Chapter 1

Modulation of visual attention by pictures conveying emotion
In our environment, many objects compete for visual selection and for representation in the limited capacity information processing system. Selection of stimuli for further processing can be biased by the physical properties of the stimuli and by the goals of the observer (Duncan & Desimone, 1995). It is well-known that salient stimuli are capable of automatically capturing attention despite our intentions (e.g., Theeuwes, 1992). An important question is whether stimuli that are associated with emotion could also automatically bias visual selection.

A large influence of threat on attention may be not surprising, considering that fast detection of threatening signals plays a significant role in the chances of survival for an organism (LeDoux, 1996; Öhman and Mineka, 2001). It has been often suggested that fast detection of threat serves to facilitate a person’s preparedness for action and to promote adaptive behavior (LeDoux, 1996). For example, the sudden appearance of a fearful face in the periphery may indicate an imminent threat or danger, demanding immediate attention. A major theory of how threatening stimuli evoke fear responses and receive enhanced attention is the fear module theory of Öhman and Mineka (2001). According to this theory, the fear module has evolved to quickly detect certain stimuli and evoke physiological and behavioral changes in response to danger. Consequently, the adaptive advantage in responding quickly to a threatening encounter probably has resulted in the visual perceptual systems being biased for quick and automatic perceptual processing of threat (Esteves, Dimberg, & Öhman, 1994; Öhman, 1986a). If so, it may be assumed that threatening stimuli are especially likely to attract attention.

Numerous studies have investigated whether attention is captured by the pictures conveying threat. However, the evidence so far has been mixed. In this chapter, the main behavioral, eye-tracking and neuroimaging findings in the literature are reviewed, and solutions for solving the existing controversies are proposed.

**Fast allocation of attention to pictures conveying emotions**

There is a long tradition of using pictorial stimuli to study whether emotions can bias attentional allocation. It has been thought that prioritized processing of emotional stimuli seems to occur through a fast and direct subcortical pathway that connects the pulvinar to the amygdala bypassing sensory cortices (e.g., LeDoux et al., 1987).
According to the preparedness theory of Seligman (Seligman, 1970, 1971), the prioritized detection of some threatening stimuli seems to be unique because they have a high evolutionary relevance. It can be argued that snakes and spiders may have a special emotional significance for humans (Öhman, Lundqvist, & Esteves, 2001) and pictures of spiders and snakes are therefore widely used in emotion research. Specifically, poisonous snakes and spiders formed a persistent threat to survival throughout most of mammalian evolution. Therefore, organisms that quickly learned to avoid them were more likely to survive, reproduce, and pass on their genes. As a consequence, a tendency to readily learn to fear snakes may have evolved in humans and other mammals. For example, primates who have been continuously exposed to snakes for millions of years are uniformly afraid of snakes (Isbell, 2006). In contrast, the lemurs of Madagascar, who have had little exposure to snakes throughout their evolution, do not fear snakes. Isbell argued that the need to detect snakes provided strong evolutionary pressure to develop perceptual capacity in animals that were potential targets of snake attacks. Therefore, humans may have an evolved predisposition to associate spiders and snakes with fear, even when they have never learned to associate such an animal with an aversive outcome themselves.

At a social level, facial expressions seem to be of special importance to the evolution of human beings. Given their biological and social significance, faces with emotional expressions are used very often in emotion research. Since humans are social beings, it seems especially important to quickly recognize emotions of other people, because emotional expressions add further meaning to faces as they reveal the state, intentions, and needs of people. Consistent with this view, it has been shown that emotional information from faces is detected very rapidly (100 ms after stimulus onset), and different facial expressions are discriminated within an additional 100 ms (for reviews, see Eimer & Holmes, 2007; Palermo & Rhodes, 2007). Ekman (1972) proposed that expressions of emotion in the human face represent biologically evolved signals. Anger, for example, is a threat signal potentially related to threat, whereas a smile is a comforting signal of friendly intentions. Therefore, facial emotions give an indication to observers of what they can expect from the people expressing them and how to adjust their own behavior accordingly. An important factor of emotional
expressions is that they can communicate behavioral intentions and can be used to affect the behavior of another person (Dimberg & Öhman, 1983; Fridlund, Schwartz, & Fowler, 1984; Juth, Lundqvist, Karlsson, & Öhman, 2005).

A key question in research on emotion and attention is whether fear-relevant pictures, such as spiders, snakes, and angry faces, can be detected automatically. When multiple items are present in the environment, it seems important to select those elements that are of high behavioral relevance to the observer. Quick selection of threat could aid the observer to quickly select an appropriate behavioral response. Therefore, many studies have focused on examining facilitating effects of emotion on attention in an environment where multiple stimuli compete for attentional selection.

A commonly used paradigm to study facilitating effects of emotion on attention is visual search. In a typical visual search task, a target stimulus is presented in an array of distractors, and the goal is to indicate as fast as possible whether the target is present or not. In order to determine if threat is more quickly detected than neutral information, response times to detecting the threatening target among neutral distractors are compared to a neutral target among neutral distractors. If threat is indeed quickly selected, the presence of a threatening stimulus should be detected faster than the presence of a neutral stimulus. Several studies have used this paradigm to measure how efficiently visual attention is directed to emotional facial stimuli. It has often been reported that angry faces when they are targets are detected faster than happy faces when they are targets among neutral distractor faces (Calvo, Avero, & Lundqvist, 2006; Esteves, 1999; Fox et al., 2000; Frischen, Eastwood, & Smilek, 2008; Mather & Knight, 2006; Öhman, Lundqvist, et al., 2001; Pitica, Susa, Benga, & Miclea, 2012). Consistent with these results, several studies revealed fast detection of threatening animals embedded with non-threatening stimuli. Because of their evolutionary relevance, most studies used pictures of spiders or snakes among neutral pictures such as flowers or mushrooms (Öhman, Flykt, et al., 2001; Soares, Esteves, & Flykt, 2009; Soares, Esteves, Lundqvist, & Öhman, 2009). In addition, some studies report distraction by pictures of snakes and spiders when searching for a neutral target.
More evidence for facilitated attention to threatening stimuli is provided by studies that used a variant of Posner’s spatial cueing paradigm. The results of visual search tasks imply that humans quickly detect potentially threatening stimuli when embedded with neutral stimuli. However, these tasks do not provide answer to the question how and at what point this preferential selection occurs. According to Posner (1982), orienting is a mechanism that the cognitive system uses to achieve attentional selection. Orienting of attention can be described as the process of moving attention to a location in space, and subsequently detecting the presence or absence of a stimulus presented at that location (Posner, 1982). Importantly, a potentially significant event, such as a threatening stimulus, may automatically trigger orienting towards its location, and consequently facilitate its detection.

Several studies have used spatial cueing paradigms to investigate whether orienting of attention to threatening stimuli is facilitated. In Posner’s classical paradigm (Posner, 1980), a cue appears briefly at a location and is followed on some of the trials by a target presented at that location (valid-cue condition), or at the alternative location on the rest of the trials (invalid-cue condition). In a task similar to Posner’s cueing paradigm, the dot-probe task, two cues simultaneously appear at the two locations. Participants have to respond as fast as possible to the target. Enhanced performance on validly cued compared to invalidly cued trials indicates that an attentional bias occurs at the stage of initial orienting of attention. To investigate facilitated attention to threatening information, several spatial cueing studies used pictures conveying threatening or emotionally neutral information as cues. If threatening stimuli indeed facilitate orienting of attention, reaction times for detecting a target on a location cued by an threatening stimulus would be faster relative to a location cued by a neutral stimulus.

