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Human Amygdala in Sensory and Attentional Unawareness: Neural Pathways and Behavioural Outcomes

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Abstract

One of the neural structures more often implicated in the processing of emotional signals in the absence of visual awareness is the amygdala. In this chapter, we review current evidence from human neuroscience in healthy and brain-damaged patients on the role of amygdala during non-conscious (visual) perception of emotional stimuli. Nevertheless, there is as of yet no consensus on the limits and conditions that affect the extent of amygdala's response without focused attention or awareness. We propose to distinguish between attentional unawareness, a condition wherein the stimulus is potentially accessible to enter visual awareness but fails to do so because attention is diverted, and sensory unawareness, in which the stimulus fails to enter awareness because its normal processing in the visual cortex is suppressed. Within this conceptual framework, some of the apparently contradictory findings seem to gain new coherence and converge on the role of the amygdala in supporting different types of non-conscious emotion processing. Amygdala responses in the absence of awareness are linked to different functional mechanisms and are driven by more complex neural networks than commonly assumed. Acknowledging this complexity can be helpful to foster new studies on amygdala functions without awareness and their impact on human behaviour.

Keywords: blindsight, hemispatial neglect, subcortical, superior colliculus, pulvinar, attention, consciousness

1. Introduction

The amygdala (Amg) is a composite subcortical structure that comprises more than 12 sub-nuclei having distinctive patterns of input-output connections with the rest of the brain [1, 2]. This histological and connectional heterogeneity reflects its multifaceted functions. In fact, the Amg has long been known to have a central role in the processing of emotions, but it also serves as an interface between emotion and cognitive functions, including decision-making, learning and attention [3, 4]. Over the past two decades, evidence has accumulated which shows that Amg exerts some of its functions also when the subject is not aware of the nature, content or even presence of the triggering emotional stimulus [5]. The present chapter will discuss findings related to Amg functions in humans during conditions in which the subject is not aware of the presence of an emotional visual stimulus. We will cover Amg main functional/anatomical afferent and efferent pathways that seem particularly relevant during emotion perception in the absence of awareness, and the consequences of such unconscious perception along several dimensions, such as expressive or instrumental actions, psychophysiological and neuroendocrine alterations or modulation of motivated behaviour. Before addressing each specific issue, there are several preliminary considerations, both theoretical and methodological, about the relevance of studying Amg's contribution to emotion processing without awareness [5, 6].

First, Amg functions and circuitry have been well preserved across evolution and appeared early during phylogenetic as well as ontogenetic development. For example, the Amg is present in reptiles, birds and mammals [1], and its neurogenesis in humans and other primates is complete at birth [7], and its connections lay down by the second week of age [8]. Therefore, studying Amg's role in the perception of emotional stimuli when visual awareness is lacking enables us to focus on processes related to basic or core aspects of emotion perception and responses. These primitive aspects of emotion processing likely evolved before more sophisticated functions like perceptual awareness and core feelings. These primordial Amg functions have been implicated in the specialization of more recent cortical functions across the primate lineage as well as during development and maturation [9], including present-day organization of the cortical visual system [10, 11]. Hence, this also provides a valuable testing ground for gauging cross-species continuity of functions and comparison. Second, by examining stimulus properties and categories that evoke Amg activity without awareness, or that by comparison fail to do so, we may be able to abstract from common taxonomies, such as those distinguishing animate from inanimate objects, faces from bodies and so on, to reveal cross-category commonalities between stimulus types and attributes that could not be anticipated by looking at cortical segregation of stimulus categories [12, 13]. Lastly, Amg clearly rests at the intersection between conscious as well as non-conscious emotional processing [14]. To the extent that these two different modes of processing incoming sensory information co-exist in the brain, assessing which operations the Amg undertakes without awareness helps to unravel functions that may be overridden, modulated or even actively blocked during conscious perception and cortical top-down regulation. This can add valuable insights to the longstanding debate on whether perceptions with and without awareness are qualitative or quantitatively different phenomena, whether and how they interact and interfere to shape

the ultimately conscious representation of the external world, and which are, if anything, the specific evolutionary benefits that determined conservation of emotion processing without awareness across evolution [6].

