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# To what extent are emotional visual stimuli processed without attention and awareness?

Luiz Pessoa

In the past few years, important contributions have been made to the study of emotional visual perception. Researchers have reported responses to emotional stimuli in the human amygdala under some unattended conditions (i.e. conditions in which the focus of attention was diverted away from the stimuli due to task instructions), during visual masking and during binocular suppression. Taken together, these results reveal the relative degree of autonomy of emotional processing. At the same time, however, important limitations to the notion of complete automaticity have been revealed. Effects of task context and attention have been shown, as well as large inter-subject differences in sensitivity to the detection of masked fearful faces (whereby briefly presented, target fearful faces are immediately followed by a neutral face that 'masks' the initial face). A better understanding of the neural basis of emotional perception and how it relates to visual attention and awareness is likely to require further refinement of the concepts of automaticity and awareness.

## Addresses

Department of Psychology, Brown University, 89 Waterman Street, Providence, RI 02912, USA

Corresponding author: Pessoa, Luiz (pessoa@brown.edu)

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## Introduction

Researchers and non-specialists alike have been fascinated by the 'unconscious' ever since Freud likened the mind to an iceberg, with only a small portion of mental processes taking place above the surface (conscious) but with the vast majority occurring below the surface (unconscious). The present review attempts to summarize our current understanding of some of the key issues that surround visual awareness and the processing of emotional stimuli. Central to many of the studies reviewed, is the idea that although neural responses (indexed by intracranial recordings, functional magnetic resonance imaging [fMRI], event-related potentials [ERPs], etc) to emotional items in many brain regions

might depend on experimental context, attention and awareness, neural responses in key limbic structures, such as the amygdala, are largely, if not completely, automatic (i.e. independent of such factors; see Glossary). I begin this article by reviewing the link between visual attention and emotional processing. I then go on to detail the visual masking studies (see Glossary) that have attempted to manipulate visual awareness explicitly by the presentation of brief visual stimuli that are masked by other images. Next, I review studies that have addressed a putative subcortical pathway involved in emotional perception (see Glossary). I conclude the review with a brief discussion of the different measures of visual awareness and will relate unaware (see Glossary) processing to the concept of automaticity. In this review, the important related literature regarding whether Pavlovian conditioning occurs without awareness is not discussed owing to space constraints; see [1,2\*\*] for further discussion.

## Does the processing of emotional stimuli require attention?

There is good evidence that the processing of emotional information is prioritized: it is fast [3] and it interferes with the ongoing processing of other information [4–6]. However, does it occur independently of attention? This question has been addressed by the determination of fMRI or ERP responses to emotional stimuli that are either attended or unattended as a result of manipulation of spatial attention, object-based attention or task instructions. In one study by Vuilleumier *et al.*, spatial attention was manipulated by having subjects fixate on a central cue and compare either two faces or two houses presented eccentrically [5]. On each trial, subjects either compared the faces to each other or the houses to each other. Four stimuli were presented, with, say, faces presented to the left and right of a central fixation cue, and houses presented below and above fixation. Thus, the focus of attention was varied by having subjects attend to the left and the right of fixation (while ignoring top and bottom stimuli) or above and below fixation (while ignoring the left and right stimuli); in each case, they indicated whether the attended stimuli were the same or not. The contrast in the fMRI response to fearful and neutral faces was not modulated by the focus of attention, consistent with the view that the processing of emotional items does not require attention. A second study by Pessoa *et al.*, however, found the opposite result [7]. Spatial attention was manipulated by having subjects focus on faces of different gender or on bars of different orientation, which were all presented on the display at the same time. Subjects were asked, in some trials, to indicate

**Glossary**

**Automatic:** A highly loaded term commonly interpreted to imply independence from 'top-down' factors, such as attention and task instructions. At times, it is linked with the less strict notion of task-irrelevant or involuntary processing.

**Binocular suppression:** Perceptual state in which the perception of a stimulus shown to one eye is 'suppressed' from conscious awareness because an 'incompatible' stimulus is presented to the other eye.

**Subcortical pathway:** A putative anatomical pathway that would link the retina to the amygdala without going through cortical areas, such as the primary and second visual areas (V1 and V2).

