently estimated as high as 94,000 human deaths each year, thus representing a significant public health problem (Kasturiratne, Wickremasinghe, de Silva, et al., 2008).

A recent theory advocates that snakes were the first predators to prey on early mammals and, as a consequence of an evolutionary arms-race, particular features of the visual system of our primate ancestors seemed to have evolved largely to help detect and avoid venomous snakes (Isbell, 2006, 2009). This evolutionary hypothesis proposed by Lynne Isbell (2006, 2009), the Snake Detection Theory, is based on converging evidence from several scientific disciplines, such as psychology, neuroscience, paleontology, biogeography, molecular biology, genetics, biological anthropology, nutrition, and geology. The theory proposes that the superior vision and large brains of primates can be at least partly attributed to predation pressure from snakes throughout primate evolutionary history. The evidence reviewed by Isbell (2006, 2009) suggests that constrictor snakes were prominent predators on the first primates (about 100 Mya), with other predators, such as raptors, emerging later in evolution (circa 20-50 Mya). The emergence of venomous snakes, which took place by about 60 Mya, provided an important milestone in the evolution of snakes as predators. As a response to this escalation in the predator-prey arms race, anthropoid primates developed an improved visual system to effectively detect and avoid snakes before they could strike. Snake venom constitutes a powerful lethal weapon, even for large prey as primates. Indeed, the death rate in humans who were bitten by a snake, which I referred to earlier in this section (Kasturiratne, et al., 2008), represents good evidence in support of the devastating effects of snake venom that occurs even in the current days.

The evolution of snakes in the development of an effective venom resulted in increased selection pressures for improved defensive strategies by primates. Given that the detection of venomous snakes is clearly demanding, as these predators are often camouflaged either in vegetation including trees, primates had to developed improved perceptual systems for an enhanced detection of such predators (see Öhman, 2009). Of particular relevance is the pattern of primate evolutionary coexistence with venomous snakes, with primates sharing a longer evolutionary history with venomous snakes (Old World anthropoids) having more advanced visual systems and showing more consistent fear of snakes, compared to primates that did not have such close history (New World and Malagasy monkeys) (Isbell, 2009). According to Isbell (2006,
the evolutionary pressures imposed to primates resulted in an improved visual system, as reflected in an improved vision, as well as in the bidirectional connections between the sensory systems (such as the visual system) and the amygdala (LeDoux, 1996; Öhman, Carlsson, Lundqvist, & Öhman, 2007).

1.7 SELECTIVE ATTENTION

Selectivity resulting from attentional mechanisms is a central feature of our cognitive activity. We are constantly subjected to a barrage of information impinging upon our senses. Given that not all the impinged information can be processed, selecting from among all the potentially available stimuli is mandatory. Indeed, this process is the most evident manifestation of selective attention (e.g., Pashler, 1998). The often cited passage by William James (1890, pp. 403-404) is commonly used to refer to the selectivity of processing:

"Everyone knows what attention is. It is the taking possession of the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought."

Attention can be divided into two broad categories: voluntary and reflexive attention. Voluntary attention refers to our ability to intentionally attend to something, thus reflecting top-down, goal-directed influences. Reflexive attention (or bottom-up, stimulus-driven), on the other hand, involves the capturing of attention by sensory events (often termed attentional capture, e.g., Gazzaniga, Ivry, & Mangun, 2009). So what are the factors that modulate the selection of a particular visual stimulus, at the expense of other stimuli present in our surroundings? According to Corbetta and Shulman (2002), the dynamic interaction between top-down and bottom-up factors will determine the direction of attention. The top-down system is a slower, goal-directed mechanism (e.g., Treisman & Gelade, 1980; Treisman, 2006) involved in the selection of sensory information and responses and influenced by factors such as expectation, knowledge, and current goals (e.g., cognitive task demands). The bottom-up system, on the other hand, is a fast (sometimes compulsory), stimulus-driven mechanism, involved in the information processing elicited by incoming sensory stimulation including, for instance, the processing of salient, unexpected, novel visual stimuli (e.g., Nakayama & Mackeben, 1989).

The interactions between goal-driven and stimulus-driven systems are well characterized by the notion of attentional control settings as suggested by Folk, Remington, and Johnston (1992). They argue that there are attentional control settings that tune the ability that some stimuli have to grab attention in accordance with their relevance for the current goals of the individual. However, to allow only stimuli that are currently relevant to influence behavior entails the risk to overlook imminent dangers or to miss more profitable options. Thus, any organism is well advised to remain sensitive for changes of the current situation despite concentrating on an ongoing action or task. For example, animals that ignore the appearance of a predator while feeding would hardly survive and are unlikely to be found among our evolutionary ancestors. Therefore, it is reasonable to assume that the evolved mechanisms are somehow able to manage a balance between facilitating the impact of currently relevant information in order to maintain an intention and continuously monitoring the environment for potentially significant information on the other hand. Yantis and Hillström (1994) hold that it should be ecologically more useful for attention to be drawn to new objects in the field since these may represent either an important threat to be avoided (like a predator) or an important opportunity to be sought out (like prey).

There is strong support for the notion that the bottoms-up and top-down systems generally operate together and mutually interact (Corbetta & Shulman, 2002; Posner & Petersen, 1990). Moreover, neuroscientific evidence supports the distinction
by suggesting partially isolated networks of brain areas performing different attentional functions (Corbetta & Shulman, 2002). The system involved in preparing and applying goal-directed (top-down) selection for stimuli and responses includes specific areas in the dorsal posterior parietal and frontal cortex. The other system is specialized in the detection of behavioral relevant stimuli, particularly when they are salient, unexpected, and potentially dangerous. It involves the temporo-parietal and ventral frontal cortex, it is largely lateralized to the right hemisphere, and it operates already at the level of striate and extrastriate cortex. This network seems to interrupt ongoing cognitive (“circuit-breaking” function) and neural activity, directing attention to stimulus that might be behaviorally important and therefore taking high priority in the brain. One hypothesis is that this network may serve as an alerting system to detect behaviorally relevant stimuli, but without high resolution spatial sensors. According to the functional brain imaging literature, information from sensory input can bypass perceptual analysis, and result in motor outputs, without involving feedback information flowing from “high” to “low” brain centers. Attention can then modulate the baseline activity at the first stage of cortical information processing, the primary visual cortex, by increasing the gain on incoming visual information. Moreover, attention may also send top-down signals and, therefore, increase the baseline activity in the striate and extrastriate cortex (Kanwisher & Wojciulik, 2000).

It is generally assumed that selective attention mechanisms involve two hierarchical stages that are functionally independent. In order to perform any type of selection in attention it is assumed that the information to be processed needs to be available, with some preattentive processing required prior the operation of selective attention. Therefore, the distinction between preattentive and attentive processes is critical in the study of selective attention. Preattentive processes are processes that operate independently of the focus of attention and, as a consequence, are applied to all of the objects in the visual field, regardless of whether an object is the focus of attention or not. These processes occur automatically and, therefore, can work in parallel across many different sensory channels without loss in efficiency (Wolfe, 2000). Attentive processes, on the other hand, require the allocation of attentional resources to a limited extent of the visual field. The later system is limited in capacity and processes information serially (Wolfe, 2000). The preattentive process describes a monitoring system, which constantly and automatically keeps track of what is happening in the environment. When this monitoring system locates a threatening stimulus, it automatically shifts the attention so as to bring that same stimulus into the focus of voluntary, conscious attention. Indeed, some studies provide indications that the emotional properties of the stimulus may influence perception prior to the analysis of its semantic meaning (Morris et al., 1999).

### 1.7.1 Selective Attention Under Load

The locus of selective attention constitutes one of the central issues in attention research. According to the early selection view, initially proposed by Broadbent (1958) and further developed by Treisman and Geffen (1967), preattentive processing only includes rudimentary perceptual processing, with attentive processes being necessary to integrate features to form meaningful objects (e.g., Broadbent, 1958). Consequently, unattended stimuli are not fully perceived and only basic physical features of the stimuli (e.g., spatial location, color, orientation) are extracted and represented in parallel. Rather, the late selection view, advanced by Deutch and Deutch (1963) and Norman (1968), held that the preattentive processing presupposes the perceptual analysis of the entire scene, including object identification. Thus, according to this view, perception is an automatic process to the extent that there remains...
available capacity. In other words, attention is not a necessary prerequisite for all the stimuli in the environment to be processed to a semantic level (e.g., Duncan, 1980).

An attempt to resolve the debate of the early versus late selection was proposed by a hybrid model, the perceptual load theory (Lavie, 1995, 2005), which combines both views. According to this theory, the locus of the “bottleneck” in the sequence of information processing is dependent on the processing load involved in the primary task. In tasks where the task-relevant stimuli place low demands on the perceptual system, task-irrelevant stimuli may be perceived (late selection). However, when task-relevant stimuli place higher perceptual demands, the perception of task-irrelevant stimuli can be prevented (early selection), since the perceptual load involved in the task consumes all the available capacity. Therefore, when the processing load is high there is an early selection, while when the processing load is low selection takes place at a later stage. Therefore, the perceptual load theory combines the view that perception is capacity-limited (early selection) and that it involves an automatic process while attentional resources are not depleted (late selection) (e.g., Eliti Wallace, & Fox, 2005).