The rest of the chapter proceeds as follows. We will first introduce a conceptual and terminological distinction between different types of emotion perceptions without awareness, as they entail profoundly different mechanisms and are sampled through distinctive experimental designs. Second, we will review neuroimaging evidences demonstrating Amg activity during emotion perception without awareness, how they have been interpreted, and current controversies and limitations. Third, we will discuss the neural timing of the Amg response during presence/absence of visual awareness for the triggering emotional stimulus, and how data acquired with high temporal resolution techniques can elucidate and accommodate apparent inconsistencies originating from fMRI results. Fourth, we will consider functional and anatomical evidence about the neural networks that seem crucial in conveying sensory information to the Amg in the absence of awareness. Fifth, we will concentrate on stimulus categories and properties that can be processed non-consciously by the Amg and finally, we will summarize the behavioural and psychophysiological consequence of emotion perception without awareness. Throughout the chapter, we will concentrate on vision because this is the best-known system in terms of connections with the Amg in human and non-human primates, and because the majority of human studies investigating Amg's role in processing emotions without awareness used visual stimuli.

2. Different types of unawareness for emotions and how they are studied

A host of techniques and experimental manipulations have been used to render emotional stimuli not consciously perceivable. For example, during backward masking an emotional stimulus (e.g. a facial expression) is briefly presented and then immediately followed by a masking stimulus (e.g. a neutral or scrambled face). If the stimulus onset asynchrony between the first and masking stimulus is sufficiently brief, then the observer cannot consciously report the presence or the emotional content of the first stimulus [15, 16]. Binocular rivalry or continuous flash suppression exploits the mutual inhibition between monocular channels in the primary visual cortex (V1) by presenting different images to the corresponding regions of the two eyes [17–19]. In such condition, only one image enters visual awareness, whereas the other image is suppressed from awareness. Other popular paradigms include dual-task designs where the subject's attention is engaged in an attention-absorbing task, such as matching judgment between neutral stimuli, while an emotional stimulus is presented at task-irrelevant and unattended locations [20, 21]. In the attentional blink, a rapid stream of stimuli is presented and subjects are asked to detect the presence of a target stimulus. However, if a second target appears in rapid succession after a first successfully detected target (typically within 500 ms), the latter fails to be reported [22]. Many other paradigms such as priming, Stroop-task, dot-probe designs or the redundant target paradigm have been used to sample emotion perception without awareness, each with its own advantages and limitations [23–27].

Although detailed coverage of these different methods goes beyond the purposes of this chapter, they can be conveniently grouped in two broad categories that entail different functional mechanisms [6]. Dual-task, attentional blink, visual search or Stroop paradigms render the emotional stimulus not consciously visible by interfering with attentional mechanisms. Psychophysical evidence indicates indeed that visual stimuli outside the focus of attention are not, or are only partially, seen consciously [28]. Accordingly, when attentional resources are engaged in a task, cortical activity that is evoked in visual areas by unattended (i.e. task-irrelevant) stimuli is suppressed or significantly reduced by top-down influences from fronto-parietal regions that control voluntary attention [29]. We refer to these phenomena as *attentional unawareness*. Emotional stimuli seem to constitute an exception, as the processing of emotional information seems less dependent on attentional resources than neutral information. As we will discuss later, this mechanism seems to depend on Amg [30].

In contrast, failure to become aware of a stimulus may also result from sensory reasons, although attentional selection mechanisms can operate normally [31]. For example, if the stimulus intensity is too weak (i.e. below the detection threshold) or the presentation time is too brief (i.e. subliminal), the stimulus often does not generate a conscious sensation notwithstanding we pay attention to it [32, 33]. Backward masking, binocular rivalry or flash suppression do not modulate attention, but temporarily interfere with normal functioning in the ventral occipito-temporal cortex, which is known to be crucial for visual awareness [18, 34, 35]. In this latter case, we refer to this type of non-conscious processing as *sensory unawareness*.