**Subliminal perception:** Perceptual state in which subjects are not aware of a stimulus, but for which behavioral or physiological consequences of having 'registered' the stimulus can be ascertained. Both 'subjective' and 'objective' awareness criteria have been used to characterize subliminal perception.

**Supraliminal perception:** Supra-threshold perceptual state in which subjects are aware of the stimulus.

**Unaware:** A perceptual condition in which subjects report that they are not conscious of a briefly presented stimulus. Often used interchangeably with the term 'subliminal'.

**Valence:** Stimulus dimension that varies from 'pleasant' to 'unpleasant'.

**Visual masking:** Experimental paradigm in which a 'target' visual stimulus is followed (and in some cases preceded) by another salient visual stimulus that 'masks' the perception of the target stimulus. Visual masking is commonly utilized to manipulate visual awareness.

whether a central face was male or female and, in other trials, to determine whether two peripheral bars had the same orientation or not. The bar-orientation task was made very difficult in an attempt to consume most, if not all, attentional resources, leaving only small amounts, if any, for the processing of the unattended faces. During the gender task, fearful faces evoked stronger neural activity than neutral faces in a network of brain regions including the fusiform gyrus, superior temporal sulcus, orbitofrontal cortex and amygdala. Crucially, such differential activation was not observed when subjects performed the difficult bar-orientation task. Thus, a strong valence (see Glossary) by attention statistical interaction was observed insofar as a valence effect (fearful > neutral) was observed during the gender task, but not during the bar-orientation task. A third study by Anderson *et al.* investigated this question by manipulating object-based attention while keeping spatial attention constant [8<sup>\*</sup>]. 'Double-exposure' images that contained faces and buildings were used, both of which were semi-transparent, and subjects were instructed to make either a male/female judgment (attend to faces) or an inside/outside judgment (attend to places). In the amygdala, similar responses were evoked to both attended and unattended fearful or neutral faces — thus, no effect of attention was observed for the two expressions. However, an interesting effect was observed with expressions of disgust, which evoked stronger signals in the amygdala during unattended relative to attended conditions.

Recent ERP studies have further addressed the role of attention during emotional perception. In a paradigm

very similar to that employed by Vuilleumier *et al.* [5], Holmes *et al.* [9<sup>\*\*</sup>] investigated ERPs when subjects were instructed to match two faces or two houses that were to the left/right or above/below fixation. When faces were attended, several ERP components were modulated by facial expression (fearful versus neutral), including very 'early' (~120 ms post-stimulus) and 'late' components (300–500 ms post-stimulus). However, early as well as late differential responses were completely eliminated in trials in which the faces were presented at unattended spatial locations (i.e. during house matching), a finding confirmed in a follow-up study [10]. Finally, a recent study that used depth electrodes as part of pre-surgical evaluation reported much larger (and earlier) responses to fearful faces in the human amygdala when attention was paid to facial expression when compared with attention to gender [11<sup>\*</sup>]; see also [12,13<sup>\*\*</sup>]. Interestingly, during the gender task stronger responses to fearful faces were only observed at 600 ms post-stimulus.

In summary, evidence for the processing of emotional items that are outside the focus of attention is mixed. These findings, however, can be reconciled if we consider the concept of attentional load [14–16]. It has been suggested that spare processing capacity is utilized for the processing of task-irrelevant or unattended items. The studies that revealed that attention modulates the processing of emotional stimuli employed very demanding tasks that might have nearly exhausted the processing capacity. By contrast, the studies that observed little or no effect of attention used less demanding tasks. However, even in the study by Anderson *et al.* [8<sup>\*</sup>] in which amygdala responses to attended and unattended fearful faces were the same, responses to unattended disgusted faces were, paradoxically, increased. Thus, it appears that during conditions of relative inattention, only coarse affective properties are registered, such as the overall valence or stimulus arousal. This would suggest that, even in such low-load cases, there are important limitations with regard to the features encoded by the amygdala for unattended information. Finally, a recent study by Bishop *et al.* [17<sup>\*</sup>] suggests that differences in individual anxiety levels are important predictors of amygdala responses during unattended conditions and could help to explain discrepancies in results from previous studies.

### Does the processing of emotional stimuli depend upon awareness?

Two influential neuroimaging papers, both of which appeared in 1998, reported that responses in the human amygdala occur in the absence of visual awareness. Awareness was manipulated by employing backward masking, as introduced by Esteves and Öhman [18] in a behavioural paradigm. In one study, fearful faces were shown for 33 ms and were immediately replaced by a neutral 'mask' face that was presented for 167 ms [19].