Additionally, in order to provide a more direct measurement of attentional orienting, several studies have measured the effect of threat on saccadic eye movements. Since there is a close coupling between eye movements covert visual
attention (Deubel & Schneider, 1996; Henderson, 2003), eye tracking has been widely used to study visual attention (Kowler, Anderson, Dosher, & Blaser, 1995; McPeek, Maljkovic, & Nakayama, 1999; Shepherd, Findlay, & Hockey, 1986). The premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umilta, 1987) states that the mechanisms responsible for covert attention and the mechanisms involved in programming saccadic eye movements are fundamentally the same. It has been demonstrated that shifting covert attention is accompanied by preparation of a saccade, and vice versa, the preparation of a saccade results in an obligatory shift of attention to the location of a saccade target (Deubel & Schneider, 1996; Belopolsky & Theeuwes, 2009a; 2012). Therefore, eye movements can serve as a direct behavioral measure of attentional orienting.

Evidence for facilitated orienting to threatening stimuli is provided by studies that used an eye movement version of Posner’s spatial cueing paradigm. Several spatial cueing studies have observed facilitated orienting to targets presented at the locations of fear-relevant stimuli such as spiders and snakes (Lipp & Derakshan, 2005), angry faces (Cooper & Langton, 2006), and IAPS pictures (International Affective Picture System; Lang, Bradley, & Cuthbert, 1999; Koster, Crombez, Verschuere, & De Houwer, 2004; Mogg, McNamara, Powys, Rawlinson, Seiffer, & Bradley, 2000). Moreover, faster eye movements to threatening compared to neutral stimuli were observed when threatening/neutral stimulus pairs were presented in the periphery, and participants were instructed to make a speeded saccade to the side where the threatening or neutral stimulus appeared (Bannerman, Milders, & Sahraie, 2010a, 2010b; Gerdes, Alpers, & Pauli, 2008; Kissler & Keil, 2008). However, in many studies, facilitated detection of threat was only observed in highly anxious individuals as compared to non-anxious individuals (Bradley, Mogg, Falla, & Hamilton, 1998; Macleod, Mathews, & Tata, 1986; Mogg, Bradley, DeBono, & Painter, 1997; Wilson and McLeod, 2003). Therefore, individual levels of fear seem to play a large role in attentional bias. This may indicate that high anxiety is associated with a disproportionate degree of attentional vigilance. Thus, although attentional biases to threatening stimuli are observed in the general population, the intensity of this bias seems to be modulated by individual differences in the level of anxiety, and differences in perceived threat intensity of the stimuli.
In sum, the studies described above provide evidence for fast orienting to threatening stimuli. However, some concerns have been raised regarding the validity of these conclusions. First, in many studies threatening stimuli were often relevant to the task goal, making it difficult to state that they draw attention automatically (Yantis, 1993). Second, it is possible that attentional bias to threatening stimuli does not consist of faster orienting to threat, but instead of subsequent processes that occur after the stimulus has been detected. Third, it is plausible that attentional capture by threatening stimuli is due to their physical properties instead of the emotion they evoke. Below, these three criticisms are examined in more detail.

**Task-relevance of threatening stimuli**

In many studies that investigated attentional capture by threatening stimuli these stimuli were not completely irrelevant to the goals of the observer. As such, in visual search tasks the threatening stimuli were often the target of search, which makes it difficult to claim that the presence of threat attracted attention involuntarily. As indicated in the Introduction, one of the criteria of automatic processing is its resistance to voluntary suppression (Jonides, 1981). In order to investigate whether threatening stimuli truly capture attention it should be disadvantageous to pay attention to them. If the detection of threatening stimuli is indeed an automatic process, one expects it to occur also when observers have to perform a task where the threatening stimuli are task-irrelevant (Yantis, 1993).

Contradictory to the view that threatening stimuli attract attention automatically, Miltner and colleagues (Miltner et al., 2004) failed to find fast detection of threat stimuli when the task goal was not to detect a target stimulus, but to judge whether the background distractors belonged to the same stimulus category. Likewise, Hahn and Gronlund (2007) demonstrated that when searching for a happy target face, an angry face distractor did not slow search time, indicating that irrelevant angry faces did not attract attention. Other evidence for importance of goal-relevance is provided in a spatial cueing task by Vromen and colleagues (Vromen, Lipp, & Remington, 2014), who demonstrated that spiders only capture attention when they are part of the task goal. In addition, Devue and colleagues (Devue et al., 2011) showed that when spider
phobics were instructed to search for a shape target singleton, the presence of spider

distractors caused more interference than butterflies with finding the target, but only
when the two types of distractors were presented in separate blocks. When spider and
butterfly distractors were mixed within a block, both of them captured attention
equally strongly. The authors concluded that the mere expectation of a feared object
(spiders and butterflies were the only black objects in the display) can determine what
objects receive priority in attentional selection. Therefore, it is difficult to draw strong
conclusions about whether fast detection of threat is truly automatic and occurs
without involvement of top-down knowledge.

In contrast to the view that threatening stimuli only capture attention when
they are part of the task goal, several studies have shown capture of attention by task-
irrelevant threatening stimuli. In a cueing task by Nummenmaa and colleagues
(Nummenmaa, Hyönä, & Calvo, 2009, Experiment 1), the goal was to make a saccade in
the direction indicated by a central color cue. A neutral/emotional picture pair was
simultaneously presented in the periphery. Saccadic reaction times were faster when
the cue pointed toward the emotional picture rather than toward the neutral picture.

Other studies measured saccadic trajectories to investigate attentional capture
of task-irrelevant stimuli. It has been shown that when a distractor stimulus interferes
with a saccade to a target, the trajectories of saccades to the target show significant
curvature toward or away from the distractor (Findlay & Harris, 1984; McPeek & Keller,
2001; Minken, Vanopstal, & Vangisbergen, 1993; Vangisbergen, Vanopstal, & Tax,
1987). In a typical task for measuring saccade curvature, saccades have to be generated
to a location that is never coinciding with the location of a distractor, and paying
attention to the distractor is never required by the task. Therefore, the distractor effect
found on saccade trajectories in this paradigm most likely reflects automatic
interference of a distractor with ongoing task goals.

A few studies examined the effect of emotional stimuli on saccade trajectories.
Nummenmaa and colleagues (2009, Experiment 3) presented a pair of pictures
conveying neutral and emotional (either pleasant or unpleasant) scenes on the left and
right side of the screen, and participants had to execute a saccade as quickly as possible
to a target on top of the screen. They showed that saccade endpoints and trajectories
deviated away from the visual field in which the emotional scenes were presented. In a
similar study, it has been demonstrated that saccade trajectories deviate most strongly
away from angry versus happy faces. Schmidt and colleagues (Schmidt, Belopolsky, &
Theeuwes, 2012, see Chapter 3) presented emotional faces pairwise with neutral faces
close to the saccade target. Their results show saccadic deviations away from an angry
face compared to a happy or a neutral face. These effects have been replicated by
(Petrova & Wentura, 2012), who demonstrated deviation away from a single angry
face, relative to a happy or a neutral face. The results of trajectory studies indicate that
threatening distractors are quickly selected and interfere with ongoing task goals.
Oculomotor interference of a threatening distractor provides strong evidence that
threat directly affects behavior, even when it is irrelevant to the task.

Attentional bias to threat: facilitation or disengagement?
Since fast detection and evaluation of suddenly emerging stimuli is essential for an
organism’s survival, attentional bias to emotion may result from facilitated detection of
an emotional stimulus. An alternative view is attentional bias may arise from a difficulty
to disengage from the emotional stimulus (see Derryberry & Reed, 2002). Delayed
attentional disengagement suggests that once attention is oriented towards a stimulus,
it is difficult to redirect it to another stimulus. For example, it has been argued that
delayed disengagement of attention from threatening stimuli can be related to
behavioral freezing (LeDoux, 1996). This freezing behavior can for example be observed
when an animal is encountered by a predator. From an evolutionary view, engaged
attention on the predator might be developed in order to help the animal select an
appropriate response without leaving the predator unattended (Belopolsky, Devue, &
Theeuwes, 2011). This monitoring component of reacting to threat can exist parallel to
fast detection of threat, since after detection, threatening stimuli may trigger elaborate
processing.