Attentional and sensory unawareness are thus qualitatively different phenomena that can be investigated to explore different Amg functions, while still remaining within the domain of non-conscious processes. For example, studying emotion perception during attentional unawareness is well-suited to examine the role of Amg in biasing orientation towards affective stimuli, and investigate what mechanism enables Amg to eventually promote privileged access of emotional signals to awareness. Sensory unawareness can instead reveal alternative pathways by which visual stimuli can reach the Amg, or their impact towards on-going activities, behaviour or judgments, while still remaining unseen. Lastly, patients with brain damage represent an invaluable additional source of information to broaden our knowledge of Amg functions without awareness. Patients with hemispatial neglect due to right temporoparietal lesions typically fail to pay attention to the contralesional (left) space, and stimuli appearing on that side often go undetected [36]. Therefore, the study of Amg response to emotional stimuli in such patients can add insights into the mechanism governing attentional unawareness. On the other hand, patients with cortical blindness following destruction of the visual cortex offer a case study to investigate the distinction between conscious and non-conscious emotion processing due to sensory causes, as opposed to attentional, and the role of Amg therein [37]. Indeed, such patients are permanently blind to stimuli presented inside the scotoma (the visual field region affected by the cortical lesion), including supra threshold and long-lasting stimuli [38–41]. Lastly, patients with focal damage to the Amg offer the ultimate ground-truth to translate correlational evidence typical of fMRI into causal evidence on Amg functions, by observing whether and how the influence of emotional stimuli during attentional or sensory unawareness is modified or abolished following Amg lesion [42].

3. Amygdala response during sensory and attentional unawareness: evidence and limits

Neuroimaging studies on healthy participants in which attention was manipulated have shown that stimulus-evoked activity in the Amg, along with that of other cortical and sub-cortical structures, is not suppressed when emotional stimuli are unattended [21, 43–45]. Although this has been sometimes interpreted as evidence of strict automaticity in Amg response to emotion, the current evidence is mixed on this issue. For example, Vuilleumier et al. [21] showed that Amg activation in response to fearful facial expressions is independent of attention, whereas Pessoa et al. [20] reported that when attention is engaged elsewhere by a demanding task, Amg response is suppressed. These apparently contradictory results may be partly explained by differences in the tasks and experimental design, which prevent simple or straightforward comparisons. In fact, in the original study by Pessoa and collaborators [20], the subjects had to evaluate the gender during trials in which attention was focused on the faces, whereas they were asked to judge the same/different orientation of peripheral bars when faces were unattended. In addition to the focus of attention on faces versus bars, therefore, the cognitive load, type of judgment and task requirements also varied between the two conditions, whereas in the study by Vuilleumier et al. [21] only the focus of attention changed. Also, Pessoa et al. [20] used a block design, which samples Amg activity across various repetitions of the same condition and is thus more liable to habituation and less sensitive to physiological responses induced by single events, whereas Vuilleumier et al. [21] used an event-related design where attention varied between single trials. Another major confounding factor concerns the different response the Amg displays to various emotion categories. For instance, Williams et al. [45] found that Amg activity in response to happy facial expressions was greater when faces were attended, whereas for fearful expressions activity was greater when the faces were unattended. Findings collected in neuroimaging studies on patients with hemispatial neglect seem more convergent towards the automaticity of Amg's activity in response to unattended stimuli. Indeed, stimuli presented in the contralateral and pathologically unattended left side of such patients can activate the Amg as well as cortical areas directly connected to it, such as the orbitofrontal cortex or the insula [46–48]. The advantage of addressing the issue of Amg automaticity in neglect patients is based on the fact that no explicit or intentional manipulation of attention is required from the subject, thereby discounting issues related to task differences and attentional load between conditions.

Investigations on sensory unawareness have consistently shown that unseen emotional stimuli elicit activity in the Amg, often along with activity in the superior colliculus and pulvinar [11, 16, 17, 19, 49–58]. But how robust is Amg's response to unseen as opposed to seen stimuli? Some reports found indeed that Amg activity during unawareness and awareness is the same, others described that in several cases, unseen emotional stimuli yield responses higher than those reported during conscious perception of the same stimuli [43, 59], whereas still others reported significantly greater activity in Amg when participants were aware of emotional expressions [56, 57, 60]. Also in this case, methodological differences seem at least partly responsible for the inconsistencies. In fact, assessing the neural bases of emotion perception during sensory unawareness ideally involves a direct comparison between perceived and

unperceived, albeit physically identical, stimuli. Evidence of this type is, however, difficult to observe in healthy individuals, because many manipulations that render a stimulus invisible for the subject inevitably also render the stimulus spatially and temporally different from its consciously visible counterpart. At present, studies on patients with cortical blindness following destruction of the visual cortex possibly provide the best opportunity to clarify the neural basis and properties of non-conscious perception of emotional stimuli. These patients are able to discriminate emotional stimuli that they report not to have seen, for example by ‘guessing’ whether the stimulus expresses happiness or fear [61]—a phenomenon known as affective blindsight—and their proficiency is associated with activity in the Amg [61–68]. As it often happens when mixed results are reported, interpretations and theoretical views on the role of Amg tend to group along two extremes: those endorsing a strict notion on Amg automaticity and independency from awareness, and those supporting that awareness is a necessary condition for Amg response to occur. We and others have proposed that neural networks for conscious and non-conscious perception of emotions are not entirely different or segregated [5, 30, 69–71]. In this context, Amg not only contributes to both modes of processing, but its initial response without awareness actually helps to determine whether the stimulus will reach awareness and how it will modulate behavioural and bodily reactions. Therefore, the temporal dimension of Amg response becomes critical to interpret its role in emotion perception without awareness, while also offering an additional framework to understand more coherently the seemingly abstracted and different findings summarized above [6].