Subjects were naïve as to the stimulus conditions, which included masked fearful and masked happy faces. Stronger responses were observed in response to fearful rather than happy faces (both masked by neutral faces), even though, upon subsequent debriefing, subjects did not report seeing any emotional faces. In another study, Morris *et al.* [20] combined backward masking with classical conditioning to investigate responses to perceived and non-perceived angry faces. Although the participants did not report seeing the masked angry stimuli (angry faces were shown for 30 ms and followed by a neutral mask that was shown for 45 ms), the contrast of conditioned and non-conditioned masked angry faces activated the right amygdala. Recent studies have also gathered evidence for unaware processing by the amygdala [21,22,23\*,24,25\*,26,27,28\*\*,29–31]. For instance, Gläscher and Adolphs [31] showed that in normal controls, but not in patients with amygdala lesions, arousal ratings correlated with skin conductance responses for both subliminal (unaware) and supraliminal (aware) conditions (see Glossary). Together with the important earlier work by Öhman and colleagues [18], these results have strengthened the view that emotional processing occurs independently of conscious awareness [32,33]. In general, a stimulus that is shown for about 30 ms before masking is considered to be at the ‘threshold’ for awareness. However, a recent study by Phillips *et al.* [28\*\*] did not observe any response in the amygdala during unaware conditions. The authors compared aware conditions, in which target faces (fearful or disgusted) were shown for 170 ms and followed by a mask that was shown for 100 ms, with unaware conditions, in which target faces were shown for 30 ms and, again, followed by a mask that was shown for 100 ms. Unlike prior studies, however, no differential responses were observed in the amygdala in association with fearful faces in the unaware condition (or in the anterior insula for unaware disgusted faces).

A crucial issue in the assessment of awareness is the criteria used to determine whether a participant is aware or unaware of a stimulus [34,35\*\*,36]. According to ‘objective’ criteria, unaware perception occurs when a subject’s performance in a ‘forced-choice’ task is at chance. Under such conditions, behavioral effects of unaware stimuli (e.g. faster reaction time to undetected fearful faces), as well as the associated fMRI signals, constitute correlates of unaware perception. According to ‘subjective’ criteria, unaware perception occurs when subjects report that they are unable to perform the task better than by chance (independent of their actual objective performance). Although some of the previous studies used forced-choice objective methods [20], they did not assess performance in a manner that is independent of response bias on an individual-by-individual basis (see [2\*\*] for a careful characterization of awareness in the context of conditioning and [37] during the perception of words). This is important because in the face of weak, noisy

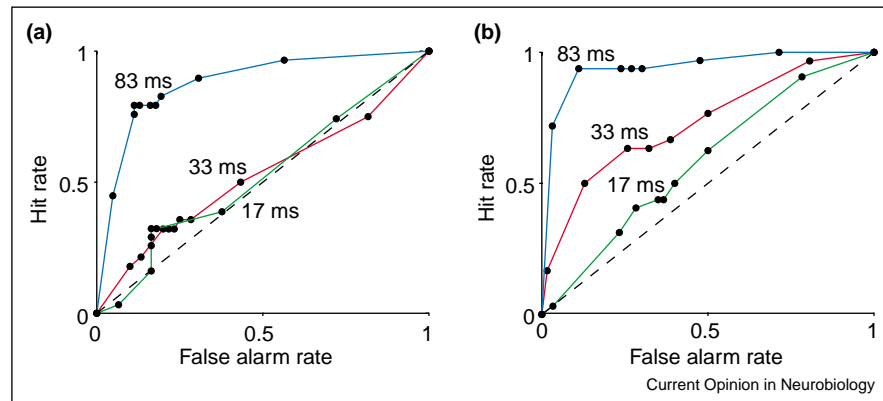
signals, subjects might indicate that they do not detect target stimuli and thus appear to be unable to detect them reliably. A recent behavioral study by Pessoa *et al.* [38\*\*] addressed these issues by analyzing performance by way of signal detection methods. The authors varied the duration (17, 33 and 83 ms) of which a target face (fearful, happy or neutral) was shown before being immediately replaced by a neutral-face mask (which was shown for 116, 100, and 50 ms, respectively, such that the target plus mask lasted 133 ms in each case). The subject’s task was to report explicitly whether or not a fearful face was presented in each trial, and also to rate their confidence in this decision. Although some subjects only reliably detected the fearful targets that were shown for 83 ms, 36% of the participants were able to detect both the 33 ms and 83 ms targets. Remarkably, some subjects could even detect fearful faces that were shown for 17 ms before masking. These results demonstrated that participants differ widely in their sensitivity to fearful faces (Figure 1). Moreover, the results revealed that even very brief (17 ms) stimuli can be incompletely masked, consistent with another recent study [39]. The findings by Pessoa *et al.* [38\*\*] also raise the possibility that the discrepancy between the results of Phillips *et al.* [28\*\*] and those of prior studies might be caused, at least in part, by variability in sensitivity among individuals, which may be related to anxiety levels [40].