Several dot-probe studies have provided evidence for delayed disengagement
of attention from threatening pictures compared to neutral pictures. When a
threatening cue was present at the invalid location, detection times of targets was
slowed compared to when neutral cues were present (Cooper & Langton, 2006; Koster, Crombez, Verschuere, et al., 2004; Stormark, Nordby, & Hugdahl, 1995). Moreover, it has been shown that saccadic eye movements away from centrally presented faces were slower when the face had an angry expression compared to a neutral expression (Belopolsky et al, 2011). Thus, threat-related stimuli seem to be effective in holding visual attention. However, consistent with studies showing facilitated attention only in anxious participants (Bradley et al., 1998; Macleod et al., 1986; Mogg et al., 1997), some studies showed that the presence of threatening cues affects the disengagement component of attention in highly anxious but not in low anxious participants (Fox, Russo, Bowles, & Dutton, 2001; Koster, Crombez, Verschuere, Van Damme, & Wiersema, 2006). Therefore, whether an emotional picture influences attentional selection seems to rely on the emotional value that an individual applies to the event.

In sum, behavioral and eye tracking studies have provided evidence for both fast detection of and slow disengagement from threatening stimuli, even when they are irrelevant to the task goal. However, a large problem faced by many studies investigating the link between emotion and attention lies in the choice of stimulus material. In the next section, the importance of solving this problem is discussed.

**Stimulus-specific differences**

In the studies described above, there are inevitable differences in low-level features among the stimuli. For example, pictures can differ in complexity, luminance, and appearance, making it hard to draw conclusions on whether it was the emotional value of the stimulus that biased attention or the physical low level features. The possible influence of low-level features has been highlighted by researchers who demonstrated that a search advantage is not specific for threatening animals, but also present for non-threatening animals, such as cats and horses among flowers and mushrooms (Lipp, Derakshan, Waters, & Logies, 2004). This pattern of results seems to indicate that among backgrounds of flowers and mushrooms, pictures of all animals rather than only threatening animals are detected faster. A possible explanation for this effect is that it is hard to control for low-level differences between stimuli, especially when using natural images. For example, a certain stimulus may have specific colors or appears on a
different background than another stimulus (see Cave & Batty, 2006).

Some studies revealed that there are effects of emotion on attention which are independent of low-level features (e.g., Lundqvist & Öhman, 2005; Öhman, Juth, & Lundqvist, 2010; Tipples, Atkinson, & Young, 2002). Most of these studies used schematic face stimuli (e.g., smileys), since they consist of only a few features, such as eyes and mouth, and can therefore easily be controlled for perceptual differences. For example, Tipples and colleagues (2002) presented features that are specific to angry faces, such as a v-shaped eyebrow, in non-face objects. No search advantage was found for v-shaped eyebrows presented in a non-face object, indicating that fast detection of schematic angry faces is not caused by perceptually distinct features of the face. In addition, some studies presented face stimuli upside down, since this is thought to disrupt holistic face processing while keeping perceptual differences intact (Tanaka & Farrah, 1993). In visual search tasks, it has been shown that detection of inverted angry faces is not facilitated compared to inverted neutral faces, indicating that facilitated attention was not driven by low-level features (e.g., Fox et al., 2000). Therefore, when investigating the effects of emotion on attention, it seems highly important to control as much as possible for low-level differences between stimuli.

In addition to low-level differences, whether a threatening picture influences attentional allocation also seems to depend on how much emotion it evokes in the observer. For example, Öhman and colleagues (2001) observed faster detection of snakes among flowers in snake phobics, but not in spider phobics, and vice versa. This suggests that individual emotional significance may be an important factor drawing attention to a particular object. An attentional bias toward threatening animals may be a unique characteristic of phobic individuals, and may not represent a typical attentional orienting response. This is consistent with findings of several studies that reported fast detection of threatening pictures in anxious participants but not in low-anxious participants. Therefore, the emotional arousal elicited by the feared stimulus may play a large role in its speeded detection.

Consistent with this view, Lundqvist, Juth, and Öhman (2014) stated that the factor of emotional arousal is probably also crucial for explaining results of visual search
tasks with emotional faces. They reanalyzed data from more than two decades and argued that emotional arousal has a stronger influence on visual search efficiency measures than valence. Specifically, they showed that relative arousal elicited by the target compared to the distractors systematically influences the outcome of visual search experiments. A happy face rated higher in arousal than its angry counterpart was likely to be detected with more efficiently than the angry face, and vice versa. The influence of arousal may thus seem a crucial factor in attentional biases to emotional stimuli. Overall, since pictorial stimuli may vary substantially in perceptual factors and in the level of arousal they elicit, the use of pictures in investigating an attentional bias to emotions should be treated with caution.

**Is attention necessary to process threat?**

A central question about prioritized detection of threat is whether it can occur without attention and perhaps outside of conscious awareness (LeDoux, 1996). In order to investigate the effect of threat on attention, researchers have often focused on the amygdala, a subcortical structure that is believed to be important for the processing of emotional stimuli (Davis & Whalen, 2001). For example, exposure to fearful stimuli has been shown to induce activation of the amygdala. The main source of visual input to the amygdala comes from higher-order visual association cortices in the anterior temporal lobe (Amaral, Price, Pitkanen, & Carmichael, 1992). An important view on the role of the amygdala in attention is that detection of fearful stimuli may be mediated by a direct pathway between the amygdala and other subcortical structures, such as the pulvinar and the superior colliculus. Such a direct connection has been frequently demonstrated in rodent studies (see LeDoux, 1996), and is supposed to operate independently and in parallel to cortical visual processing (Whalen et al., 1998). A direct pathway to the amygdala bypassing the visual cortex implies that evaluation of fearful signals does not rely on conscious appraisal of these signals, and fearful signals can be evaluated quickly and efficiently. Therefore, it is suggested that the subcortical pathway underlies automatic detection of threat (LeDoux, 2000; Liddell et al., 2005; Morris, Öhman, & Dolan, 1999).
Several studies have suggested that the amygdala is activated even when the threatening stimuli are presented outside the focus of attention. It has for example been shown that when participants were instructed to either attend to pairs of houses or pairs of faces, the amygdala responded to fearful faces regardless of whether they were attended or not (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Vuilleumier, Armony, Driver, & Dolan, 2001). In contrast, activity in the fusiform face area (FFA), which appears to depend on the degree of attention toward faces (Wojciulik, Kanwisher, & Driver, 1998), was considerably modulated by whether faces appeared at attended versus unattended locations. These results support the view that the threatening content of an event can be processed even when attention is allocated elsewhere.

Additionally, there are several demonstrations of amygdala activation to stimuli that are not consciously perceived. For example, several studies used a backward masking procedure, in which a stimulus is presented for a brief period of time and followed by a mask stimulus. Backward masking blocks processing of visual stimuli in the primary visual cortex (Rolls & Tovee, 1994; Rolls et al., 1999). It has been demonstrated that amygdala activation to the presentation of fearful faces is enhanced compared to neutral faces, and that this activation occurred even when participants were not aware of the presentation of the faces because they were masked (Whalen, et al., 1998). In addition, a number of studies have used binocular rivalry to examine preferential processing of emotional stimuli. In binocular rivalry, different stimuli are simultaneously presented to each eye but only one of them usually reaches consciousness at a particular time. Several studies revealed that during binocular rivalry, emotional stimuli preferentially access conscious perception with respect to neutral stimuli (Alpers & Pauli, 2006; Bannerman, Milders, De Gelder, & Sahraie, 2008; Williams, Morris, McGlone, Abbott, & Mattingley, 2004). Moreover, Pasley and colleagues (Pasley, Mayes, & Schultz, 2004) showed that when fearful faces and control pictures of chairs were presented to participants under binocular suppression, neural activity in the left amygdala discriminated between these two complex object types. In contrast, no differential activity was found in inferior temporal cortex (IT), a visual area involved in object recognition.
On the contrary, it has been argued that when processing resources are sufficiently used (for example, by performing a challenging task), visual processing of emotional stimuli is significantly reduced, which challenges the view that emotional stimuli are processed automatically (Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Pessoa, Oliveira, & Pereira, 2011). Moreover, in a study of a patient with complete amygdala lesions (Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009), it was shown that reaction times for detecting fearful faces among distractor stimuli were within the normal range, and fearful facial expressions broke into consciousness faster than happy faces during binocular suppression to the same degree as in control subjects. These findings demonstrate that the amygdala is not essential for non-conscious, rapid fear detection, and argue against the existence of a direct subcortical visual pathway.