The work developed by Lavie (1995, 2005) holds that stimuli that are task-irrelevant (distractors) are not processed beyond a fairly superficial level when perceptual resources are fully occupied in an ongoing task. In contrast, when the perceptual load involved in the task is low, and perceptual capacities involved in the task are not exhausted, there are more resources available for processing the distractors. Importantly, the concept of perceptual load is defined within the specific task or context, with an increased perceptual load meaning that either there is an increase in the number of items to be perceived, or that the same number of items is kept but their perceptual identification is more demanding on attention (e.g., heterogeneous displays).

According to the biased competition theory (Duncan, 1996), the competition among multiple stimuli for neural representation can be controlled by biases that favor one particular stimulus at the expense of other competing ones, with both bottom-up and top-down mechanisms modulating these biases. Recently, it has been proposed that the objects’ competitive interactions in the visual cortex, along with the biasing mechanisms to resolve the competition in favor of the target object, may constitute the neural mechanism underlying perceptual load (Torralbo & Beck, 2008). Therefore, the manipulations of perceptual load may also result in an increased sensory competition, with selective attention biasing the competition in favor of the attended stimulus. According to this perspective, a task is characterized as having a high perceptual load when it involves a strong competition among potential targets and therefore a top-down bias is needed to resolve the ongoing competition and select the target. On the other hand, if the task involves a low perceptual load, there is a minimal competition among potential targets and thus little top-down bias is needed for the selection of the target (Beck & Kastner, 2009). The competition may also be resolved by bottom-up mechanisms, with their source in stimulus-driven signals (e.g., a salient item that contrasts against its background). Interestingly, although bottom-up mechanisms may take place in the visual cortex, it is possible that some stimuli (emotionally salient) may be biased through connections with the amygdala (see Beck & Kastner, 2009, for a review).

1.7.2 The Visual Search Paradigm

In a relatively recent development (Hansen & Hansen, 1988), visual search task has become a major tool to examine the reciprocal links between attention and emotion (see Yiend, 2009, for a review). Indeed, it is deemed as an effective tool for investigating selective attention to different categories of visual information (see Wolfe, 2000, for a review). It captures important aspects of our visual world, as we
constantly search for specific items in cluttered scenes. In a typical visual search task
the observer is presented with a series of displays showing a variable number of items.
The displays are presented one at a time and the task is to look for a target item (a
stimulus that differs from the remaining ones, i.e., the distractor items). The target
stimulus is present on half of the trials and absent on the other half, where only
distractor items are presented. The participant’s task is to decide, as quickly and
accurately as possible if there is a target stimulus among the distractors, and to press
different response buttons depending upon their decision (presence or absence of a
target item), with both reaction times and accuracy being recorded.

In order to provide a direct measure of search efficiency, reaction times
are commonly analyzed as a function of the set size, estimating the time taken to
process each stimulus in the visual search displays (Wolfe, 1998). The pattern of results
seems to depend on the different combinations of targets and distractors that are used in
the experiment. While in some cases the presence of distractors have a small
interference with the target detection (reflected in shallow slopes), in other cases
increasing the number of distractors significantly increases the search time it takes to
detect the target (reflected in steeper slopes) (Duncan & Humphreys, 1989; Wolfe,
1998).

According to a theory proposed by Duncan and Humphreys (1989), the
speed of the search process is strongly related to the similarity between targets and
distractors, as well as to the similarity among distractors (distractor-distractor
similarity). This perspective hence assumes that there is a continuum in the visual
search process. Specifically, searches are easier with increased similarity within
distractors and, on the other hand, searches are difficult with an enhanced similarity
between targets and distractors.

In cases where targets and distractors are similar, the target does not
differ from the surroundings (i.e., the distractors) which results in less efficient target
detection rates. In this scenario, the individual items in the display may require scrutiny
to discern which item corresponds to a distractor or, instead, to the actual target.
However, in situations where the target stimulus is dissimilar from the distractors, then
distractors can be perceptually grouped, which results in a more efficient search to
detect the target stimulus. In a similar way, when the class of distractors is similar (i.e.,
homogeneous), they can easily be grouped together, thus giving a higher saliency to the
target, and facilitating its detection (Duncan & Humphreys, 1989; Rauschenberger &
Yantis, 2006; Wolfe, 1998).

The visual search literature shows that stimuli differing in the power to
draw attention (usually designated saliency) may differ in their ability to affect visual
search performance (e.g., Constantinidis & Steinmetz, 2001). Thus, stimuli displaying
the highest salience because they differ substantially from their surroundings in some
simple visual feature are more likely to improve the search rates (e.g., a red item is
undoubtedly more salient when presented against a background of green items) (e.g.,
Theeuwes, 1992; Yantis, 1998). Although most versions of the visual search task
typically use highly artificial stimuli (e.g., lines, letters), in the studies included in this
thesis (I-IV) we have used more ecologically valid stimuli (photographs of the stimuli
in their natural background). We designed the several experiments in this thesis
carefully in order to avoid potential perceptual confounds. Although in study I we used
a varied mapping design, with every stimulus category being presented both as targets
and distractors, in the remaining studies (II-IV), we used a constant mapping design,
i.e., the same class of distractors was used across trials with different target conditions
(see Shiffrin & Gardner, 1972). Hence in study I, although we could examine both
target and distractor effects, there were dissimilarities between the two classes of
stimuli, making it hard to disentangle target and distractor related effects. However, in
studies II-IV, while using the constant mapping design, we tried to avoid such problem while keeping constant the class of distractors (pictures of fruits).

1.7.3 Selective Attention to Emotional Stimuli in Participants Diagnosed with Anxiety Disorders

Selective attention towards potentially dangerous stimuli is decisive since it allows the opportunity to engage in a defensive behavior, thus increasing the chances of avoiding harm. The emotion of fear then carries an obvious adaptive value. However, fear may become dysfunctional and turn into anxiety disorders, such as phobias. The attentional system of anxious individuals seems to be particularly sensitive to the presence of fear-related stimuli in the environment by rapidly identifying the potential threats and quickly eliciting appropriate defensive responses (e.g., see Fox, 2004, for a review). Thus, we can assume fundamental biases in information processing may be underlined by individual differences in the emotional responses to environmental stimuli.

Anxiety has been associated to a hypervigilant fear detection system (Eysenck, 1992), with extensive evidence showing that individuals with clinical anxiety disorders (e.g., Mathews & MacLeod, 1985), as well as nonclinical individuals with high trait-anxiety scores (e.g., Fox, 1993), have emotion-related biases in attention. However, the effects of state versus trait anxiety (acute anxiety and more endurable and stable levels of anxiety, respectively) underlying the attentional mechanisms have not yet been clarified, although a recent study has contributed with interesting findings (Pacheco-Unguetti, Acosta, Callejas, & Juan Lupiáñez, 2010). The results from this study showed that the different types of anxiety (state and trait) seem to be associated with different attentional networks. While trait anxiety appears to be related to difficulties in the executive control network, state anxiety is linked to an improved functioning of the alerting and orienting networks.

The assumption that threatening information engages attention more effectively in anxious individuals has been widely supported in both generally anxious (e.g., Mathews & MacLeod, 1994) and specific phobic groups (e.g., Lavy & van den Hout, 1993), particularly in tasks involving competition between stimuli for further cognitive processing. This preferential processing selectivity towards threat-related stimuli represents one of the most relevant clinical consequences in the maintenance of anxiety disorders (e.g., Williams, Watts, MacLeod, & Mathews, 1997). This biased processing may, on the other hand, result in the perception of the world as an unsafe, uncertain, and dangerous place, which would then increase the state anxiety levels of these individuals (Mogg, Millar, & Bradley, 2000). Further supporting the role of attentional bias in maintaining anxiety in individuals diagnosed with anxiety disorder are results showing that this preferential processing seems to diminish and even disappear after successive treatment of anxiety disorders, namely treatment for specific phobias (e.g., Mattia, Heimberg, & Hope, 1993).
2 AIMS OF THE THESIS

Inspired by the snake detection theory (Isbell, 2009), the general aim of this project was to establish meaningful differences in the attentional processing of two classes of fear-relevant animal stimuli, snakes and spiders, as compared to different categories of neutral stimuli. We also wanted to examine whether such processing would be modulated by the perceptual load involved in the visual search settings. Finally, we wanted to assess if the differences between the fear-relevant and the neutral classes of stimuli would be particularly obvious in participants who were highly fearful of either of the fear-relevant stimuli. Overall, the research intended to provide new insights into fear and fear-related disorders.