## Does a fast subcortical visual pathway support emotional perception?

### Anatomical evidence

In primates, the retina projects to both the lateral geniculate nucleus of the thalamus (LGN) and the superior colliculus. The LGN pathway continues to the primary visual area (V1) and from there to a series of extrastriate regions. In monkeys, the amygdala receives inputs from the inferior temporal area (TE) in the temporal cortex. Thus, highly processed inputs are sent to the amygdala by way of a cortical pathway [41] (Figure 2). An important theme that has arisen from recent studies of unaware emotional perception concerns the existence of a putative retino–collicular–pulvinar–amygdala ‘subcortical pathway’, which could provide the substrate for the automatic processing of facial expression. The existence of a ‘fast’ subcortical pathway, like that described above, has been documented to be present in the auditory domain [42,43] and, in the visual domain, a similar subcortical pathway has been reported in rats [42,44,45]. But, does it also exist in primates? In non-human primates, the superior colliculus projects to the pulvinar nucleus of the thalamus, and there is some evidence that indicates that the pulvinar projects to the amygdala [46]. However, a crucial link along the pathway has yet to be demonstrated. Projections to the amygdala from the pulvinar appear to originate in the medial aspect, whereas the collicular input projects to the inferior aspect of the pulvinar. Interconnections between the inferior and the medial nuclei of the

Figure 1



Sensitivity to fearful target faces as characterized by receiver operating characteristic (ROC) curves. The diagonal dashed line indicates chance performance (i.e. the same number of false alarms and correct detections [hits]). Better-than-chance behavior is indicated by curves that extend in the direction of the upper left corner. The area under the ROC curve is the non-parametric sensitivity measure A', which indicates the extent to which subjects can tell fearful targets from non-fearful stimuli. Data are shown from two representative individuals that were tested after being shown the target face for varying lengths of time (83 ms [blue], 33 ms [red] and 17 ms [green]) before being masked. (a) The first subject was only able to detect 83 ms targets and (b) the second was able to detect both 33 ms and 83 ms targets, and showed a trend in detecting 17 ms targets (assessed statistically by comparing A' values relative to an area of 0.5, which is the value expected by chance) [38\*\*].

pulvinar have not been described, leaving the question of the presence of a subcortical visual pathway to the amygdala open (Figure 2).

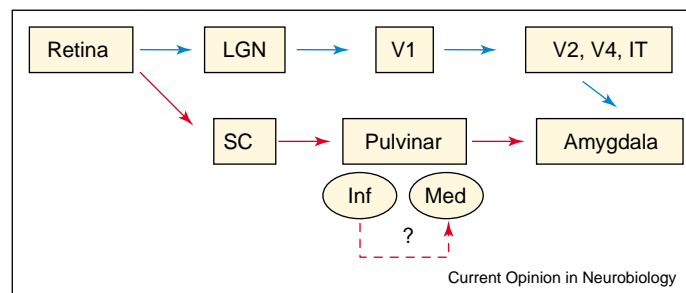
**Functional evidence: blindsight, binocular rivalry and spatial frequencies**

In the absence of a completely documented subcortical pathway, support for its existence has been strengthened by studies of the blindsight patient GY who has right hemianopia caused by left occipital lobe damage. Such studies have revealed that, remarkably, GY is able to discriminate between emotional facial expressions presented in his blind hemifield [47], a phenomenon called affective blindsight [48]. Recently, GY was scanned with fMRI in a study in which he was exposed to lateralized

presentations of fearful or happy expressions in either his blind or his intact hemifield [49]. Despite the absence of normal vision in his blind hemifield, the presentation of fearful faces resulted in enhanced amygdala responses. Given the apparent lack of an intact cortical route to the amygdala, these results suggest that information reached the amygdala by way of a subcortical pathway.