In sum, although it remains unclear whether emotional stimuli can be processed prior to awareness, the studies described above indicate that the amygdala is at least partly involved in allocating attentional resources to emotional stimuli. Given the broad connectivity of the amygdala with other subcortical and cortical structures, the effect of the amygdala on behavior can probably be mediated through many routes, for example, via both the visual cortex and prefrontal cortex (Pessoa & Adolphs, 2010). Through this connectivity, and because of its significant role in emotion detection, the amygdala is likely to be involved in prioritized detection of emotionally relevant events in the environment.

Conclusions
When an individual is suddenly confronted with an unexpected situation, it is important to immediately adjust behavior accordingly. Just as a perceptually salient stimulus attracts attention, pictures with an emotional value seem to bias attention and influence behavior. In addition, some studies showed that instead of facilitated attention to threat, it takes longer to disengage attention away from threat after it has been attended, relative to neutral stimuli. There are however still some limiting factors with regard to the use of emotional pictures. First, studies using emotional pictures generally lack control over perceptual features of the stimuli. It can therefore not strictly be concluded that the attentional effects are driven by emotion, and not by
feature differences such as complexity and luminance. Second, although pictures conveying threat can be considered aversive, they only seem to impose a symbolic representation of threat, and never signal an actual threatening outcome. This view is supported by several studies that only found an attentional bias to threatening pictures in highly anxious or phobic individuals.

To resolve these problems, it seems essential that the perceptual features of the emotional and neutral stimuli are kept equal. Several studies have overcome this problem by using stimuli that have identical physical features, and associating some of them with threat using a fear conditioning procedure. In classical conditioning, an initially neutral stimulus is paired with an aversive outcome, such as an electric shock or an aversive noise, while another neutral stimulus is not. Since the neutral stimuli can be completely controlled for physical differences, it is likely that attentional effects will be caused by the threatening value of the stimuli. Crucially, another major advantage of using a fear conditioning paradigm is that stimuli will be associated with a real aversive outcome and will therefore pose a genuine threat that is very likely to be appraised as aversive. The chance of receiving an electric shock or aversive noise can evidently be considered much more threatening than observing a threatening picture, especially in individuals that are not so vulnerable to pictorial threat. The next chapter gives an overview of research on attentional selection of initially neutral stimuli that have been associated with a threatening outcome through conditioning.
Chapter 2

Modulation of visual attention by fear-conditioned stimuli
Fear can be viewed as an adaptive behavioral response, allowing us to predict, react, and adjust to past, present, and future threat. Threatening events usually do not arrive without notice, but are signaled by certain cues. For example, a predator may announce its presence by movements, sounds or odors. The contingency between such cues and dangerous outcomes are learned very quickly, such that a state of fear can be elicited by a cue alone (e.g., Rescorla & Solomon, 1967). In case of future detection of the same conditioned cues, defensive responses in anticipation of the predator’s attack could help an organism to increase survival chances. Thus, associative learning between a cue and an outcome can account for the development of an emotional response. This conditioned response allows the organism to anticipate a dangerous event and to prepare for the appropriate course of action. Conditioned fear can easily be induced in the laboratory settings and there is a long history of inducing fear in laboratory animals (Bekhterev, 1913), as well as in humans (Watson & Rayner, 1920). It is likely that emotional behavior is closely related to basic associative learning processes.

**Classical and operant fear conditioning**

The term *classical conditioning* refers to the learning of an association between two stimuli that are initially unrelated (Pavlov, 1927). In a classic conditioning design, an initially neutral stimulus (CS) becomes a conditioned stimulus through an association with an unconditioned stimulus (US), while another neutral stimulus remains unpaired. For example, in Pavlov's initial conditioning experiments, he rang a bell before giving a dog food. After a few repetitions, the dogs started to salivate in response to the bell. In this example, the bell is the conditioned stimulus, and the food is the unconditioned stimulus. Thus, the response to the bell was acquired through previous experience. One powerful form of Pavlovian conditioning is *fear conditioning* (Davis, 1992; Fendt & Fanselow, 1999; LeDoux, 2000). Simply stated, classical fear conditioning involves learning that certain environmental stimuli predict aversive events. Fear conditioning in humans typically uses a tone or a light as a CS and a mild electric shock or an aversive noise as a US. Under these circumstances a small number of CS–US pairings produces robust fear learning as is reflected in responses related to fear, such as increased heart rate, skin conductance responses (SCRs), and potentiated startle. A well-known
example of fear conditioning in humans is the Little Albert experiment by Watson and Rayner (1920). When Albert's hand touched the rat, the experimenters banged a steel bar with a hammer behind his head (US), which caused him to startle, fall forward and cry. Afterwards, when the rat (CS) was placed near Little Albert's hand, he withdrew his hand and began to cry. Fear conditioning can thus turn arbitrary stimuli into cues that signal potential threat on the basis of past experiences. Therefore, classical conditioning is a form of associative learning involving the formation of connections between a neutral stimulus and a stimulus with innate behavioral significance.

Another form of conditioning is operant conditioning, sometimes referred to as instrumental conditioning. Operant conditioning is a method of learning that occurs through rewards and punishments of behavior. For example, in Skinner's operant conditioning experiment (Skinner, 1938), pigeons were put in a chamber and were free to make simple, repeatable responses. When the animal correctly performed a particular response, such as pressing a lever, the chamber mechanism delivered food or another reward. Eventually, the animal learned that the particular behavior was associated with reward, and repeated that behavior frequently in order to obtain more reward. Likewise, fear can be quickly acquired through operant conditioning in which the presentation of an aversive stimulus is conditional upon behavior. In that case, a response (e.g., pressing a button on a keyboard) is followed by an electric shock or an aversive noise. As a result, one learns to avoid making the response that was followed by the aversive experience. Most contemporary learning theorists regard classical conditioning as reflecting stimulus-outcome associations and operant learning as reflecting response-outcome associations (Kirsch, 1985; Rescorla, 1988, 1991). Operant conditioning situations produce expectancies that particular behaviors will produce particular outcomes (e.g., that food can be found in a particular location), and classical conditioning produces expectancies that certain stimuli will be followed by other stimuli (e.g., that an electric shock will be presented soon after the bell is sounded).

In daily life, we are continuously confronted with a large number of stimuli in our environment. Since the capacity of our visual system is limited, stimuli that seem relevant to are in competition for attentional selection with less relevant events.
general, it is thought that stimuli automatically attract attention when they are more salient than others. A stimulus can be considered salient when it differs in physical features such as color and size. Such a physically salient stimulus can attract attention automatically, even when task goals require attention to be directed to another location (e.g., Theeuws, 1992). Recently, it has been argued that salience is not limited to perceptual features, but can also be defined as having a high behavioral relevance (Awh et al., 2012). In the previous chapter, we discussed evidence for the view that pictures that convey threat, such as angry faces and snakes, are preferentially selected over neutral ones, even though they interfere with voluntary task goals. It is thought that such stimuli are more salient than neutral ones because of their high behavioral relevance. Following this line of reasoning, it can be argued that cues that predict a behaviorally relevant outcome are also likely to attract attention automatically. If a cue is likely to be followed by something aversive or threatening, it is clearly beneficial for an organism to quickly direct attention to it, especially if that helps him to avoid the danger (Frijda, 1986). Therefore, the ability to quickly select items that predict threat is crucial when it comes to survival chances.