The specific goals of the thesis were:

- To compare the attentional processing of evolutionary-relevant animal stimuli (snakes and spiders) and non-evolutionary-relevant animal stimuli (cats and fish), both in a normal sample and in a sample composed by highly fearful participants (of either of the fear-relevant animals, i.e., snakes or spiders) (Study I)

- To investigate whether there were differences between the attentional and emotional processing of highly feared stimuli but with a distinct evolutionary relevance (snakes and spiders) in contrast with mushroom stimuli. We also assessed whether the perceptual load involved in the task modulated the processing of fear targets. Finally, we examined possible dissociations between snake and spider fearful individuals (Study II)

- To further establish theoretically meaningful differences between the effect of snake and spider pictures on human attention in visual search settings. Specifically, we studied whether snakes were more easily spotted than spiders (and mushrooms) in peripheral vision and in visually taxing contexts (increased number of items and heterogeneous displays) (Study III)

- To extend the data base by examining visual search for snakes, spiders, and mushrooms in a new, ecologically relevant, visually degraded condition (short stimulus presentations). In line with the studies II and III, we also assessed whether the level of perceptual load would modulate the facilitated detection of snakes and spiders. Finally, we examined whether the attentional priority for both fear-relevant categories was influenced by the participant’s prior fear (Study IV)
3 METHODS  

3.1 PARTICIPANTS

Participants were undergraduate students attending different courses at several universities in Portugal (ISCTE - Instituto Universitário de Lisboa, Lisbon; ISLA, Superior Institute of Leiria, Leiria, and Universidade Lusófona de Humanidades e Tecnologias, Lisbon). They all volunteered to participate and gave informed consent. Participants were recruited at several classes and through advertisements placed at the various faculties. A total of 338 individuals (mean age=22 yrs) participated in the different studies, with a strongly biased female to male ratio (295/43). The gender bias is consistent with studies showing significantly higher self-reported fear in females than in males, with fear of snakes and spiders displaying the largest sex differences (Arrindel, 2000).

Participants were all screened for snake and spider fears by answering the Portuguese versions of the Snake Phobia (SNAQ) and Spider Phobia (SPQ) Questionnaires, translated from the original version developed by Klorman, Weerts, Hastings, Melamed, and Lang (1974) (for details see section 3.4). Moreover, following the same procedure as that introduced by Öhman and Soares (1994), and subsequently used by other authors (e.g., Carlsson et al., 2004), we selected participants based on their animal fears. Those scoring high on the SNAQ and low on the SPQ were considered for the snake fearful group. The opposite criterion was used to allocate participants in the spider fearful group (i.e., low scores on the SNAQ, and high scores on the SPQ). Moreover, participants scoring low to medium on both questionnaires were assigned to the control or non-fearful group. It was only in Study I, Experiment 1, that participants were not selected based on their prior fear, although in Experiment 2 of the same study both snake and spider fearful individuals were combined into the same group. This was not the case in studies II and IV, where two independent groups of snake and spider fearful participants were compared to a control group. It should be noted that in Study III the data was not analyzed according to the allocation of participants into the fearful and non-fearful groups. The enrolment strategy in this study was to obtain a sample of participants with matched levels and variance of snake and spider fears, as the main purpose of the study was to investigate differences in the attentional process of snakes and spiders (with mushrooms as a neutral control) in visually taxing contexts. More information concerning the selection procedures is given in each of the studies I-IV.

3.2 ETHICS

A consultation with the Regional Research Ethics Committee at Karolinska Institutet assured that the Swedish law for ethical evaluation of research was not applicable for the experiments in this thesis.

Participants were informed about the nature of the tasks they were asked to perform, and they were given the option of discontinuing their participation at any time during the study. The individuals were payed 5 Euros (in the form of a photocopy card) for their participation, although care was taken not to influence the participants decision's to participate or not in the experiment.

3.3 STIMULI

The human attentional system has evolved to effectively monitor stimuli which are crucial to the predatory defense system (e.g., Öhman & Mineka, 2003). Snakes provide the best representation of such unique stimuli, deeply grounded in evolution (for reviews see Isbell, 2006, 2009; Öhman, 2009; Öhman & Mineka, 2003), which motivated our choice to use pictures of snakes as one of the fear-relevant
stimulus. In addition, we opted for spiders as the comparison fear-relevant stimulus. According to epidemiological data, both stimuli are among the most feared by humans (Agras et al., 1969), and among the most frequent members in the clinical category of animal phobias (APA, 2000). Also, snakes and spiders do not differ in ratings of valence, arousal and dominance collected from large samples of participants (Lang, Bradley, & Cuthbert, 2005). Therefore, we carefully matched the fear-relevant stimuli in terms of their association with danger, because the danger or threat was a central parameter in this thesis.

Although the attentional system has evolved towards the efficient processing of animal stimuli (see New, Cosmides, & Tooby, 2007; Öhman, 2007a), few studies have compared fear-relevant and fear-irrelevant animal stimuli (Lipp, 2006; Lipp, Derakshan, Waters, & Logies, 2004; Tipples, Young, Quinnlan, Brooks, & Ellis, 2002; Rinck, Reinecke, Ellwart, Heuer, & Becker, 2005). Therefore, in Study I, we compared fear-relevant stimuli (snakes and spiders, collapsed into the same category) with animal control stimuli supposedly without evolutionary mediated fear relevance (cats and fish), and with equivalent ratings (neutral) of valence, arousal, and dominance (Lang et al., 2005). However, in studies II-IV, we compared snakes and spiders (not collapsed into the same category) with mushroom stimuli, as well as with fruits, which were included as the background stimuli. The selection of the latter two stimulus categories was based on the fact that both stimuli lacked relevance in an evolutionary perspective and both coexist in the same ecological environments as the snakes and spiders.

All picture stimuli were matched so that they would display the central objects against a background involving their typical ecology (e.g., grass or other vegetation, sand, gravel, pebbles, and parts of stones). The picture sets included several exemplars of each category (9 exemplars in study I, and 18 in studies II-IV), all with the same size within each study. The pictures from study I were the same as those used by Öhman et al. (2001a). In studies II-IV, these pictures were retained, with the remaining ones being carefully selected from the Internet (except for the fruits, which all came from the Internet). Although it is not possible to completely rule out potential low-level physical feature differences between the different pictures, we opted for “real” pictures to ensure a more ecologically valid study. In summary, we have carefully chosen our stimuli based on theoretical (evolutionary) considerations, and we have tried to keep track of their emotional valence, likely evolutionary relevance, and perceptual features.

3.4 SELF-REPORTED QUESTIONNAIRES

Fear of snakes and spiders was assessed by SNAQ and SPQ, respectively, in studies I-IV (Klorman et al., 1974). The questionnaires included 30 (SNAQ) and 31 (SPQ) true or false statements that were translated into Portuguese using forward and backward translation procedures. The questionnaires have been shown valid and reliable psychometric characteristics across several samples (e.g., Fredriksson, 1983; Klorman et al., 1974). Moreover, they have proved to be effective measures to allow the allocation of snake and spider fearful individuals (e.g., Öhman et al., 2001a). The use of both questionnaires has been extended to research (e.g., Carlsson et al., 2004) and treatment settings (e.g., Hunt et al., 2006; Murris & Merckelbah, 1996, for studies using SNAQ and SPQ, respectively), with the latter studies showing that both questionnaires were sensitive to therapeutic changes and correlated with other subjective and behavioral measures of snake and spider fear.

We have recently collected normative psychometric data on the Portuguese translation of the SNAQ and SPQ (Esteves, Silva, & Soares, in preparation). The reliability of the scales were satisfactory according to the data
collected with undergraduate Portuguese students (N = 633) (SNAQ: Cronbach’s α = .91, and SPQ: Cronbach’s α = .92). Moreover, three months test-retest reliability was high (see Muris & Merckelbach, 1996, for similar findings). As previously reported in other studies (e.g., Agras et al., 1969), our normative data also showed sex differences indicating that females reported higher levels of fear than males.

In study II, in the addition to the SNAQ and SPQ, we also used Portuguese versions of the Spielberger Trait Anxiety Inventory (STAI-T) (Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983), and The Hospital Anxiety and Depression Scale (Zigmond & Snaith, 1983) to assess the levels of anxiety and depression. These questionnaires also have good psychometric characteristics and are regularly used in research and clinical practice (e.g., Mogg, Bradley, Dixon, Fisher, Twelftree, & McWilliams, 2002; and Öst, L.-G., 1985, respectively).

### 3.5 Behavioral Measures

#### 3.5.1 Visual Search Task

Different variations of the visual search task were used across the different studies. In study I, the visual stimuli were arranged in a 3x3 grid (i.e., 9 cells).

![Visual Search Task](image)

Figure 1. One example of a grid with one target picture, a snake, presented among spider distractors, that was used as stimuli in the visual search task in Study1.

In study III, experiment 1, the visual display was also presented in a grid, with the pictures arranged on an imaginary rectangle that was divided equally into a 6 x 6 grid (i.e., 36 cells).
Figure 2. Example of the grids presented in study III, Experiment 1. (a) Arrangement of the images in the display in the four foveal locations (A), twelve parafoveal locations (B), and twenty peripheral locations (C) (1.2°, 3.4°, and 5.7°, respectively), in Experiment 1; (b) Example of a display with 3 items and a target picture (mushroom) in the periphery; (c) Example of a display with 12 items and a target picture (snake) in the parafovea; (d) Example of a display with 18 items and the target picture (spider) in the fovea.