4. Timing of Amg response: fast signals for slow measures

The speed of processing has always been regarded as one hallmark of non-conscious emotion perception [72]. However, human studies on Amg engagement in emotion processing without awareness typically used fMRI, which has high spatial but poor temporal resolution. In fact, fMRI studies usually average together events occurring during a temporal window of about 2 s, due to the sluggishness of blood oxygen level-dependent (BOLD) response. On the other hand, non-invasive methods with higher temporal resolution in the order of milliseconds, such as EEG and MEG, have traditionally had limitations in sampling neural activity in deep structures such as the Amg [73]. Nevertheless, recent technical advancements in sources analysis, such as the synthetic aperture magnetometry (SAM) and sliding windows analysis, increased precision and sensitivity in detecting MEG signals from deep brain structures.

One early study combining MEG and MRI methods reported early event-related synchronization in the Amg at 20–30 ms after stimulus onset, whereas synchronization in the primary visual cortex occurred later at about 40–50 ms after stimulus onset [74]. A more recent MEG study revealed a dissociation between rapid Amg response to automatic fearful face processing and a later response that interacted with voluntary attention. On each trial, participants had to discriminate the orientation of peripheral bars while task-irrelevant neutral or fearful faces were presented centrally. Rapid increase in gamma band activity in response to threatening faces (30–60 ms) was shown to be independent of task load and under attentional unawareness, while a significant interaction of emotion with attention manipulation was seen at later

latencies (280–340 ms), subsequent to fronto-parietal activity [75]. Coherently, two other MEG studies used dynamic causal modelling (DCM) to test the explanatory power of the automatic Amg response mediated via the subcortical route versus a model predicting only cortical mediation associated with stimulus awareness over Amg activity. Early brain activity was better explained by a model including an automatic Amg response via the subcortical pathway, whereas at longer latencies both models had comparable explanatory power [76, 77]. Therefore, MEG data offer new clues to resolve the longstanding controversy concerning automaticity of Amg response based on fMRI results, as described above [78]. On such bases, it seems that Amg automaticity is a function of time, and these findings have been interpreted according to a two-stage model of emotion-attention interaction. Early Amg responses afford early discrimination between threat and neutral stimuli. These responses occur independently of awareness and attention, possibly because the influence of the fronto-parietal cortex in reducing the representation strength of task-irrelevant and unattended emotional information during attentional competition requires more time to be effective. Conversely, later Amg responses are modulated by attention because the same top-down fronto-parietal mechanisms have had sufficient time to enhance the representation of task-relevant and attended information. Notably, both the early automatic and later attention-modulated Amg responses lie within the time window of one volume acquisition of fMRI studies, likely resulting in the contamination of the rapid effects [6].

Admittedly, intracranial electrophysiological recordings offer the most reliable source of evidence concerning both automaticity of Amg response and its dependency on attention and visual awareness. Three recent studies addressed this issue by recording signals directly from electrodes implanted in the Amg of patients undergoing pre-surgical assessment of pharmacologically intractable epilepsy. Pourtois and colleagues [79] employed the same dual-task paradigm previously used by Vuilleumier et al. [21] to gauge Amg automaticity with fMRI measures. Recordings from lateral Amg in patients with temporal lobe epilepsy showed an early neural response, in the 140–290 ms post-stimulus onset that differed between fearful and neutral faces. Notably, this early response occurred independently of, and prior to, attentional effect starting at 700 ms post-stimulus onset. Likewise, Sato et al. [80] showed greater gamma-band activity in response to fear compared to neutral faces between 50 and 150 ms. Even though this study confirmed early responses to emotional stimuli, sensory or attentional unawareness was not manipulated and stimuli were projected centrally for 1 s. Lastly, a recent study by Ménzéd-Bértolo et al. [81] found fast Amg responses at 74 ms post-stimulus onset, which were specific for fearful faces compared to neutral or happy facial expressions. Moreover, fast Amg responses were selective to the low spatial frequencies' components of fearful faces. This sensitivity to low spatial frequencies is important because it is in keeping with the properties of the magnocellular pathway, which is supposed to relay visual signals to the Amg via a subcortical pathway devoted to fast and non-conscious emotion perception.