Several studies examined how stimuli that have been previously associated with threat influence the attentional system. In general, such experiments start with a classical fear conditioning paradigm in which two neutral stimuli, such as geometrical shapes, are presented one by one in the center of the screen. On some presentations, one of the neutral stimuli (the CS+) is paired with an aversive outcome (US), such as a white noise or an electric shock. The other neutral stimulus (CS-) is never paired with an aversive outcome. Thus, after fear conditioning, an initially neutral cue has acquired emotional significance. Importantly, there is a large advantage of using fear-conditioned cues over pictures conveying threatening information. Since the initially neutral stimuli can be completely controlled for perceptual differences, it can be ensured that a possible attentional effect is driven by the emotion associated with it. In addition, the stimuli will pose a genuine threat that is very likely to be appraised as aversive, because the chance of an aversive event (e.g., receiving an electric shock or hearing a loud noise) can be considered much more threatening than observing a
threatening picture. Thus, the use of fear-conditioned stimuli may substantially add to the discussion whether stimuli with an emotional value attract attention.

**Fear conditioning and attention**

As described in Chapter 1, attentional biases to threat can be caused by both facilitated attention to threat and by subsequent processes that occur after the threatening stimulus has been detected. Since fast detection of threatening stimuli is essential for an organism’s survival, detection of a threatening stimulus may be facilitated compared to a neutral stimulus. In addition, an attentional bias may arise from trouble to disengage attention from the threatening stimulus. In that case, it can be argued that after quick selection of threat, the threatening stimulus requires elaborate processing in order to select an appropriate behavioral response. For example, it is important to quickly detect a suspicious movement, but it may be inefficient to directly attend to a new location afterwards, since the intentions of the source of movements are yet unclear. To examine how stimuli that are associated with threat modulate the attentional system, many studies have used a variation of Posner’s (1980) exogenous spatial orienting task. In this task, attention is oriented to a spatial location through the presentation of a peripheral stimulus (cue), followed by a response-target presented at the same (valid trial) or at the opposite (invalid trial) spatial location as the cue. Fast responses to validly cued locations indicate efficient allocation of spatial attention to the cued location, whereas slow responses to invalidly cued locations indicate slow disengagement of attention of the cued location. If cues that predict threat indeed attract attention automatically, responses to locations cued by a fear-conditioned stimulus should be faster than neutrally cued locations. In contrast, slow responses to locations invalidly cued by a fear-conditioned stimulus (i.e., the target is presented at an uncued location) would indicate a difficulty in disengaging attention from threat.

Several spatial cueing studies that used fear-conditioned cues demonstrated delayed disengagement from threat, facilitated attention to threat, or a combination of both. In a study by Van Damme and colleagues (Van Damme et al., 2004), response times to locations previously occupied by a fear-conditioned cue were faster compared to a neutral cue. Thus, threatening cues facilitated directing attention to their location
in comparison to neutral cues. However, threatening cues did not impair disengagement of attention from their location in comparison to neutral cues. In contrast, Massar and colleagues (Massar, Mol, Kenemans, & Baas, 2011) only observed slower disengagement of attention from threatening cues, but not facilitation of attention. Koster and colleagues (Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004) performed a spatial cueing task in which the CS+ was paired with an aversive noise throughout the experiment. One of two locations on the screen could be cued by a colored frame. One of the colors served as the CS+, the other remained neutral. On some trials, the aversive noise was presented simultaneously with the fear-conditioned frame (CS+). The authors reported evidence for facilitated engagement to fear-conditioned cues, reflected in faster reaction times to targets preceded by a fear-conditioned cue compared to a neutral cue. Moreover, response latencies to invalidly cued targets were slower compared to neutral cues, indicating that threatening cues delayed disengagement of attention (see also Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2005). Facilitation and delayed disengagement of attention to threatening cues during a spatial cueing task was also observed by Van Damme and colleagues (Van Damme, Crombez, Hermans, Koster, & Eccleston, 2006) who used an electrical shock as US. Overall, these results show that after an initial shift of attention to potential threat, it takes longer to disengage attention to a new location.

In contrast to fast allocation and delayed disengagement, Stormark and colleagues (Stormark & Hugdahl, 1996; Stormark, Hugdahl, & Posner, 1999), demonstrated a quick shift of attention away from fear-conditioned cues. When a location was invalidly cued by a fear-conditioned stimulus, targets on the opposite location were quickly detected, compared to when neutral cues were present. The authors suggested that this effect can be explained by a tendency to quickly shift away from threat, which could be part of a strategy to avoid further processing of aversive information. However, since in these studies the time between cue and target onset was relatively long (600 ms), the effect could be explained by inhibition of return to the previously attended location (Posner & Cohen, 1984).

In sum, there is evidence that attentional bias to signals of threat consists of both facilitated engagement of attention and difficulty in orienting attention away from
threat signals. The latter finding is in line with many studies on emotion attention using pictorial signals of threat (Fox et al., 2001; Fox, Russo, & Dutton, 2002; Yiend & Mathews, 2001). Although a disengagement delay does not seem particularly adaptive, dwelling of attention on threatening stimuli may be an important factor when trying to cope with threat. When the source of threat is being monitored, increased dwell time for threat would facilitate the identification and evaluation of the implied threat (Belopolsky, Devue & Theeuwes, 2011). When dealing with a threatening situation, initial selection and subsequent processing of threat both seem to be important for reducing the risk of being harmed.

Importantly, in a real life setting, threatening stimuli are never presented on their own but are accompanied by many other inputs that compete for visual selection. The preferential selection of threatening stimuli over neutral ones when they are in competition seems to be an important adaptive behavior. For example, when an observer has a goal to search for food in his environment, it is important that any potentially threatening object wins the competition for attentional selection, and overrides the goal to attend to the food. It therefore seems to be of particular importance to study the attentional effects of threatening stimuli when they are in competition with other items in the visual field.

Notebaert and colleagues (Notebaert, Crombez, Van Damme, De Houwer, & Theeuwes, 2010) used a visual search task to investigate whether signals of potential threat interfere with search goals. In their study, participants had to search for a target among distractors. All search items were presented in circles of different colors. One of the colors served as the CS+ and was previously paired with an electrical shock during a classical conditioning procedure. On congruent trials, the target always appeared inside the CS+. Moreover, in the experimental group, the CS+ occurred at a certain location in the visual display on 80% of the trials. In the control group, the CS+ appeared equally often at all locations. Results showed that in the control group, the CS+ caused both facilitation and interference in the visual search task. When the target was presented inside the CS+ circle, reaction times were faster compared to neutral circles. When the target appeared in a neutral circle, the presence of the CS+ circle slowed down search
times. In contrast, in the experimental group, the spatially predictable CS+ caused facilitation but no interference. The authors suggest that the lack of an interference effect in the experimental group could indicate that the spatial predictability of the CS+ prepared participants for a quicker disengagement of attention from the threatening stimulus. When there is a high chance of threat to appear at a certain location, a threatening outcome can be better anticipated, and an appropriate response can be prepared. In addition, the authors showed that search time on congruent trials did not attenuate with increasing set size compared to baseline trials (where the CS+ was absent). The authors concluded that the CS+ was prioritized over other stimuli, but did not automatically attract attention (see also Notbaert, Crombez, Van Damme, De Houwer, & Theeuwes, 2011).

A study by Schmidt and colleagues (Schmidt, Belopolsky, & Theeuwes, 2014, see Chapter 4) provides further evidence supporting the hypothesis that threatening stimuli interfere with search for a neutral target among deviant neutral distractors. In their study, a diamond shape (CS+) was associated with an electrical shock in a classical conditioning procedure, while a differently colored diamond (CS-) was never associated with a shock. In a subsequent visual search task, participants had to search for a circle among diamond distractors. On 50% of the trials, the CS+ or CS- was present as a distractor. The results showed that the presence of an irrelevant distractor that was previously associated with a shock slowed search more than a distractor without fear association, indicating that learned fear associations have the ability to capture attention even if we try to ignore them. These results support the view that threat-predicting cues prioritize attention when they are in competition with neutral cues, and therefore interfere with current goals.