In the remaining visual search tasks (study II, study III, experiment 2, and study IV), the pictures were arranged around an imaginary circle, thus keeping constant the distance the eyes had to move from the central fixation point.

Figure 3. Two examples of the circular displays used as stimuli in the visual search task in studies II-IV. The picture on the top is representative of studies II and IV, and involves one target picture, a snake, presented among a background of fruits. The picture on the bottom is one example of a display used in study II, Experiment 2, and includes a neutral target picture (a bird), presented in a heterogeneous background (different exemplars of fruits).
In study I, every combination of targets and distractors were used. Specifically, the grid could include fear-relevant targets (a snake or a spider) among fear-irrelevant distractors (cats or fish), or the reverse. Moreover, the fear-relevant target stimuli could also be presented among fear-irrelevant distractors (i.e., a snake target among spider distractors and vice-versa), as the fear-irrelevant targets could be presented against fear-irrelevant distractors (i.e., a cat among fish, and vice-versa).

However, in the remaining studies (II-IV), the target stimulus (a snake, a spider, or a mushroom), was presented against a background of emotionally neutral distractors (fruits). Therefore, while in study I we used a varied mapping design, i.e., all stimuli were used as both target and distractors, in the remaining studies (II-IV), a constant mapping design was used, since we kept the same distractors in the different target conditions (see Shiffrin & Gardner, 1972).

3.5.2 SAM

Studies I-II included rating tasks in which participants were asked to indicate their subjective evaluation of the stimuli, using the affective valence and arousal scales of the Self-Assessment Manikin (SAM) (Lang et al., 1997), with the scales ranging from 1 to 9. The purpose of the rating tasks was to examine whether the emotional properties of the stimuli were important to how they affected attention. While in study I participants were instructed to rate all the picture set included in the visual search task, in study II only a sample of pictures included in the search task was rated by the participants. In the latter study, a follow-up rating task, aiming at examining group differences in the emotional processing of a diverse set of emotional stimuli, was also included. This picture set comprised photographs selected from the International Affective Picture System (IAPS) database (Center for the Study of Emotion and Attention, 1993), depicting the two fearful categories (snakes and spiders), emotionally unpleasant (other threatening animals and injured people), emotionally pleasant (pleasant animals and babies), and emotionally neutral (neutral objects, e.g., a basket) pictures. This rating task was made available through a Web application, specifically created for the study. Participants were given the URL and a password to get access to the rating session.

3.6 STATISTICAL ANALYSES

For the visual search tasks we excluded error trials in the Reaction Time (RT) analysis. Moreover, we replaced outlier RTs that were greater than ± 3 * standard deviations (SD) from the individual’s mean by the mean ± 3 * SD. Prior to the statistical analyses we also logarithmically (log10) transformed the RT data (studies I-IV), and Arcsin transformed \( \sqrt{x+0.5} \) the accuracy data (study II) in order to follow the requirements of a normally distributed data. However, the values were back-transformed to RTs (in ms) and accuracy (in %) in the text and in the figures to facilitate interpretation of the data.

Analyses of Variance (ANOVAs) were run separately for correct RTs and for response accuracy in all studies (I-IV), with Tukey HSDs as follow-up tests. However, when appropriate, we used t-tests for explicitly predicted effects (studies I and II). We also run one-way Analyses of Variance in study II. Significance levels were set at \( p < 0.05 \) and partial \( \eta^2 (\eta_{p}^{2}) \) was supplied as estimates of the effect size. Finally, in studies II and III (Experiment I) we analyzed the data separately for slope coefficients, which was calculated based on a least-square estimated line of the regression of detection latencies on number of items for each participant and experimental condition.
4 RESULTS AND DISCUSSION

4.1 FINDING THREATENING AMONG NON-THREATENING ANIMALS (STUDY I)

A cross two visual search tasks we examined attentional selectivity to animal stimuli with and without evolutionary fear-relevance (snakes and spiders; cats and fish, respectively). In contrast with Experiment 1, in which participants were not selected based on their prior fear, in Experiment 2 we selected participants who reported high fear of either snakes or spiders (but not both), and a control group with low fear of either animal. Participants were also required to subjectively rate the pictures from each of the stimuli categories involved in the visual search task, in experiment 2.

As previously mentioned in section 3.5.1, we used a varied mapping design, allowing what we deemed the conclusions of interest, i.e., conclusions about threat detection speed (fear-relevant target among neutral distractors) and distraction effects of threat (neutral target among fear-relevant distractors). The results from Experiment 1, with non-selected participants, showed no asymmetry in reaction time and accuracy data between fear-relevant and neutral animals when they served as targets and distractors, respectively. Instead, the results showed that the processing of fear-relevant targets among fear-relevant distractors increased the latency of target detection and reduced the accuracy rates, which was interpreted as a delay in the disengagement of attention.

The findings from Experiment 2, with participants selected based on their prior fear, showed that fearful participants were specifically sensitized to select their target feared stimulus in the display (see Figure 4), with the emotional ratings mirroring this effect. This finding provided further support for the preferential allocation of attention to feared animals among non-feared ones.

Figure 4. Mean reaction times (RTs) in milliseconds for fearful and non-fearful (“control”) participants to locate a discrepant target stimulus that could be feared (a snake deviant for snake fearful participants or a spider deviant for spider fearful participants), non-fearred but fear-relevant (FR) (a spider deviant for snake fearful participants or a snake deviant for spider fearful participants), or non-fear related (Non-FR) (cat or fish), in study I, Experiment 2.

4.2 DISSOCIATIONS BETWEEN ANIMAL FEARS (STUDY II)

As in study I, most studies in the literature on attention that have used fear-relevant animals (snakes and spiders), as well as participants fearful of each animal stimulus, have collapsed the fear-relevant stimuli and the fearful individuals into single groups or conditions (e.g., Öhman et al., 2001a). This has had the
unfortunate effect of leaving potentially informative differences between snakes and spiders and between snake and spider fears unreported. In study II we wanted to investigate theoretically meaningful differences between snakes and spiders and between snake and spider fears. Moreover, in order to address some other questions left open from Study I and from the literature with animal stimuli, we used the visual search task to examine whether target performance to fear stimuli would deteriorate in highly demanding displays (displays with more items). Since increments in the number of distractors are said to increase the perceptual demands of the task (Lavie, 1995), we manipulated this factor by including small, medium and large displays (with 6, 12, and 18 pictures, respectively). As mentioned in section 3.5.1, we used a constant mapping design, i.e., the distractor pictures were always emotionally neutral (fruits). This methodological choice intended to avoid potential differences in the variability between fear-relevant and neutral stimuli, which could have occurred in the varied mapping design, used in study I. Thus, in the present visual search task we used snakes, spiders, and mushroom targets, presented among backgrounds of neutral distractors (fruits).

Attention (visual search task) and emotion data (subjective ratings) were collected from sixty participants (snake fearful, spider fearful and controls). The emotion measures involved two subjective rating tasks, one that included the pictorial stimuli involved in the visual search task and a follow-up task with snakes and spiders, combined with other emotional stimuli (negative, positive and neutral). The results from both measures showed that while spider fear was highly specific (see Figures 5 and 6), snake fear was associated with a more generalized enhanced evaluation of all negative stimuli. Consistent with this were the more elevated depression scores in snake fearful participants, which were taken as suggesting more signs of psychopathology in this group.

* p <.05

**Figure 5.** Detection differences (ms) between the control (mushrooms) and the fear target conditions (spiders or spiders) as a function of the prior fear of participants (Spider Fear, Snake Fear or the Control Group), with a larger detection difference indicating a larger facilitating effect of threat on target detection (study II).
* p<.05. ** p<.01. *** p<.001

Figure 6. SAM ratings of valence and arousal in study II, for Spider (feared for spider fearful participants and fear-relevant but not-feared for snake fearful participants), Snake (feared for snake fearful participants and fear-relevant but not-feared for spider fearful participants), Threatening Animals, Injured People, Neutral Objects, Pleasant Animals, and Pleasant Babies, by the Spider Fearful Group, Snake Fearful Group, and the Control Group in the follow up task. The SAM ratings of valence vary from one (low in unpleasantness) to nine (high in unpleasantness). The SAM ratings of arousal vary from one (low arousing) to nine (high arousing).