The present findings raise two interrelated issues of the utmost relevance. The first one concerns how visual information exploitable for non-conscious emotion perception reaches the Amg. The second relates to the encoding properties of the pathway(s) that channel visual information to the Amg without awareness, thereby defining which visual properties, stimulus attributes and categories can undergo emotion processing and trigger appropriate responses. In the next two sections we will deal separately with each of these issues.

5. Pathways to the Amg relevant for non-conscious emotion perception

The canonical pathway for the transmission of visual information from the retina to the Amg passes through the occipito-temporal cortex along the ventral stream, with the main projection originating from the anterior part of the inferior temporal cortex (TE) [82]. However, earlier studies in rats underlined the role of midbrain structures in providing a rapid but coarse analysis of the affective value of auditory as well as visual stimuli and in relaying such information to the Amg, hence bypassing the primary sensory cortices [72, 83–87]. Neuroimaging data on healthy subjects in which sensory unawareness for emotional stimuli had been induced by experimental manipulations have revealed that the superior colliculus, pulvinar and Amg constitute a functional network that shows increased positive covariation of activity in response to non-consciously perceived emotional signals [11, 16, 54, 57, 88, 89]. By contrast, the major cortical pathway relaying visual input to the Amg does not show substantial activity and functional connectivity under the same conditions of sensory unawareness but does so during conscious perception of emotional stimuli [17, 56, 57]. Similar findings have been reported in patients with affective blindsight presented with unseen facial and bodily expressions. This indicates that a functional subcortical pathway to the Amg is engaged in emotion perception during sensory unawareness [5, 65, 66, 68, 90–94]. The involvement of the superior colliculus and pulvinar is in keeping with their connectional pattern and physiological properties. Notably, the superficial layers of the superior colliculus (SC) receive direct retinal input only from the magnocellular and koniocellular channels originating from the parasol and bistratified retinal ganglion cells, respectively [95–97]. Also the medial subdivision of the inferior pulvinar receives direct projections from the retina, in addition to input originating from the superior colliculus and targeting the centromedial and posterior subdivisions of the inferior pulvinar [6]. Hence, these subcortical structures are ideally positioned to convey visual input to the Amg and bypass transient or permanent inactivation of the visual cortices. The functional role of the superior colliculus and pulvinar in processing emotional expressions has also received independent support from recent single cell recordings in monkeys [98]. In fact, a subpopulation of neurons in the superior colliculus responds to face and face-like visual stimuli, and its response properties are not influenced by low spatial frequency filtering of the images. Moreover, neural response magnitude and latency to face stimuli in the superior colliculus significantly correlate with those in the pulvinar. Another cell recording study from the same group showed that monkey pulvinar neurons display differential activity to specific emotional expressions [99].

Granted the role of a subcortical functional pathway to the Amg devoted to processing emotion under sensory unawareness, are these structures also anatomically connected, thereby forming a structural pathway? While tracer studies have demonstrated the existence in birds and rodents of anatomical connections between the superior colliculus, pulvinar and Amg, similar evidence in primates was lacking until recently [14, 100]. Yet Day-Brown et al. [101] have shown in tree shrews that projections to the lateral Amg originate also from the dorsal pulvinar. This latter part of the pulvinar receives visual input from the superior colliculus, thereby forming a disynaptic pathway to the Amg. The authors suggested that this pathway potentially relays non-topographic visual information from the SC to the Amg, its functional role being that of alerting the animal to potentially dangerous signals [101]. In an attempt to verify whether such

anatomical connections also exist in the human brain, we used diffusion tensor imaging (DTI) and tractography techniques to characterize *in vivo* the connectivity between the superior colliculus, pulvinar and Amg in normal observers and its changes in blindsight GY are the initials of the patient's name that it has been tested in the paper. This way of report the name is to protect the privacy of the patient [102]. We found fibre connections between pulvinar and Amg and also between superior colliculus and Amg via the pulvinar in the healthy observer as well as in the patient GY. The destruction of the visual cortex led to qualitative and quantitative modifications along the pathways connecting these three structures, and the changes were confined to the patient's damaged hemisphere, thereby strongly supporting the notion that the subcortical route conveys visual information critical for sustaining affective blindsight and non-conscious emotion perception. A recent tractography study by Rafal and collaborators [103] used a different tractography method in 20 healthy subjects, as well as in eight monkeys, to trace possible direct connections between colliculus, pulvinar and Amg. The results in humans were closely comparable to our previous findings, and the study also provided the first anatomical evidence of direct connections between Amg, pulvinar and colliculus in the monkey brain.