**Oculomotor competition between fear-conditioned and neutral cues**

It has been often suggested that emotions reflect states of action readiness (Frijda, 1986). The function of fast selection would be to prepare an organism to initiate rapid action when threat is present. When stimuli are competing for attentional selection, eye movement behavior provides direct information of which stimulus was selected preferentially over another. Key evidence for competition within the oculomotor
system modulated by threat comes from studies measuring saccadic latencies towards or away from threatening pictures (e.g., Kissler & Keil, 2008; Bannerman et al., 2009, 2010) and deviations in saccadic trajectories when a threatening picture was present (Nummenmaa et al., 2009; Petrova et al., 2013; Schmidt et al., 2012), which are thought to reflect oculomotor competition for attention between locations in space. So far, only two studies have used eye movements to examine the effects of fear-conditioned stimuli on attention. Mulckhuysse and colleagues (2013) investigated if fear-conditioned stimuli influence saccadic pathways in a similar way as threatening pictures do. Participants had to make speeded eye movements to a target while a fear-conditioned (CS+) or neutral distractor (CS-) was presented in the periphery. The results showed that long-latency saccades deviated more strongly away from the CS+ than from the CS- distractor. Moreover, short-latency saccades deviated more strongly toward the CS+ than toward the CS- distractor. Consistent with studies using pictorial stimuli, these results indicate that the oculomotor system is able to differentiate between a threatening and a non-threatening event very early in time. Since the stimuli were completely task-irrelevant, the results suggest that fear-conditioned stimuli interfere with ongoing behavior even when there is no incentive to pay attention to them.

One other study investigated oculomotor competition between fear-conditioned and neutral stimuli. Schmidt and colleagues (Schmidt, Belopolsky, & Theeuwes, 2015, see Chapter 5) briefly presented two differently colored cues left and right from fixation. Shortly after the cues disappeared, participants were instructed to make speeded eye movements to the left or right, indicated by a centrally presented arrow. During the experiment, one of the cues (CS+) was on some trials combined with an electrical shock (US). Results showed that saccadic latencies to locations previously occupied by the CS+ were faster than saccades in the opposite direction. A comparison with trials in which only neutral cues were presented indicated that this difference was caused by both facilitation of saccades to CS+ locations, and slower saccades away from CS+ locations. Comparisons of saccades with a neutral baseline suggested that the early bias toward fear-conditioned cues may indeed arise through facilitation towards the threatening cue. Thus, the presence of a potentially threatening stimulus interfered
with execution of a voluntary saccade, which indicates that conditioned fear has a direct influence on visual selection. Interestingly, in this study, the CS+ was always presented simultaneously with a neutral stimulus. Therefore, besides the CS+, there was another cue that signaled the US, namely the stimulus that was always presented together with the CS+, the paired stimulus (PS). Similar to the pattern observed for the CS+, faster saccades to paired stimuli were observed when presented together with a neutral stimulus, as well as slower saccades to the opposite location. Thus, even though participants did not explicitly learn a contingency between the PS and the US, the PS still acquired a threat value and attracted attention to its location. Presumably, participants implicitly learned that the paired stimulus was also part of the compound that formed the CS+. Therefore, it is likely that cues that are implicitly associated with fear are also relevant for behavior and elicit oculomotor competition when presented together with a completely neutral stimulus.

The time course of attentional biases to threat

The results of the studies described above demonstrate that threatening events can be quickly selected over other competing demands for attention. As stated in Chapter 1, threatening events can be considered more salient to an observer compared to neutral events because they have high behavioral relevance. When an item in the visual field is more salient relative to other items, it is thought to attract attention in a bottom-up, i.e. automatic, way, even when the goal is to look for another item. Importantly, it has been proven that the bottom-up processing of salient events is short-lived (e.g., Donk & van Zoest, 2008). After a limited time interval, the visual system no longer holds information concerning the relative salience of objects, and salient objects do not automatically influence attentional selection anymore. Therefore, attentional competition from threatening stimuli is likely to dissipate very quickly. However, it may be argued that a threatening stimulus does not lose its behavioral value after it has been selected. It has been suggested that when some time has passed, salience-driven effects can eventually be followed by the voluntary deployment of attention (Koch & Ullman, 1985; Wolfe, Cave, & Franzel, 1989). It may be that after initial automatic orienting, voluntary attention is preferentially deployed to the threatening stimulus, since it still contains
more relevant information than neutral stimuli.

In a follow up to their 2015 study, Schmidt and colleagues (Schmidt, Belopolsky, & Theeuwes, submitted, see Chapter 6) investigated if fear-conditioned cues are preferentially selected over neutral ones, after initial processing. Participants had to make speeded eye movements towards locations previously occupied by either a location that was previously fear-conditioned or by a neutral location. The direction of the eye movement was indicated by an arrow which appeared 50 ms or 600 ms after termination of the stimuli in a random manner. If fear-conditioned stimuli only induce attentional selection very early in time, a validity effect is expected only in the 50 ms condition. However, if fear-conditioned stimuli still induce attentional selection after the initial selection, the 600 ms condition would also show a validity effect. For both the 50 and the 600 ms conditions, the results showed facilitated attention towards locations validly cued by fear-conditioned compared to neutral stimuli, and delayed disengagement of attention from invalidly cued locations. These effects were replicated in an experiment using a 1000 ms delay between cue and arrow presentation. Thus, potential threat still induced attentional selection long after the source of threat had been removed. However, preferential selection of threatening stimuli long after removal is probably caused by a top-down set of the observer, i.e., the observer voluntary attended to the location previously occupied by the threatening cue since it contained behaviorally relevant information.

The results of the study by Schmidt and colleagues (2015) indicate that initial orienting to potential threat is most likely under bottom-up control. Since bottom-up allocation of attention is short-lived (Donk & van Zoest, 2008), subsequent engagement of attention to threat can most likely be attributed to top-down goals of the observer. This view is strengthened by fact that participants got verbal instructions about the stimulus-outcome contingency, and therefore may have had a voluntary preference to attend to threat. Note, however, that no behaviorally relevant information was present at the validly cued location at the time of eye movement in the long delay conditions. Perhaps, the location previously occupied by the threat-related cue had become associated with threat until the end of the trial.
Attention to cues signaling safety

The results described above demonstrate that a stimulus that conveys threat is quickly selected. However, threatening signals are not the only type of information that can be considered behaviorally relevant. Any signal that contains relevant information, compared to signals conveying no information, should be selected preferentially by the visual system. For example, just as a threatening cue contains important information about a possible aversive outcome, a safety cue holds crucial information about when the outcome is not aversive, and signals a possible escape. Therefore, safety signals could be considered behaviorally relevant and may produce an attentional orienting effect. Such a response would require the allocation of attention both to the identification of potential safety stimuli and to the initiation of an appropriate response. The visual system may process safety signals in a preferential way, since avoidance of an aversive outcome seems a highly relevant behavior for an organism that is confronted with a threatening situation. A high motivation to escape from threat may be reflected in an attentional bias to signals of safety, compared to signals conveying more ambiguous or no information.

To test whether signals of safety are preferentially selected, Schmidt and colleagues (submitted, see Chapter 6, Experiment 3) performed a spatial cueing task similar to the one described in the previous paragraph. Participants got verbal instructions only about the contingency between one of the colored cues and a ‘safe’ outcome. They were told that when the safety cue was presented during the experiment, the chance of receiving an electrical shock was zero. In contrast, when any other cue was present, they had a chance of receiving a shock on random trials. SOAs of 50 and 600 ms between cue offset and target onset were randomly used. The results showed that in the 50 ms SOA condition, saccadic latencies in validly cued trials did not differ from invalidly cued trials, indicating that safety cues were not preferentially selected over neutral ones early in time. However, a validity effect was observed for safety trials in the 600 ms SOA condition. This validity effect was driven by slower responses to trials with an invalid safety cue, compared to an invalid neutral cue. Therefore, when given enough time to process information about competing cues, the voluntary execution of an eye movement was interrupted by the presence of a cue that
signaled safety. Although this effect is similar to the validity effect observed for threatening cues in the 600 ms SOA condition, quick facilitation to threat in early stages of processing seem specific to cues with a highly threatening value. The initial eye movement to the threatening cue appears automatic. Additionally, when there is enough time to evaluate the competing stimuli, attention can be voluntary deployed to behaviorally relevant information other than threat.