Further support for the notion of a subcortical pathway has been obtained in studies of binocular rivalry. During rivalry, different incompatible images are presented to each eye [50]. The ensuing perceptual state is not one of fusion; instead the observer experiences alternation of the images. With prolonged viewing, each image undergoes a period of dominance followed by a period of suppression.

Figure 2



Visual pathways to the amygdala. In addition to the regular cortical pathway (blue arrows), it has been proposed that the amygdala also receives information by way of a fast, subcortical pathway that includes the superior colliculus (SC) and pulvinar (red arrows). However, a crucial link along the pathway has yet to be demonstrated (dotted arrow). Projections to the amygdala from the pulvinar originate in the medial (med) aspect, which is not the part of the pulvinar that receives collicular input (the inferior [inf] aspect) Moreover, interconnections between the inferior and the medial nuclei have not been described. If such a subcortical pathway exists in primates, it is unclear whether it is functional in normal vision and whether it is capable of supporting emotional perception. Abbreviations: IT, inferotemporal cortex; LGN, lateral geniculate nucleus of the thalamus; V1, V2 and V4, primary, second and fourth visual areas.



Because retinal stimulation is kept constant, although the percept alternates every few seconds, binocular rivalry is well suited for the investigation of the dissociation between physical stimulation and visual awareness [51]. Two recent studies made use of this dissociation to investigate the neural correlates of perceived and suppressed states. Pasley *et al.* [52\*\*] presented images of fearful faces or of chairs to one eye and an image of a house to the other eye. To minimize the chances of 'mixed' perceptual states (i.e. incomplete suppression) the house image moved sharply back and forth continuously for the duration of the presentation of the face or chair image to the other eye (approximately 1.5 s). During such suppression states, fearful faces evoked stronger responses in the left amygdala than chairs. Crucially, such differential activity was not observed in occipitotemporal sites that demonstrated responses to faces and chairs during normal viewing [52\*\*]. In another study, Williams *et al.* [53\*\*] presented images of houses to one eye and happy, fearful or neutral faces to the other. To minimize 'blending' of the two images, stimuli were presented briefly (for 500 ms) and the authors exploited each participant's bias in sensitivity to particular wavelengths so that one of the images would initially dominate over the other. Suppressed fearful faces evoked stronger responses bilaterally in the amygdala than neutral ones. However, no differential activity was observed in the fusiform and the parahippocampal gyri. The main conclusion stemming from these studies is that amygdala activation to fearful faces occurs independently of visual awareness (i.e. during binocular suppression; see Glossary). By contrast, object-responsive extrastriate visual regions appear to reflect conscious perceptual states more directly [54–56].

Another interesting way in which the subcortical pathway has been targeted is by the use of visual stimuli that might selectively activate it. Visual responses in the superior colliculus and in the pulvinar are sensitive to low spatial-frequency (LSF) information; however, they are largely insensitive to high spatial-frequency (HSF) signals. At the same time, brain regions along the cortical pathway are capable of processing fine visual shape information. Vuilleumier and co-workers [57\*,58] showed that although the response of the fusiform cortex to faces was influenced more by fine HSF information, the amygdala response to fearful expressions was selectively driven by coarse LSF cues. These results raise the possibility that the visual inputs to the amygdala are partly distinct from inputs to the ventral extrastriate visual cortex.

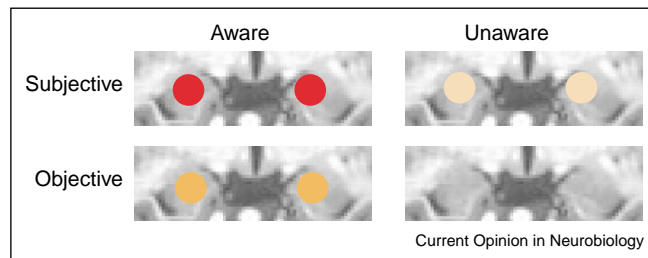
#### A functional pathway?