Clearly, the existence of such a subcortical pathway does not exclude the possibility that the Amg receives visual input also from other structures, nor the role of cortical areas in different forms of conscious or non-conscious emotion perception [104]. For example, both the lateral geniculate nucleus and the pulvinar send collateral projections that bypass V1 and target extrastriate visual areas, including areas along the ventral stream that can then relay visual information back to the Amg. Also, two other disynaptic subcortical pathways to the Amg have been recently demonstrated in mice, along with their functional role in triggering innate defensive responses to threatening visual stimuli. Both these pathways originate from the superior colliculus, but one includes the parabigeminal nucleus as intermediate station leading to the Amg [105], whereas the other involves the lateral posterior nucleus of the thalamus [106]. Whether these and other potential pathways beyond the well-documented colliculus-pulvinar-Amg one play a crucial role for emotion perception without awareness in humans remains to be established. Lastly, these two-route perspective involving cortical versus subcortical input to the Amg has been often conceived or presented as alternative to the two-stages account discussed above, as emerging from analyses of the temporal profile of Amg responses. However, there is no necessary contradiction between these two views nor must they be seen as mutually exclusive. Conversely, empirical evidence seems to indicate they co-exist in the intact brain, and they gain new coherence when considered under the light of the distinction between sensory and attentional unawareness introduced above [6]. In fact, when V1 is not able to process visual information normally, because of either experimental manipulation inducing sensory unawareness or permanent damage to V1, the subcortical route seems the primary non-canonical pathway to convey rapidly visual information to Amg and sustain non-conscious emotion processing. During attentional unawareness in healthy subjects or in patients with neglect, however, the visual cortex is normally functioning and coarse magnocellular input can also reach the Amg from cortical areas in the ventral stream through an initial forward sweep [30, 71]. This can afford rapid processing of unattended stimuli prior to voluntary attentional control [79, 107] or fine-grained and conscious stimulus perception.

6. Stimulus categories and properties triggering amygdala response without awareness

Facial expressions effectively communicate other's emotions during social interactions and, until recently, most investigations of human emotions predominately concentrated on processes associated with viewing faces (e.g. Ref. [108]). It is therefore not surprising that research on emotion perception without awareness primarily used facial expressions [16, 53, 54, 109]. This has contributed to the prevailing assumption that Amg activity during non-conscious emotion perception is selective for facial expressions [10, 110]. However, recent investigation seems to challenge this view from two parallel lines of findings. On the one hand, Amg activity contingent upon sensory and attentional awareness in healthy as well as brain damaged patients emerged from non-facial stimuli, thereby extending evidence of non-conscious emotion processing to other stimulus categories. Bodily expressions of emotions, both static and dynamic, have been the most extensively studied non-facial stimuli [46, 47, 62, 67, 68, 92–94, 110, 111]. Stimuli that represent evolution-determined threats, such as spiders and snakes, have also been tested under conditions of sensory and attentional unawareness. These stimuli induced enhanced physiological arousal and amygdala activity [112–115] particularly in individuals who were phobic to these types of stimuli, and activated Amg also when unattended because they were presented in the affected side of patients with hemispatial neglect [47]. On the other hand, the alleged special status of faces in triggering non-conscious perception and Amg activity is at odds with negative evidence when non-emotional facial attributes are tested, such as personal identity or gender [116]. Furthermore, facial expressions of complex social emotions, such as arrogance or guilt, also fail to undergo non-conscious emotion processing in patient with affective blindsight (Celeghin, Adenzato, et al., in preparation).