The results also showed an enhancement in the search advantage of spider targets, compared to snake targets, although this advantage was canceled with an increased in the perceptual load involved in the largest displays. It was suggested that the detection of snakes seems to be more dependent on bottom-up, stimulus-driven processes whereas spiders appear to be less dependent on attentional efficiency and highly selective for fearful groups (more associated with top-down, conceptually-driven processes).
4.3 ATTENTIONAL PRIORITY TO SNAKES IN VISUALLY TAXING CONTEXTS (STUDY III)

In study III we pursued the investigation of whether there were dissociations in the attentional processing of a highly feared and evolutionary-relevant stimulus (snakes), and a highly feared but with a disputed evolutionary relevance stimulus (spiders), and the effects of perceptual load on the processing of such stimuli. We included two attentional tasks in order to further establish theoretically meaningful differences between the effect of snake and spider pictures on human attention. In Experiment 1 the task involved the detection of a target stimulus (snake, spider, or mushroom) that could appear in foveal, parafoveal, or in peripheral visual locations and amongst emotionally neutral backgrounds (fruits). The set size of the visual displays was also manipulated (3, 6, 12, or 18 pictures). In Experiment 2 the stimuli of interest (snakes, spiders, and mushrooms) were task-irrelevant. The participants looked for birds among fruits and on some trials, a snake, a spider, or a mushroom replaced one of the fruits. Moreover, the perceptual load (set size - 4, 6; and similarity of the background pictures - homogeneous and heterogeneous backgrounds) was manipulated.

The results from Experiment 1 showed that snakes were more quickly and more accurately detected than spider and mushroom stimuli, independently of the number of items to be searched in the display, with this effect being particularly evident when targets were located in the peripheral vision (see Figure 7). The findings from Experiment 2 were conceptually similar to those of Experiment 1 by showing that snakes interfered significantly more with RTs to the target bird than the other task-irrelevant stimuli, particularly when the perceptual load was high (i.e., larger set size) (see Figure 8). The findings also showed that in the foveal stimulus presentation of Experiment 1, and in the low perceptual load of Experiment 2, the difference between snakes and spiders was much smaller with even a tendency of larger attention effects of spiders than of snakes (see Figures 7 and 8). The specific differences in attention to two commonly feared animals were consistent with ideas of snakes as a central agent in the evolution of primate defense systems (Isbell, 2006, 2009).
Error bars represent standard errors (s.e.m.). *** indicates \( p < 0.001 \), ** indicates \( p < 0.01 \), * indicates \( p < 0.05 \).

**Figure 7.** Results from study III, Experiment 1, relating attentional efficiency (a) and behavioral measures (b, c) to locate a discrepant target stimulus that could be a snake, a spider, or a mushroom presented among neutral distractor stimuli (fruits), in Experiment 1. a) Slopes across different set sizes (3, 6, 12, 18) (expressed as the mean search time [in milliseconds]/searched item) for locating the target picture as a function of eccentricity (fovea, parafovea, periphery); b) Mean percentage of accurate responses for detecting the different target stimuli as a function of eccentricity; and c) Mean reaction times (RTs) in milliseconds (ms) to detect the target picture in displays with different set sizes and at different eccentricities.

* \( p<0.05 \), ** \( p<0.01 \), *** \( p<0.001 \)

**Figure 8.** Mean Reaction Times (RTs) in milliseconds (ms) to locate a discrepant target (bird) in the different type of distractor conditions (snake, spider, mushroom, and no distractor), in study III, Experiment 2. The upper panel refers to the homogeneous displays, whereas the lower panel illustrates the heterogeneous displays, both as a function of the set size (4; 6). Longer RTs indicate larger interference scores.
4.4 FAST DETECTION OF SNAKES WITH BRIEF STIMULUS EXPOSURES (STUDY IV)

In study IV we further investigated dissociations in the search processing for snake and spider stimuli (compared to mushroom stimuli), when these were presented among a background of neutral pictures (fruits) in a visual search task. Moreover, as in Study II, we also wanted to assess the effects of prior fear (snake and spider fear) in the detection of fear vs neutral stimuli, and whether the effect was modulated by the exposure durations of the displays and by the number of items presented.

In Experiment 1 we used very brief exposure durations of the displays (150ms vs 300ms) while also manipulating the number of items presented (4, 6, 8). In Experiment 2, longer exposure durations were compared (300ms, 600ms, and 1200ms), together with small (4) and large displays (8) conditions. The shorter durations of the displays (150ms in Experiment 1, and 300 in Experiment 2), and the larger set sizes (8), represented the higher perceptual load conditions, in contrast with the lower load conditions involved in trials with longer exposure duration of the displays and smaller set sizes (e.g., 300ms and displays with 4 items, in Experiment 1).

Corroborating the results from the previous studies, the present findings showed that the evolutionary-relevant stimulus (i.e., snakes), compared to spider and mushroom stimulus, were consistently associated with higher attentional efficiencies (shorter reaction times and higher accuracy rates). Also in line with the previous studies (II-III), the snake advantage effect was particularly evident under the shortest stimulus durations (<300 ms compared to 600 and 1200 ms) (see Figure 9), and in the most perceptually demanding conditions, i.e., with large stimulus sets (8 rather than 6 or 4 items) (see Figure 10). This then strengthened the notion of snakes as a biologically given prototypical fear stimulus (see Öhman, 2009; Öhman & Mineka, 2001). Unfortunately, the findings did not show consistent effects for prior fear.

* p < .05. ** p < .01. *** p < .001

Figure 9. Mean Reaction Times (RTs) in milliseconds (ms) to locate a discrepant target stimulus that could be a Snake, a Spider, or a Mushroom, in displays exposed for 300ms, 600ms, and 1200ms, in study IV, Experiment 2.
* p<.05. ** p<.01. *** p<.001

Figure 10. Mean accuracy proportions to locate a discrepant target stimulus that could be a Snake, a Spider, or a Mushroom, in displays exposed for 300ms, 600ms, and 1200ms that included four (upper panel) or eight items (lower panel), in study IV, Experiment 2.
5 GENERAL DISCUSSION
5.1 ATTENTIONAL PRIORITY TO ANIMALS

Throughout evolution perceptual systems have been fine-tuned to allow effective, dynamic interactions with the environment. In line with this perspective, it has been argued that, driven by evolutionary pressures, our perceptual mechanisms were shaped in order to constantly assess the presence of animals in our surroundings. Moreover, these biased perceptual mechanisms seem to occur even without the interference of variables such as the current goals of the individual (see Öhman, 2007; New, Cosmides, & Tooby, 2007).

Öhman and his co-workers (2001a) were pioneers in using animal stimuli (snakes and spiders) in a visual search paradigm. Their point of departure was that if snakes and spiders are fear stimuli routed in evolution, then these stimuli should be more quickly detected among stimuli that did not share such evolutionary origin (flowers and mushrooms) than vice-versa. The results supported such predictions and, together with convergent results from different experimental tasks (e.g., Flykt, 2004; Lipp et al., 2004; New et al., 2007), there is a body of evidence consistent with the notion that an attentional priority for animals represents a genuine phenomenon (see Öhman, 2007a). This notion leads to the question of whether all animals are alike or whether there are subcategories of animals that are particularly relevant in an evolutionary viewpoint. The literature on fear, phobias, and preparedness (e.g., Seligman, 1971) has emphasized potentially important differences within the category of animals, by distinguishing those that have provided a major source of threat to our ancestors (e.g., Isbell, 2006, 2009), and those that supposedly were not sculpted by such evolutionary forces. The data from visual search studies on this problem are not conclusive as most studies do not include non-threatening animal distractor stimuli (e.g., Öhman et al., 2001a). However, there are a few studies using such control stimuli (e.g., beetles, butterflies, dragonflies: Rinck et al., 2005; horses, cats, and rabbits, Tipples et al., 2002) that have failed to report differences between the detection of threatening and non-threatening animals (Lipp, 2006; Rinck et al., 2005, Experiments 2 and 3; Tipples et al., 2002).

In study I we intended to further investigate the processing of fear-relevant and fear-irrelevant animal stimuli in a visual search setting that closely resembled that of the study run by Öhman et al. (2001a) (see Figure 1). Therefore, we compared the fear-relevant category (snakes and spiders), with a different animal category, that of non-threatening animal stimuli (cats and fish). The subjective ratings concerning the stimuli involved in the two visual search tasks, in study I, supported the choice of the different categories of emotional stimuli (fear and non-fear-related), with the data showing higher unpleasant and arousal scores to the fear-relevant stimuli (snakes and spiders) compared to the non-fear-relevant stimuli (cats and fish), which were rated as emotionally more positive and mildly arousing. As described in section 4.1, the results from experiment 1 did not show asymmetric differences in the detection of fear-relevant and fear-relevant animal stimuli, as reflected by the lack of significant effects in reaction time and accuracy data when either class of stimuli were presented as targets or as distractors (for similar findings see Lipp 2006; Tipples et al., 2002). In line with this pattern of results was the main effect of target stimulus in experiment 2, with no detection latency differences between the non-feared but fear-relevant stimulus (i.e., snakes for spider fearful individuals and spiders for snake fearful individuals) and the neutral stimuli (cats and fish) being observed. Interestingly, the results from experiment 1 showed an increased distraction effect when the fear-relevant categories were presented simultaneously in the display (a snake target.
among spider distractors and vice-versa). Accordingly, there are several findings showing that threat related stimuli produce distraction effects when the task involves the detection of a fear-irrelevant target (e.g., Rinck et al., 2005; Thorpe & Salkovskis, 1997). However, in study I, the distraction effect was confined to the conditions where there was a massive presentation of threat (i.e., a snake target presented among spider distractors and vice-versa) (see Figure 1).