To summarize, although important aspects of the anatomy of the subcortical pathway remain to be determined, several functional studies have advanced the notion that some form of coarse processing takes place subcortically and that it partly supports emotional perception. How-

ever, a more direct test of this pathway, possibly similar to that in the auditory domain in rats (see [59] for a discussion of 'primary' and 'non-primary' routes in visual and auditory modalities), is needed to more conclusively support this concept in primates. Several important issues remain to be addressed. First, can the type of coarse processing that occurs in the superior colliculus and the pulvinar [60] support emotional perception? Although global, holistic information is important for face processing [61], expression-related information might also rely on relatively fine-grained information [62–64]. Likewise, all but a very coarse evaluation of scenes might rely on fine spatial information [60,65]. Thus, even if a subcortical pathway exists, is it functional during normal vision? Second, can the influence of other potential anatomical pathways be ruled out? For instance, in monkeys the pulvinar projects to the second visual area (V2) as well as to more anterior inferotemporal regions (see [66]). Moreover, Gattass and co-workers [67] recently showed that orientation and/or direction selectivity was altered in 91% of the cells in V2 after inactivation of the pulvinar. Third, is processing along the subcortical pathway also modulated by attention? In view of the findings that show that attention, at least when severely depleted, is needed for the processing of emotional items, it is important to establish how the subcortical flow of information depends upon attention. Fourth, does perception during masking and binocular suppression rely on the subcortical pathway? Although masking results have often been interpreted in terms of the subcortical pathway, previous findings show that considerable cortical information is available from neuronal responses, even under backward masking conditions [68,69]. During binocular rivalry, in addition to the states of dominance and suppression, 'mixed' states are possible. Thus, differential responses in the amygdala during rivalry do not rule out the possibility that cortical signals are involved. A further complication is that direct recordings in the amygdala of patients with intractable epilepsy did not reveal any evidence for a neuronal representation of perceptually suppressed images in the amygdala or in other medial temporal lobe structures [70]. It is unclear why single-neuron responses in the amygdala correlated with subjective perceptual states but were independent of awareness in imaging studies.

A different line of work that might help us to understand the role of cortical and subcortical pathways concerns the timing of processing of emotional expressions. ERP and magnetoencephalography work has been largely inconclusive, with some results favoring very fast processing (<150 ms) [9\*\*], and others favoring relatively longer latencies [71]. Single-neuron responses in human ventral prefrontal cortex appear to distinguish between emotionally negative versus neutral complex pictures within 120–160 ms [72]. Intracranial field potentials also indicate that responses in the amygdala might differentiate between

Figure 3



Hypothetical amygdala activation as a function of subjective and objective awareness measures. The colors reflect activation strength (lighter colors indicate weaker activation; darker colors indicate stronger activation). Activation is predicted to be absent during objectively unaware conditions and present during subjectively unaware conditions. Moreover, responses would be evoked for both aware conditions, but would be stronger for subjectively aware conditions. Thus, objective awareness would constitute a more elementary form of awareness ('primary' awareness as proposed by Snodgrass and co-workers [2,36]) than subjective awareness ('secondary' awareness), which would require some level of self-knowledge.

aversive and non-aversive stimuli quite quickly (150–250 ms) [73]. Such rapid processing is consistent with the view that the ventral prefrontal cortex and the amygdala provide an initial coarse categorization of emotional stimuli, which might then bias the processing of emotional information elsewhere — perhaps in a similar fashion to that proposed for the processing of context [74].

### Strong versus weak automaticity

At the center of the debate of the role that awareness has in emotional perception is the question of how to characterize visual awareness. Both objective and subjective criteria have been employed in the past [34–36]. Although both methods have the potential to provide valuable information concerning awareness, they constrain the underlying visual processes and brain mechanisms in different manners. This is especially relevant when linking experimental findings to the notion of automaticity. The term 'automatic' is commonly interpreted to imply independence from top-down factors, such as attention and task instructions — 'strong' automaticity. At other times, it is linked with the less strict notion of task-irrelevant or involuntary processing — 'weak' automaticity. Objective and subjective awareness are implicitly associated with strong and weak notions of automaticity, respectively. Studies that reveal amygdala responses during subjective unawareness [19] inform us in terms of weak automaticity; they reveal that although subjects were subjectively unaware of the stimuli, it evoked responses. However, evidence for automatic responses during objective unawareness would require an objective performance assessment that is independent of response bias (i.e. by the signal detection theory) for every individual [38<sup>••</sup>]. However, in neuroimaging studies, such assessments remain to be carried out in a satisfactory manner. Thus, it is conceivable that the amygdala evokes automatic responses when subjects are subjectively unaware of emotional stimuli, but does not respond when subjects are objectively unaware (Figure 3).