A certain degree of functional similarity between these different stimulus categories, resulting in their similar role in sustaining non-conscious emotion processing and Amg response, challenges theories exclusively concerned with analysis of the specific visual features. In fact, evidence suggests an approach that cuts across gross physical stimulus differences, as there exist between facial and bodily expressions, or between these latter and snakes, to focus more on the functional properties of visual signals. Under the assumption that the special role of faces is not fixed by their physical properties but by their functional ones, the findings reported above converge with the idea that non-conscious emotion processing is not specific for faces, but rather for biologically primitive emotional signals that can be encoded from low spatial frequencies, that are clearly associated with action tendencies and to which we are evolutionary prepared to respond [5]. Accordingly, complex affective scenes derived from the international affective picture system (IAPS) cannot be processed non-consciously in patients with affective blindsight [117] and do not activate Amg under attentional unawareness tested in patients with neglect [118].

Evidence therefore suggests that the analysis of the emotional content of complex scenes, facial identity or expressions of social emotions may depend critically on conscious visual perception and on the detailed processing of the high spatial frequency information that is typically performed by the cortical visual system [119]. We have already discussed findings

about fast Amg responses for low but not high spatial frequency fearful expressions [81, 120]. In an attempt to determine the causal role and behavioural consequences of Amg activity during non-conscious perception of low spatial frequencies expressions, we have recently tested two patients with affective blindsight in a combined behavioural/fMRI experiment. Fearful and neutral faces were filtered so as to contain only low or only high spatial frequency information. We reasoned that, if non-conscious emotion perception during sensory unawareness relies on a subcortical pathway to Amg and magnocellular channels, then the patients should be able to correctly guess the emotional expressions of faces filtered for displaying only low spatial frequency information and this behavioural effect should be associated with Amg activity. Conversely, the same expressions filtered in high spatial frequency should knock out the behavioural effect and Amg response should drop significantly. Preliminary evidence indeed confirms our hypothesis and provides direct support for the role of subcortical structures in mediating affective blindsight.

7. Consequences of Amg activity during non-conscious emotion perception

What are the consequences of Amg activity without stimulus awareness? Do they alter on-going behaviour, psychophysiological reactions or expressive responses towards normally seen environmental stimuli? And, lastly, are these responses felt consciously, even though they cannot be linked to the external triggering event?

Non-conscious perception of emotional stimuli associated with Amg activity often induce behavioural consequences that are accompanied by characteristic psychophysiological correlates of changes in the emotional state of the (unaware) observer. These behavioural and psychophysiological outcomes are often different from those associated with conscious perception, as they tend to be stronger and faster in the former case [35, 47, 67]. This suggests that non-conscious perception of emotional stimuli is not simply a degraded counterpart of conscious perception, but a different mode of processing visual signals.

For example, emotional stimuli that are unattended nevertheless interfere with on-going tasks [25, 121], and behavioural consequences include delayed disengagement of attention [122], faster and easier detection than neutral stimuli, as shown in visual search [123, 124], attentional blink paradigms [22] or in patients with neglect [35, 125–128]. Notably, damage to the Amg abolishes some of these behavioural effects [42]. Likewise, attitudes and preferences towards neutral stimuli may be shifted towards more positive or more negative evaluations depending on whether the neutral stimuli are preceded by, or paired with, unperceived emotional stimuli [129, 130]. For example, consumption behaviours or preference judgments can be influenced by exposure to masked facial expressions, despite subjective feelings remain unaltered [131, 132]. Notably, however, when subjects are aware of the presence and nature of the emotional stimuli these effects sometimes disappear [130, 133].

Psychophysiological changes that are associated with non-conscious perception of emotional stimuli include enhanced skin conductance [15, 134] increased frequency of eye blink

(indicating startle reactions or avoidance) [64], changes in stress hormone levels [135], increased pupil dilation [47, 67] and heart rate changes [136]. These changes index arousal and their function is to prepare the organism for reacting to impeding and salient events. Similarly, undetected emotional stimuli also induce spontaneous facial reactions that reflect the affective valence of the stimuli, as recorded using electromyography (EMG) [67, 137]. This spontaneous tendency to synchronize our facial expressions with the emotional meaning of other individuals' expressions is likely to play a part in social interactions [138].