The use of a varied mapping design in study I possibly accounted for the difficulty in disentangling target versus distractor-related effects. Moreover, it is likely that negative priming effects (slowed RTs to targets that were previously presented as distractors, e.g., being slowed at responding to a cat target in a snake background right after the snake was a target in a cat background) could have occurred. Therefore, we opted to use a constant mapping design in the following studies presented in this thesis (studies II-IV), thus exclusively investigating target-related effects and avoiding the problem of potential differences in variability among fear-relevant and non-fear-related stimuli. Moreover, since our study, as well as other related studies (e.g., Rinck et al., 2005), failed to separate the effects of target versus distractor-related effects possibly because the designs engaged both voluntary and reflexive attention, we opted to investigate these effects separately (voluntary attention: studies II-IV; reflexive attention: study III, Experiment 2).

Since the visual search task is very sensitive to the visual conspicuity of the stimuli, it is reasonable that the lack of differences between detection latencies for fear-relevant and neutral stimuli in study I could have been influenced by some perceptual characteristics of the stimuli (e.g., color saturation, luminance, size). If targets are to be distinguished from the distractor stimuli, as it is always the case in visual search, the task related anticipations seem to adapt not simply to the target set but rather to the most simple features that allow a reliable distinction of target and distractors (Duncan & Humphreys, 1989). For instance, while photographs of neutral animal stimuli (cats and fish) were clearly distinct from the background, the "natural" background in which fear-relevant stimuli (snakes and spiders) were presented was more complex, showing e.g., grass or other vegetation, sand, and gravels (see Figure 1). Thus, the threat-advantage to fear-relevant stimuli could have been compromised by the fact that the neutral stimuli were more easily distinguished and grouped together.

The experimental control of the perceptual variables clearly poses a problem when measuring visual search latencies for complex pictures. In order to keep more ecologically valid studies we kept real photographs of the stimuli but, instead of having animal control stimuli, we used a different category of an emotionally neutral stimulus, i.e., mushrooms, with the advantage that it is an ecologically valid stimulus (coexists in the same ecological environment as snakes and spiders). Moreover, the stimuli of interest, i.e., snakes, spiders, and mushrooms, were presented among other emotionally neutral stimuli, i.e., fruits, which also coexist in the same ecological environment as the latter stimuli (see section 3.3 for the details on the stimulus selection). Most importantly, the results from the studies using such stimuli (II-IV) were hardly reconciled with the visual conspicuity of the stimuli. A cross studies II-IV, both snake and spider stimuli were consistently associated with faster detection and higher accuracy than the control stimuli, i.e., mushrooms. Moreover, if the visual conspicuity of the stimuli would have accounted for our findings, then we would have not obtained interactions between the stimulus category and other factors, such as the number of items in the display (set size) (studies II-IV) (see Figures 7, 8, 10), the eccentricity of the target (study III, Experiment 1) (see Figure 7), and the exposure duration of the displays (study IV) (see Figures 9 and 10). Further, if it was simply perceptual effects one could not expect the interactions with prior fear, obtained in study II. These strong
interactions across the studies are difficult to account for by general characteristics of the stimuli.

5.2 SNAKES AND SPIDERS: DANGEROUS BUT DIFFERENT

In studies II-IV, we investigated potential differences between stimuli that are carefully matched in terms of their association with danger, because this emotion is a central parameter in the present set of studies. As alluded to in an earlier section (3.3), snakes and spiders are among the most feared stimuli by humans according to epidemiological data (e.g., Agras et al., 1969), and they are also among the most frequent members in the clinical category of animal phobias (APA, 2000). In study I, as well as in most other studies in the literature (e.g., Öhman et al., 2001a), researchers typically collapse snakes and spiders into one single group, predicated on the assumption that the stimuli hold an equivalent phylogenetic-mediated relevance. However, it is reasonable to assume that snakes and spiders may differ. As the first predators that preyed on early mammals (Isbell, 2006), snakes are regarded as the founding category of predatory fears (see section 1.6.1), whereas this does not seem to be the case for spiders. Instead, several studies have suggested that disgust may play a central role in the common aversive behavior towards spiders (e.g., Davey, Cavanagh, & Lamb, 2003; Gerdes, Uhl, & Alpers, 2008). Wiens, Peira, Golkar, and Öhman (2008) reported further consistent findings by showing that disgust sensitivity was more closely correlated with spider than snake fear. Indeed, in a recent study where different types of anthropods were compared (spiders with e.g., bees and wasps), spiders showed the highest ratings on disgust, as well as on subjective ratings of dangerousness (Gerdes et al., 2008). The disgust hypothesis holds that the emotional responses to spiders have been culturally propagated, with a relatively recent historical origin in the devastating epidemics that struck Europe in the Middle Ages (Davey, 1994).

Although snakes still constitute a major deadly threat to humans in the current days (see section 1.6.1), only some spiders get direct contact with humans and, therefore, only a few are considered to cause significant morbidity or mortality in humans (e.g., Steen, Carbonaro, & Schwartz, 2004). Typically, spiders prey upon other spiders or insects and, therefore, unlike venomous snakes, spider venom did not evolve to harm humans (Gerdes et al., 2008). Moreover, spiders are dangerous primarily when they are on the body, and then touch is a more important detection modality than vision. Hence, although snakes and spiders share important features, they appear to differ in the likelihood of an evolutionary association with predation on primates. Against this background, we sought to establish theoretically meaningful differences between the effect of snake and spider pictures on human attention in visual search settings across studies II-IV. The demonstration of a more efficient detection of snakes than that of spiders in visual scenes involves a specificity that invites an evolutionary interpretation (see Isbell, 2009).

5.2.1 Detecting Snakes and Spiders in Different Regions of the Visual Field

According to Isbell (2006) the evolutionary pressure to detect potentially deadly snakes in visually demanding perceptual situations (e.g., when they are camouflaged in foliage or vegetation) resulted in a strong influence on the evolution of the outstanding visual abilities of the higher primates. Snakes obviously provide a more deadly threat than spiders, and therefore it is clearly advantageous that they can be quickly and accurately detected at some distance, even if presented in the peripheral visual field. Based on evolutionary assumptions, we hypothesized that the need to detect snakes at a distance, would allow safe avoidance or escape, which could have shaped human peripheral vision to allow rapid identification of such stimuli.
Our findings (study III, Experiment 1) supported this hypothesis by showing more efficient searches when the snake targets, compared to spiders and mushrooms, were presented in the peripheral visual field, as opposed to the parafoveal and foveal visual fields. The results from Experiment 1, in study III, also showed that spider targets presented in the fovea resulted in more shallow slopes across number of distractors than snakes (and mushrooms, to some extent, as the difference between this stimulus and spiders was marginally significant) (see Figure 7). Participants were instructed to fixate the central fixation cross, and hence foveally presented targets did not require any shift of attention. Because of their more invariant shapes, spiders and mushrooms may in fact be more easily recognized than snakes once they are focused. Snakes, on the other hand, can be more or less straightly elongated, sinusoidally shaped, or coiled, which might delay confident recognition yet be sufficient to tag attention when presented peripherally. Therefore, the results cogently suggest that snakes, but not spiders, are tuned specifically to shift attention to peripherally presented stimuli.

Starting from the assumption that a central component of fear is to prioritize attention to potentially threatening stimuli while trying to assess more information in the environment, Susskind, Lee, Cusi, Feiman, Grabski, and Anderson (2008) examined concurrent perceptual and facial changes, as well as psychophysiological responses to fear stimuli. Their results are consistent with our findings by showing that fearful facial expressions served to alter the information intake by enlarging the field of vision, allowing a more effective scanning with faster flicks of saccades, which, in turn, resulted in a quicker detection of objects in the periphery. The opposite effects were found for disgust, which seemed to dampen the sensory input. This set of findings is in line with the suggestion that the predatory defense system is linked to fear of snakes (which is then central to fear in general) (e.g., Öhman & Mineka, 2001, 2003). Spiders, on the other hand, are associated with concerns of contamination rather than concerns of physical harm and therefore are more prone to elicit avoidance (thus restricting our perceptions) (e.g., Davey et al., 2003).

A recent study corroborated these findings by showing that while fear increased the attentional blink, disgust reduced it (Vermeulen, Godefroid, & Mermillod, 2009). This argument fits in the dissociations between snake and spider stimuli at different eccentricities found in our study III (Experiment 1).

5.2.2 Finding Snakes and Spiders Under Brief Durations

The preferential attention toward snake stimuli implies that such processing might take place at preattentive levels and that it should be followed by a fast attentional engagement of attention. Therefore, we further predicted that the processing advantage for the evolutionary-relevant stimuli (snakes), compared to the other threatening stimulus with a disputed evolutionary origin (spiders) would also be evident in a new, ecologically relevant, visually degraded condition (short stimulus presentations) (study IV). Although there are studies supporting the notion that fear stimuli are predicated on early, automatic processing mechanisms (e.g., Öhman, 1993; 2000; 2008) by, for example, presenting this stimulus category under conditions of limited conscious awareness (e.g., Carlsson et al., 2004), this effect has not yet been investigated in visual search settings.