### Conclusions

In summary, important contributions have been made to the study of emotional visual perception in the past few years. Several findings support the notion of the autonomy of emotional processing. In this view, emotional processing would be largely automatic and take place irrespective of the focus of attention and independently of visual awareness. Although this view is attractive to a large majority of the research community, this notion has been recently challenged by several studies that reveal important limitations of the notion of complete automaticity. For instance, emotional perception has been shown to be modulated by attention in both fMRI [7] and ERP [9<sup>••</sup>,10] studies. At the same time, recent masking studies also challenge earlier findings that subliminal visual stimuli evoke reliable amygdala responses [28<sup>••</sup>,38<sup>••</sup>]. Overall, future research on the theme addressed in this review should focus less on whether emotional processing can take place without attention and awareness and instead should focus on determining the extent to which attention and awareness modulate emotional perception. It is likely that the answer to these questions will strongly depend on task conditions and on task demands, and will reflect the highly context-sensitive nature of visual processing in general.

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Papers of particular interest, published within the annual period of review, have been highlighted as:

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2. Wong PS, Bernat E, Snodgrass M, Shevrin H: **Event-related brain correlates of associative learning without awareness.** *Int J Psychophysiol* 2004, **53**:217-231.

Great controversy exists as to whether conditioning can take place without awareness. In particular, Lovibond and Shanks 1 have questioned previous reports of unaware conditioning by challenging the validity of previous measures of awareness. In this recent study, Wong *et al.* carefully assessed awareness and showed that although subjects were objectively unaware of the conditioned stimuli (in a presence/absence task) ERP responses revealed that neural changes occurred in response to the conditional stimuli.

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In this study, the effect of object attention on the processing of emotional faces was investigated. Spatial attention was kept fixed while attention was shifted between faces and buildings that were shown in 'double-exposure' images. Amygdala responses to fearful faces were not modulated by attention. Interestingly, fMRI responses in the amygdala to disgusted faces evoked stronger responses when the faces were unattended, which suggested that during conditions of inattention coarse processing of disgusted faces led to them being treated as fearful faces.

9. Holmes A, Vuilleumier P, Eimer M: **The processing of emotional facial expression is gated by spatial attention: evidence from event-related brain potentials.** *Brain Res Cogn Brain Res* 2003, **16**:174-184.

The authors measured ERPs when subjects were instructed to match two peripheral faces or two peripheral houses. Valence-dependent differential responses were notably absent during trials in which the faces were unattended. The results provide evidence that the processing of emotional expression is strongly modulated by spatial attention. Interestingly, the experimental manipulation was essentially the same as that employed in the fMRI study by Vuilleumier *et al.* [5], who reported that attention had no effect on amygdala responses. Although it is probable that the ERP responses measured by Holmes *et al.* did not originate in the amygdala, it is reasonable to assume that modulations of other cortical regions by the amygdala should have been picked up if the processing in the amygdala was independent of attention.

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Depth-electrode ERPs were obtained in humans, which showed responses to fearful faces with a latency of 200 ms. Such expression-related responses were only observed when subjects performed an explicit expression-related task, but not when subjects performed a gender-related task.

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The concept of strong automaticity would predict that experimental context should have little or no effect on the responses evoked by fearful faces. In this study, the authors showed that task-relevant targets evoked stronger responses in the amygdala than task-irrelevant distracters (i.e. stimuli subjects did not respond to) when a sequence of target and distracter faces were continually shown. In fact, distracter faces, regardless of their valence (or amount of repetition), evoked negligible activation, indicating top-down attenuation of behaviorally irrelevant stimuli.

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Individual so-called 'state' anxiety levels were used as an explanatory covariate in the determination of fMRI responses in the human amygdala to attended and unattended fearful faces. Spatial attention (in a paradigm similar to that of Vuilleumier *et al.* [5]) modulated responses to fearful faces in low-anxiety participants, but not in high-anxiety individuals.

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