A different source of evidence on the impact of stimulus processing without awareness comes from studies that used indirect manipulations. For example, studies on patients with affective blindsight have used indirect methods to investigate possible online interactions between consciously and non-consciously perceived emotions, as well as the influence exerted by the former over on-going recognition of seen stimuli [63, 139–141]. A classic example of such indirect methods is the redundant target paradigm, in which stimuli are presented either singly to the intact field or paired simultaneously with another stimulus in the blind field. Typically, reaction times (RTs) to the seen stimulus are faster during redundant stimulation than during single presentation to the intact field. With such method, unimodal (visual/visual) and cross-modal interactions (visual/auditory) between consciously and non-consciously perceived emotional stimuli have been observed in such patients. For example, presenting a facial expression to the blind field of patients with blindsight biases their judgment of the emotional prosody of a sentence fragment [90, 117]. For example, a fearful prosody in the voice is perceived as more fearful when it is presented synchronously with a fearful facial expression in the blind visual field, and this effect is associated with enhanced Amg activity. These findings converge with the notion that emotion processing with and without stimulus awareness co-exist and interact in the intact brain, though they can be dissociated because of focal brain damage or experimental manipulation.

But can the bodily changes and responses triggered by unseen emotional stimuli be themselves experienced consciously as feelings? The classical view is that we become aware of such bodily responses when linking them to conscious representations of their external (e.g. an angry expression or a sudden noise) or internal causes (e.g. our thoughts). In fact, some evidence indicates that we are unable to report a conscious feeling despite the fact that, at the same time, our behaviour reveals the presence of an affective reaction triggered by the exposure to an external stimulus of which we are unaware. Despite this, however, it is conceivable that we can become aware of our physiological changes without any conscious representation of their underlying causes. This seems to be a common situation in clinical conditions such as alexithymia, pathological anxiety or depression. Also, one study on patients with affective blindsight has shown that the presentation of an unseen stimulus previously paired with an aversive event enhances eye-blink startle reflex, and this enhancement corresponded to the reported level of negative emotional feelings [142].

8. Concluding considerations

If emotional stimuli can be processed without awareness, activate the Amg, and still induce coherent responses, what role is left for consciousness in emotions? Some clues come from

the observation that the responses observed when emotion processing is accompanied by awareness are often quantitatively or qualitatively different from those induced by unconscious processing. Enhanced influence of non-consciously perceived emotional signals on physiological or expressive responses is in line with evidence that cortical activity and awareness may exert an inhibitory modulation over subcortical areas or automatic responses [143–145]. The fact that such inhibition is absent during non-conscious perception of emotional stimuli could also explain the apparently paradoxical finding that subcortical activity can be enhanced during non-conscious compared to conscious perception of emotional stimuli in healthy subjects [43, 58]. Likewise, conscious perception of the eliciting stimulus can overrule subjective affective experience in response to an aversely conditioned stimulus, and the decoupling between phenomenal affective experience and actual physiological changes is associated with increased activity in the ventrolateral prefrontal cortex [129, 142]. These findings contradict the common assumption that emotional feelings merely reflect cortical readouts of peripheral and autonomic arousal. Therefore, the added value of the conscious perception of emotional stimuli seems primarily that of integrating representations of the external and internal world in order to achieve context-dependent and higher-order decoupling and flexibility between sensory input and behavioural output. Consciousness also allows control and planning, as well as anticipation of desirable or functional responses.

From the opposite vantage point, emotions seem to play a prominent role in the generation and development of state consciousness. The basic physiological reactions triggered by emotional stimuli involve the moment-to-moment mapping of our bodily states and interoceptive information crucial for homeostatic regulation. Because homeostatic processes provide the sense of invariance that accompanies every subjective experience, they constitute a neurobiological mechanism for the invariance of the sense of self and the continuity of our first-person experience of the world [146–148]. On this picture, basic aspects of the physiological reactions to emotional stimuli overlap with physiological responses related to corrections of homeostatic imbalance and thought to be necessary for the general level of consciousness [146, 149, 150]. It is not a coincidence that these emotional responses are controlled by neural structures in the brainstem that also control the level of consciousness. Accordingly, several scholars consider raw emotional feelings as the precursors or basic forms of consciousness, and have rooted it in subcortical processes rather than (only) in full-blown subjective cognitions implemented in higher-order cortical structure [145, 149, 151–153]. In keeping with this perspective, children with total congenital absence of the cerebral cortex can nevertheless exhibit appropriate affective responses and feelings can be even strengthened [154]. Moreover, direct electrical brain stimulation in subcortical and brainstem structures that evoke observable behavioural and physiological reactions associated with reward and punishment in animals, also induce conscious affective feelings when stimulated in humans [145, 153]. Therefore, even when we remain unaware of the external determinants of an emotional response, such that the eliciting stimulus does not become a content of our conscious visual experience, the chain of physiological reactions it triggers nevertheless contributes to modulate our state of vigilance and behaviour, which are constitutive components of our state of consciousness.

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