We hypothesized that if snakes are indeed less dependent on attentional resources to be identified, as the results from study III (Experiment 1) seem to show, then the processing of snake targets will require fewer fixations (see Rayner, 1998), which will result in an enhanced attentional priority for snakes with brief exposure durations (150ms; 300ms). Confirming our predictions, the results of study IV showed, across two visual search experiments in which we varied the stimulus duration of the displays (Experiment 1 – 150ms; 300ms; Experiment 2 – 300ms, 600ms, 1200ms), that
snakes (compared to spiders and mushrooms) were consistently associated with a faster and more accurate detection. This effect was particularly evident under the shorter stimulus durations (<300ms), compared to 600ms and 1200ms, which implies that the first fixation must have been especially likely to be sent to the snake target stimulus (see Figure 9).

The findings from study IV suggest that snakes, rather than spiders, are somewhat specifically tuned to guide attention on the basis of primitive processing strategies that can operate on very limited visual information. This, in turn, is consistent with the existence of a special mechanism responsible for the rapid detection of threatening information based on a “quick and dirty” analysis (Öhman, 2007b; LeDoux, 1996), calling on an attentional shift in order to prime defensive responses to what could turn out life-threatening events. Our results suggest that snakes may indeed represent such prime example.

5.2.3 Attention to Snakes and Spiders Under Load

Unlike in the study by Öhman et al. (2001a), in study I we did not manipulate the set size of the grid. Thus, we could not examine the efficiency of the search by means of slope coefficients (see section 1.7.2). In studies II, III (Experiment 1) we wanted to investigate the differences between snake and spider stimuli also in terms of search efficiency (along with the RT and accuracy data). Specifically, we intended to study potential differences between snakes and spiders in their sensitivity to be modulated by perceptual load (see Lavie, 1995; Desimone & Duncan, 1995). Based on evolutionary considerations, we assumed that the astute detection of snakes would result in a faster and more accurate detection of this stimulus in cluttered visual scenes, thus scenes where the perceptual demands were higher (e.g., displays with more items).

The variation of set size represents one of the most common manipulations of load in the literature (e.g., Torralbo & Beck, 2008), with increments in set size involving higher load conditions (e.g., Lavie & Cox, 1997). In the second experiment included in study III, in addition to the variation in set size, we also used another common manipulation of perceptual load, the similarity of the background items (e.g., Beck & Kastner, 2009; Duncan & Humphreys, 1989; Öhman, Juth, & Lundqvist, 2009). Specifically, in the homogeneous condition, the background pictures (fruits) were identical, which facilitated their identification and left more resources for efficient detection of the critical extra distractors. On the other hand, in the heterogeneous condition, all fruit pictures were different and had to be individually discarded, presumably leaving less resource for processing of the critical distractors (see Figure 3).

In studies I, II, III (Experiment 1), and IV, the stimuli of interest (snakes, spiders, and mushrooms) were “task-relevant”, i.e., they were actively looked for by the participants (top-down attentional control) as a requirement to follow the instructions and accomplish the task (e.g., Bernstein & Taylor, 1979). In the set of experiments involving top-down attentional control in which perceptual load was manipulated, we predicted that if evolutionary relevant stimuli are indeed driven by preattentive perceptual processes (e.g., Öhman, 2008, for a review), this effect should be independent of the level of perceptual load of the visual field. However, results consistent with the perceptual load theory (e.g., Lavie, 1995) would show that when perceptual resources are fully occupied (more distractors), stimuli are not processed beyond a superficial level, and would thus generally impair the odds of locating the target stimuli. Conversely, in low-load conditions (few distractors), the perceptual resources are not exhausted and therefore selecting targets among distractors can be based on a fuller processing of the target with a better differentiation between the stimulus categories.
Although in study II there was a main effect of target showing faster detection of spiders, compared to snakes, an interaction between this factor and the set size of the displays showed that the effect was modulated by the number of distractors involved in the displays. Specifically, in displays involving a high perceptual load (with 18 items, compared to 12, and 6), the advantage for spider targets was dissipated. More importantly, the slope data showed a somewhat more efficient search for snakes, compared to spiders and mushrooms. This advantage in detecting snakes under high perceptual load conditions (e.g., more items in the display), compared to the control conditions, was consistent throughout studies II-IV, suggesting that its processing did not depend on general capacity limits. The snake advantage was shown in RT and accuracy measures (studies II, III, IV), as well as in the slope measures (studies II-III, experiment 1) (e.g., see Figure 7). Hence, snakes showed apparently paradoxical results from the perspective of Lavie’s theory (1995; 2005), by producing a substantial and highly reliable attentional efficiency at the high load (large set size, heterogeneous backgrounds) conditions. In fact, it seems that snakes can pass the early filter imposed by the high load conditions, while spiders and mushrooms cannot and, therefore, are more affected by the task load.

Our findings also presented indications that spider stimuli seemed to be more dependent on attention, by showing that they were processed to an equivalent extent than snakes (and in some conditions somewhat overcoming the preferential processing of snakes, as in the foveal conditions, in study III, Experiment 1 - but see section 5.2.1), when the task was less perceptually demanding (low-load conditions).

Perceptual load can be viewed as a need to resolve competitive interactions for neural representation in the visual cortex between simultaneously presented stimuli, with top-down and bottom-up processes influencing such competition (Torralba & Beck, 2008) (see section 1.7.1). Importantly, such competition among stimuli “may be biased in favor of an emotionally salient item via connections with the amygdala” (Beck & Kastner, 2009, p. 1159), which could then be mediated by the low road to the amygdala (LeDoux, 1996). Since snakes seem to be detected in the absence of attention - they can be located in peripheral vision (study III, Experiment 1) (see section 5.2.1) and under very short exposure durations (study IV) (see section 5.2.2), its detection holds a privileged role in biasing stimuli in the competition for neural representation in the high perceptual load conditions. Spiders, on the other hand, are more dependent on attention, must be foveally processed (see section 5.2.1), and require longer exposure durations to be efficiently processed (in comparison with mushrooms) (see section 5.2.2). Therefore, spider stimuli do not appear to play a biasing role in competition for neural representation in the high perceptual load conditions, as snakes do. Moreover, and previously mentioned, snakes are unquestionably more lethal threats than spiders, which makes their accurate detection amid a complex environment (e.g., when they are camouflaged in foliage or vegetation), clearly advantageous in terms of survival.

5.2.4 The Interference of Lurking Snakes and Spiders

The findings reviewed above are supplemented by the results from study III, Experiment 2, showing that the snake advantage effect was also apparent when snakes serve as task-irrelevant distractors. Indeed, although snakes entering an attentional spotlight that searches for something else can become immediate targets of defensive maneuvers, a snake in the path of an unsuspecting foot provides a more acute danger, and its quick, automatic detection would carry considerable adaptive value. Therefore, study III (Experiment 2), examined the effects of lurking snakes (compared to spiders and mushrooms), which is unrelated to any goal driven activity. This experiment directly assessed automatic attention capture and therefore is the one that most directly tests the perceptual load theory, because here the stimuli of interest (snakes, spiders, and mushrooms) were completely task-irrelevant. Thus, subjects were looking for birds among fruits and on some trials, a snake, a spider, or a mushroom replaced one of the
fruits. The question of interest then was whether this distracting stimulus slowed the RT for finding the target (the bird) to different degrees. In addition, we varied the perceptual load of the task by including 4 or 6 fruits on different trials, and by having identical (homogeneous) or different (heterogeneous) fruit pictures. The results were conceptually similar to those of study III (Experiment 1) and IV by showing that snakes interfered significantly more with RTs to the target bird than the other task-irrelevant stimuli, but only when the perceptual load was high (i.e. when the background set of stimuli have 6 rather than 4 fruits) (see Figure 8). However, spiders showed some tendency to the opposite effect, i.e., they showed, albeit inconsistently, more interference with RTs when the background stimulus set was small (4 rather than 6) (this numbers are taken from one of Lavie’s papers that establish the concept of perceptual load: see Lavie & Cox, 1997). This result means that spiders behaved as expected from Lavie’s perceptual load theory, the mushrooms had no distractive effects, but that snakes again showed a striking difference from spiders (and mushrooms). The results also suggest that spiders could successfully get access to neural representation when perceptual load was low. However, with high perceptual load, spiders did not have sufficient strength to resolve the stimulus competition in their favor, and hence no task interference was produced (see Beck & Kastner, 2009). Thus, attention seems to come into play not as a crucial ingredient for fear detection, but as a factor that modulates the degree of specificity in such detection.