Together, these results imply that when stimuli signaling important information and neutral stimuli compete for attentional selection, information signaling stimuli interfere with voluntary task goals. In addition to events conveying safety or threat, other stimuli with a high behavioral relevance, such rewarding outcomes like money or food, are also likely interfere with voluntary saccade goals. However, not every type of information seems to bias target selection very early in time, and quick and automatic selection seems to be specific to stimuli signaling direct threat.

**Neural structures involved in fear conditioning and attention**

A large body of evidence points to the amygdala as the key neural system involved in fear conditioning (Davis, 1997; Fendt & Fanselow, 1999; Lavond, Kim, & Thompson, 1993). For example, it has been demonstrated that a patient with bilateral amygdala pathology does not show Pavlovian fear conditioning to cues paired with loud noise (Bechara et al., 1995). Moreover, patients who have received a unilateral amygdalectomy for the treatment of epilepsy also have deficits in auditory fear conditioning (Labar, Ledoux, Spencer, & Phelps, 1995), and patients with amygdala damage fail to recognize fear in facial expressions (Adolphs, Tranel, Damasio, & Damasio, 1995; Adolphs et al., 1999). Functional neuroimaging has extended these lesion studies by revealing amygdala activation during Pavlovian fear conditioning (Buchel, Dolan, Armony, & Friston, 1999; LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998; Schneider et al., 1999). These sources of evidence are consistent with the view that the amygdala is involved in fear conditioning and processing of emotional information.

The amygdala receives sensory inputs from diverse areas of the brain (e.g. thalamus, neocortex, olfactory cortex, hippocampus) and sends projections to
various autonomic and somatomotor structures that are assumed to mediate specific fear responses, such as periaqueductal gray matter for freezing behavior and lateral hypothalamus for sympathetic activation (Kim & Jung, 2006; LeDoux, 1996). In humans, the amygdala consists of several anatomically and functionally distinct nuclei, including the basolateral complex, the centro-medial nucleus and the cortical nucleus. It is generally accepted that sensory information enters the amygdala through its basal and lateral nuclei (BLA; Aggleton, Vann, Oswald, & Good, 2000; LeDoux, 1996), where CS–US association formation is believed to take place (but see Pare, Quirk, & Ledoux, 2004 for an alternative view). This evidence has been obtained from studies employing permanent and reversible lesions of the amygdala and neurophysiological recordings of amygdala spike firing during learning. These nuclei are connected with the central nucleus (CeA), which is thought to be the main amygdaloid output structure sending projections to various autonomic and somatomotor centers involved in mediating specific fear responses (Kim & Jung, 2006).

It should be noted however that activity in the amygdala evoked by a CS+ decreases over time (Buchel & Dolan, 2000; Buchel et al., 1999; LaBar et al., 1998). This observation has a direct impact on the role of the amygdala in classical fear conditioning. It has been argued that that brain systems that mediate learning, in which the amygdala plays a central role, do so by enabling associative plasticity that encodes sensory contingencies that are being acquired. Following acquisition, the learned association will be expressed at a cortical level reflecting changes in synaptic connection strengths (McGaugh, Cahill, & Roozendaal, 1996). However, after an association has been learned, there is no need for further modulation of plasticity, and systems mediating it disengage, as reflected in a decline in amygdala activation. Several neuroimaging studies have indeed reported activation of brain structures involved in learning and memory that interact with the amygdala during fear conditioning. A prominent role is fulfilled by the hippocampus, which is transiently involved in consolidating contextual fear memory (Dolcos, LaBar, & Cabeza, 2004; Phelps, 2004; Phillips & Ledoux, 1992; Richardson, Strange, & Dolan, 2004). Therefore, it has been suggested that the role of the amygdala in fear conditioning is not limited to encoding and storing Pavlovian CS-US associations, but is also strongly involved in consolidating
memories for negative experiences outside of the amygdala (Cahill & McGaugh, 1998; Dunsmoor, Murty, Davachi, & Phelps, 2015; McGaugh, 2000). The view that multiple memory systems are engaged during learning and memory tasks is supported by evidence showing that humans with amygdala damage show intact declarative memory for a fear conditioning experience, despite failing to exhibit fear responses to conditioned stimuli (Bechara et al., 1995).

**Attentional modulation by fear-conditioned cues:**

**evidence from neuroimaging studies**

The amygdala is thought to be part of a direct visual pathway that connects the thalamus and the visual cortex through the superior colliculus, and allows fast processing of sensory input (LeDoux, 1996). Evidence for a direct pathway to the amygdala bypassing the visual cortex comes from studies showing that the amygdala responds to presentations of masked fearful stimuli (Morris, Buchel, & Dolan, 2001; Morris et al., 1998; Whalen, et al., 1998). In addition, amygdala activation was observed in a blind sight patient who observed fearful faces presented in the cortically blind field (Morris, DeGelder, Weiskrantz, & Dolan, 2001). Therefore, a direct connection between the amygdala and the thalamus may allow for fast detection of events with a threat value. In addition, since many behavioral studies have observed modulation of spatial attention by threatening signals, it is likely that these signals might also influence other brain systems known to be critically involved in the control of spatial attention. It is particularly informative, for instance, to observe the overlap between brain regions involved in attentional orienting and those that are sensitive to threat.

If neural activity in the amygdala has a prominent role in modulating spatial attention allocation to threatening stimuli, then amygdala neurons should represent threatening stimuli within a spatial framework. Furthermore, neural activity should reflect the allocation of attention to stimuli signaling aversive events. Several researchers have linked neural activity in the amygdala to spatial attention. It has for example been shown that the amygdala encodes information about both the spatial location and reward value of visual stimuli (Ousdal et al., 2014). Furthermore, it has been shown that an intact amygdala is crucial for guiding gaze towards emotionally-
relevant features of fearful face stimuli (Adolphs et al., 2005), which may suggest that the amygdala helps with directing the visual system to pay attention to and identify emotions. Thus, the amygdala seems to encode information about both the emotional value of a stimulus and its spatial location.

Few neuroimaging studies directly examined modulation of spatial attention by fear-conditioned stimuli. Armony & Dolan (2002) used a spatial cueing paradigm in which a fear-conditioned and a neutral face were presented left and right from fixation. Afterwards, a dot was presented on one of the locations, and participants had to localize the dot as fast as possible. Importantly, since the fear-conditioned stimuli were completely task relevant, the use of a spatial cueing paradigm allowed for measurements of involuntary attention to a threatening location. The results showed that attention was modulated by the affective value of the stimuli. Moreover, it was demonstrated that responses in the amygdala and extrastriate visual cortex were enhanced by fear-conditioned stimuli. In addition, when attention was allocated to fear-conditioned stimuli, the fronto-parietal neural network and the lateral orbitofrontal cortex (lOFC) were activated. The fronto-parietal network is thought to underlie the control of spatial attention and is active when attention is directed to visual locations (Corbetta, 1998). The authors argued that the lOFC can transfer information about the emotional value of a stimulus from the amygdala to cortical areas subserving spatial attention. Activation of the lOFC may be an interface between spatial attention and fear conditioning. In addition, Pourtois and colleagues (Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2006) performed a spatial cueing task with fearful and neutral faces as cues. They demonstrated a modulation of intraparietal sulcus (IPS), which is crucially involved in the control of spatial attention. These results demonstrate that fearful cues can act as exogenous cues for subsequent target presented at the same location.

**Attentional orienting to behaviorally relevant stimuli**

Although this chapter so far has focused on fear learning, there is a large body of evidence for fast attentional orienting to other stimuli that are behaviorally relevant. For example, stimuli that convey a positive outcome may be equally important to be
detected quickly as negative ones. In fact, it has been suggested that any stimulus may benefit from an increased attentional processing when it is appraised as relevant to the observer (Sander, Grandjean, & Scherer, 2005). At a behavioral level, several studies have demonstrated that pictures with a pleasant arousing content may attract attention in a similar way as threatening stimuli seem to do. Using a Posner spatial cueing paradigm, it was shown that participants responded faster to locations previously occupied by pictures depicting food stimuli, relative to tools, after food deprivation (Mohanty, Gitelman, Small, & Mesulam, 2008). Moreover, it is well documented that substance-related visual cues (e.g., cigarettes or cocaine-related pictures) involuntarily capture attention in substance users (Ehrman et al., 2002; Field & Cox, 2008; Franken, Kroon, & Hendriks, 2000; Lubman, Peters, Mogg, Bradley, & Deakin, 2000; Stormark, Field, Hugdahl, & Horowitz, 1997). In addition, it has been shown that erotic images rendered invisible to observers with continuous flash suppression have been shown to attract observers’ attention, reflected in faster manual response times to their location relative to neutral images (Jiang, Costello, Fang, Huang, & He, 2006).

It is highly plausible that information relevant for reproductive behavior is also prioritized by our attention system. For example, quickly recognizing physical attractiveness can be considered adaptively beneficial. It might be advantageous to recognize attractiveness quickly because they provide an indication of reproductive fitness, which may influence decisions in mating behavior. Several studies have shown that when people have the choice to do so, they look at attractive individuals longer and more frequently (Aharon et al., 2001; Leder, Tinio, Fuchs, & Bohrn, 2010). Humans may have a predisposition to direct attention to attractive faces because of their biological and social significance, and this view is strengthened by evidence that even newborn babies look at attractive faces longer (Geldart, Maurer, & Carney, 1999). It has been shown that the presentation of a task-irrelevant attractive face interferes with endogenous cueing of spatial attention (Sui & Liu, 2009) and attention is allocated selectively to attractive opposite-sex others (Duncan et al., 2007). Thus, mating-related motives may guide the selective processing of attractive people.
Besides positive events, aversive events other than threat also seem to influence attention. Following disgust induction, participants orient toward pictures representing disgust relative to neutral pictures (Vogt, Lozo, Koster, & De Houwer, 2011). Moreover, when targets were presented 200 ms following the onset of a centrally presented picture, they were identified less accurately and more slowly when these pictures were disgust-evoking relative to fear-evoking and neutral pictures (van Hooff, Devue, Vieweg, & The, 2013), indicating a slower disengagement of attention from pictures depicting disgust.

Similar to stimuli which obtained an aversive value through fear-conditioning, learned associations between initially neutral stimuli and a positive outcome also seem to influence visual spatial attention. A large body of evidence points toward modulation of attention by stimuli that are associated with monetary reward. It has been demonstrated that initially neutral stimuli associated with value through reward learning can capture attention automatically. Specifically, a task-irrelevant distractor previously associated with a large reward slows visual search more than an equally salient distractor previously associated with a smaller reward (Anderson, Laurent, & Yantis, 2011b). Capture of attention by rewarding stimuli was even observed when participants were tested over a half year later, without the need for further reward learning (Anderson & Yantis, 2012). Moreover, the effects of reward on behavior seem to be even stronger for participants with reward-seeking personalities (Hickey, Chelazzi, & Theeuwes, 2010), indicating that motivational state (in this case, desire to earn money) is an important factor in the effect of emotion an attentional allocation. This view is supported by studies showing capture of attention by substance related cues in users but not in non-users (for a review see Field, Munafo, & Franken, 2009).

Some studies have tested whether an initially neutral cue can influence attention by merely being associated with a behavioral task goal. Vogt and colleagues (Vogt, De Houwer, & Moors, 2010) performed a task in which neutral words, such as 'field' and 'ship', were associated with a task goal, namely collecting as many points as possible during the task. In a subsequent dot-probe task, words associated with the temporary goals held attention longer than semantically related words, suggesting that
these goals influenced the allocation of attention. In another dot-probe study, it was shown that attention was automatically deployed to stimuli relevant to a temporary goal even when stimuli that signal threat were simultaneously present, suggesting that an individual’s current and temporary goals guide early attentional processes (Vogt, De Houwer, Crombez, & Van Damme, 2013). Moreover, it has been shown that induced goal relevance caused attentional biases towards goal-relevant stimuli and that such biases disappeared when the goal was fulfilled, that is, when the stimulus was not relevant anymore (Engelmann & Pessoa, 2007). These findings support the view that the allocation of attention is not entirely stimulus driven but is also guided by previous experience (Awh et al., 2012).

Consistent with behavioral studies, there is evidence that amygdala activity is not only associated with stimuli conveying negative outcomes but also with positive outcomes (De Martino, Kumaran, Seymour, & Dolan, 2006; Johnsrude, Owen, White, Zhao, & Bohbot, 2000; Ousdal, Reckless, Server, Andreassen, & Jensen, 2012; Ousdal et al., 2014) as well as facial displays of happiness (Breiter et al., 1996; Yang et al., 2002). It has therefore been argued that the amygdala is rather a valence non-specific relevance detector than a detector of fear (Sander, Grafman, & Zalla, 2003). Although the amygdala clearly responses to stimuli that predict threat, its role can be considered more general, by providing other brain regions with associative information concerning biologically relevant events, including items high in arousal but of neutral valence, such as novel and erotic stimuli.

In sum, preferential processing of threat seems to be generalized to other events with a high behavioral relevance, and the amygdala seems to be just as important for processing positive reward and reinforcement as it is for negative. Both valuable resources and dangers benefit from privileged processing, and behaviorally significant stimuli such as food, money, or signals of threat have shown to be effective cues for capturing attention. Depending on the current emotional and physical state of the organism, relevant objects need to be quickly selected from an environment and appropriately processed to fulfil short and long term goals.
Conclusions

Several studies have used a fear-conditioning procedure to examine how stimuli with a learned threat value modulate our attentional system. Evidence of behavioral and eye tracking studies have shown that stimuli that are associated with potential threat are detected preferentially over neutral ones, even when they are irrelevant to current task goals. Facilitated attention to threat has been observed when fear-conditioned stimuli are in competition with neutral ones. In addition, some studies find delayed disengagement of attention from cues signaling threat, or a combination of quick selection and delayed disengagement. When a potentially threatening event is present, initial selection and subsequent processing of threat both seem to be important for reducing the risk of being harmed.

The use of fear-conditioned stimuli has extensively contributed to a long history of research on emotion and attention. In contrast to many studies that used pictorial representations of threat, fear-conditioning studies provide clear evidence that attentional bias is driven by fear, and not by possible low-level feature differences. In addition, since fear-conditioned stimuli signal genuine threat that is very likely to be appraised as aversive, they are prioritized for attentional selection in a healthy, non-anxious population. Importantly, the results of fear-conditioning studies underline the view that attentional allocation is not only determined by bottom-up and goal-driven factors, but also by items with a high behavioral value (see Awh, et al., 2012).

Attentional bias for stimuli signaling threat is in line with converging evidence for the evolutionary function of attention to threat. The biological value of this quick orienting may be seen in the heightened spatial awareness of a potential threat that needs to be conquered. However, preferential processing of emotional information does not seem to be specific to stimuli conveying threat. Other signals that signal behavioral importance, such as reward or safety, also seem to modulate our attentional system. Whether an event is considered relevant seems to depend on one’s personal goals and emotional states. Items that are relevant to those goals need to be quickly selected from an environment and appropriately processed. Emotions seem to add relevance to events, which thereby acquire their preferential processing.
MODULATION OF VISUAL ATTENTION BY FEAR-CONDITIONED STIMULI