5.2.5 Snakes as the Archetypal Fear Stimulus?

The consistent bulk of results from the present research showed that snakes, compared to spiders (and mushrooms) were consistently more effective in engaging (studies II, III - Experiment 1, IV) and shifting (study III – Experiment 2) attention (see Posner & Peterson, 1990), and that this preferential processing was particularly evident under the most demanding perceptual conditions (i.e., high-load conditions) (Lavie, 1995, 2005). Specifically, the privileged attentional processing of snake stimuli was most evident among many distractors (studies II-IV) (e.g., see Figures 7, 8, and 10), in peripheral vision (study III – Experiment 1) (see Figure 7), at brief exposure times (< 300ms) (study IV) (see Figure 9), and when unexpectedly presented among the background stimuli (study III – Experiment 2) (see Figure 8). Snake stimuli were generally superior to spider stimuli (reflected in shorter RTs, higher accuracy scores, and more shallow slopes), as illustrated in the main effects of target (see section 5.2.3 for one exception in study II) and in a number of interactions showing a favored processing of snakes. Thus, our strategy to establish a foundation in terms defined by specific experimental paradigms appeared to produce a consistent set of findings with well-controlled stimuli, thus extending the empirical base for claiming that snakes are special.

Our set of results support the notion that snakes, but not spiders, have effects that are independent of attention, and presumably mediated by the subcortical pathway to the amygdala (LeDoux, 1996). This route (via the superior colliculi and pulvinar nucleus of the thalamus, e.g., Vuilleumier, 2005) is based on magnocellular pathways from the retina and is served by large rapidly conducting neurons, which mediates gross, low spatial-frequency information directly to the amygdala for rapid threat detection (Vuilleumier, Armony, Driver & Dolan, 2003). Indeed, the primary effect of snakes might be related to a recruitment of the fast magnocellular/amygdala system (e.g., Gazzaniga et al., 2009) for rapid guidance of attention to its spatial location. Moreover, because the processing of snakes seems to be carried out independently of available resources, they are relatively immune to disruption from other ongoing operations, thus being more based on bottom-up processes (see Pashler, 1998). Spiders, on the other hand, and as previously mentioned, seem to be more dependent on attention, with recent findings corroborating this notion by
showing the amygdala activation towards spiders was modulated by the allocation of attention (Alpers, Gerdes, Lagarie, Tabbert, Vailt, & Stark, 2009).

In summary, our set of findings suggest that it seems particularly important to detect snakes early and automatically, that is, in peripheral vision, and when the scene is perceptually complex and allows good camouflage for lurking snakes (and other dangers). We hypothesize that the specificity of our findings would likely be found with other objects that are perceptually similar to snakes (e.g., worms or eels), or even to venomous and non-venomous snakes. As previously discussed in section 1.2, there is a maximal benefit of fear, with a “quick and dirty” analysis of the stimuli being error prone, but likely to be biased by evolution to risk false positives – detecting “threats” that in reality are innocuous – rather than false negatives.

The very specificity of snake processing speaks in favor of an evolutionary explanation, particularly one that derives from Isbell’s (2009) Snake Detection Theory (for a more detailed description, see section 1.6.1). The evidence demonstrated that snakes are special and may indeed represent the archetypical fear stimulus, with a biologically given relevance. Our findings fit well with recent literature showing that attention is prioritized to snakes in complex visual displays not only in adult humans (e.g., Ohman et al., 2001a), but also in children (LoBue & DeLoache, 2008) and infants (LoBue & DeLoache, 2009), as well as in lab-reared, snake-naïve rhesus monkeys (Shibasaki & Kawai, 2009), which provides a strong suggestion that this privileged processing does not depend on prior experience to this stimulus.

The present research offers important contributions to the study of fear and attention, although we are aware that there is a substantial distance to travel before we get even close to what we know about faces, for instance. However, a research program can now be envisioned with the aim of diminishing this distance. As a gradual understanding of the phenomena is built, the research focus can be broadened to new paradigms.

5.3 THE EFFECTS OF PRIOR FEAR ON ATTENTION AND DISSOCIATIONS BETWEEN SNAKE AND SPIDER FEARS

It is generally accepted in the literature that when the emotional and personal significance of the stimuli is emphasized, threat stimuli seem to capture attention even more efficiently for individuals that are selected to be highly fearful of such stimuli (for an overview see e.g., Cisler & Koster, 2009). This, in turn, suggests a top-down, conceptually-driven effect of emotion and personal significance on attention. The findings from study I supported this notion by showing that fearful individuals, compared to non-fearful ones, showed a preferential processing of the congruent feared stimulus, which strengthened the notion that fear significance is an important factor drawing attention to a particular spatial location. However, the significant differences in the RT data were restricted to within-participants differences (although this was not the case in the rating data, where both within and between differences were shown). Even so, the results indicated that participants who actually perceived the fear-relevant stimuli as dangerous and emotion provoking showed enhanced sensitivity to these stimuli, as reflected in the shorter latencies to their detection. This agrees with the observation that the presence of feared stimuli in the environment of fearful individuals grants these objects salient meaning by significantly pulling participant’s attention towards them, and increasing arousal and negative emotional feelings of threat (e.g., Williams et al., 1997). Indeed, in study II, the results relating trait anxiety showed no significant differences between fearful and non-fearful individuals. Therefore, it is reasonable to assume that our findings may have in fact only reflected the alerting and orienting networks to the fear stimuli, as
participants were particularly afraid of this type of stimuli and consequently were under acute states of state anxiety (see Pacheco-Unguenttu et al., 2010).

As mentioned in earlier sections of the present thesis, there are indications in the literature showing that while snake fear is associated with the predatory defense system (e.g., Öhman, 2009), spider fear is more likely to be mediated by disgust (Matchett & Davey, 1991). Thus, because snake and spider fear seem to be mediated by different emotions (spiders might be more disgusting than feared, and snakes might be more feared than disgusting), the lumping of the two specific fears may result in difficulties disentangling the results.

The studies that collapse spider and snake fearful participants into one single group (e.g., Globisch et al., 1999), including our own (study I), are predicated on the nosological categorization of phobias (including specific phobias, such as animal phobias) by the DSM-IV-TR (APA, 2000), and in distinct psychophysiological data towards feared stimulus by animal phobic individuals (e.g., Hare & Blevings, 1975). As a result of this common practice, it is not possible to investigate potential differences in responses between these individuals. Since there are scarce data pointing to the relevance of such differentiation (Lipp & Derakshan, 2005; Wiens et al., 2008), we sought to explicitly compare these two groups of animal phobic individuals (in our case highly fearful individuals) in studies II and IV, with an adequate statistical power.

Our results showed that snake and spider fears may in fact differ, although the evidence was not consistent. While in study II there was a clear dissociation between the two types of animal fear, reflected in attention and emotion measures, in study IV this dissociation was not evident. In study II, the results showed specificity towards the feared stimulus in spider fearful individuals, with the snake fearful participants not differentiating between their feared stimulus (snakes) and the non-feared but fear-relevant stimulus category (spiders). Moreover, the latter group of participants also showed a more generalized enhanced evaluation of other classes of negative stimuli, in a follow-up rating task. However, in study IV, where we manipulated the stimulus durations of the displays, as well as the perceptual load, our findings were not consistent and were somewhat difficult to interpret. Although there was an interaction effect between prior fear and attention in the experiment where very brief displays were presented (Experiment 1 - 150ms, 300ms), the result was compromised by the fact that indistinguishable effects were observed in the snake fearful and in the control group. In addition, and providing further interpretational difficulties, spider fearful participants did not find spiders faster than snakes. Furthermore, in the experiment with longer exposure durations (Experiment 2), the interaction effect was not observed. We suggested that the use of displays with varying stimulus durations (very short, 300ms, and longer, 600ms, and 1200ms), intermixed across conditions, could have abolished the prior fear effects due to goal-driven strategies.

The evidence for a facilitated processing of feared stimuli in fearful individuals appears to be mixed, with some studies using the visual search task documenting such privileged processing (e.g., Öhman et al., 2001a; Rinck et al., 2005; Experiment 1), while others fail to provide such evidence (e.g., Rinck et al., 2005, Experiments 2 and 3; Miltner et al., 2004). Unfortunately, our set of findings did not contribute to resolve the contradictory studies in the literature. While some studies use clinical samples, others use non-clinical samples (such as our studies I, II, and IV), with different cutoff points in the SNAQ and SPQ (see methods section of the studies, for details), which may contribute to the inconsistency of the findings.
The results presented in this thesis suggested that the differentiated emotions associated with snake and spider fear may have had different effects on attention (see Susskind et al., 2008; Vermeulen, 2009). Therefore, future studies should consider not collapsing both groups of participants into one single group. Alternatively, the studies investigating the effects of prior fear on attention could opt to compare both groups or, alternatively, include one single group. In such case, our results suggest that the group of spider fearful individuals, given their specificity (see study II for details), may be more adequate to study than the group of snake fearful participants. Further research is needed to clarify the inconsistencies between studies and investigate potential moderators in the effects of prior fear on attention. For instance, it would be relevant to clarify the dissociation of trait and state anxiety in the different attentional processes involved in fear (see Pacheco-Unguenttu et al., 2010). Finally, further examination of the dissociations between snake and spider fearful individuals are also recommended.
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