Amygdala's "unfelt" emotions?

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Abstract

Participants saw "hybrid" pictures of faces composed by superimposing neutral expression in high spatial frequencies (HSF, 7-128 cycles/image) over different emotional expressions in low spatial frequencies (LSF, 1-6 cycles). While explicitly judging them as neutral, participants rated the hybrids as friendly when the emotion showed in the low frequencies was positive, and as unfriendly when the emotion shown in the low frequencies was negative. A young female patient (S.S.), whose left anterior temporal lobe had been surgically removed to treat a brain tumor, showed a change in unconscious preferences in the above test when the hybrids' low frequency emotion was either sadness or fear, while she failed to explicitly label both fear and anger. Given (1) the amygdala's sensitivity only to lowest spatial frequencies, and its "blindness" to the highest frequency, and (2) fusiform's sensitivity to the highest frequencies and not to the lowest ones, as indicated by previous neuroimaging studies (Vuilleumier, Armony, Driver, & Dolan, 2003; Winston, Vuilleumier, & Dolan, 2003), the present study confirms the amygdala's fundamental role in the response to fear, while suggesting its role in the unconscious response to other "negative" emotions like anger and sadness.

Keywords: Amygdala; Consciousness; Emotion; Facial Expressions; Implicit Perception; Spatial Frequency; Hybrids

Emotions in historical perspective

The existence of "unfelt" emotions—an oxymoron or nonsense at first glance—has become increasingly accepted within contemporary psychology (Barrett, Niedenthal, & Winkielman, 2005) and philosophy (e.g. Lacewing, 2007; Prinz, 2005), since it would seem very difficult to make sense of human behavior without it. This has not always been the case, though. As recently as 1999, Frijda wrote about affect as "hedonic experience, the experience of pleasure and pain". Clore (1994) had been even more stringent, explaining how emotions are never unconscious because "emotion involves an experience, and one cannot have an experience that is not experienced [and] they must be felt, and feelings are by definition conscious" (pp. 285-290).

Ever since William James' classic paper "What is an emotion" (1884) appeared, emotions have been considered explicit and conscious by definition. James, when talking about the bodily sensations involved in an emotion, writes that "our feeling of the same [bodily] changes as they occur IS the emotion", maintaining the subjectivity and necessary conscious characteristic of an emotion[1].

Cognitive science, around the middle of this century, became the science of thinking and reasoning as a reaction to behaviorism, and was therefore most interested in the unconscious: The focus of cognition was the *process* and not the *product*, and while the latter is accessible to awareness, the former is not. Leaving out consciousness, it left out emotions. James proposed "we are afraid because we run", turning upside down the most natural explanation laypersons would give themselves for the origin of emotions. According to James (1884) it was the specific signature of any emotion in terms of bodily reactions, such as heart rate, sweat and so on, that made one feel that specific emotion. Not long after, another psychologist, sir Walter Cannon (1915), working in his colleague Bard's laboratory, opposed the idea of bodily sensations as the origin of feelings on the

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[1] James' article was published in a philosophy journal, *Mind*. At the time, there were no specialized psychology journals.

base of two considerations: (1) The autonomic nervous system (ANS), which controlled all those reactions, was known to react uniformly, no matter what activated it. This would take away the specificity of the response, and therefore its discriminatory power; (2) The ANS response was way too slow to account for emotions by itself. Only in the early 1960 James's theory was revived by Schachter and Singer (1962), who put a cognitive attribution between the physiological feedback and the feeling: While the body was aroused by the ANS, the context would supply information enough to discriminate the right feeling to feel and (quickly) give it a label. This way, emotions got their place back in cognitive psychology, however only as a conscious phenomenon. Nevertheless, an important question had not been answered yet: What causes the bodily reactions in the first place? Some years later Lazarus (1966; 1991) in his studies on stress and coping, filled in the gap between stimulus and bodily response: He adopted Arnold's (1960) term *appraisal* as "the mental assessment of the potential harm or benefit of a situation" – i.e., an unconscious evaluation. While appraisal research went on for many years, a paper appeared in 1980 on preferences formed without conscious awareness of the stimulus. Zajonc (1980) published the results of a series of studies on a phenomenon called the mere exposure effect, where participants, asked to choose between novel stimuli and stimuli they had been previously exposed to, tended reliably to prefer the latter ones. Mere exposure leads to preference. When exposed subliminally to stimuli (exposing time could be as short as 1 ms) participants also showed clear preference for the old ones with respect to the new ones, even if recognition rate remained at chance level (Kunst-Wilson & Zajonc, 1980). Moreover, according to Bornstein and Dagostino's (1992) meta-analysis of the studies on the mere exposure effect, it appears that the influence of these stimuli be greater when they remain subliminal than when they are available to consciousness.

What does *unconscious* mean?

The existence of unconscious emotions that do not rise to the surface of awareness but still affect behavior has now long been recognized and tested.

Rorschach's (1942) inkblot technique, Machover's (1949) Draw-a-Person test, and Murray’s (1943) Thematic Apperception Test (TAT) are examples of major instruments to (elicit and) measure emotional behavior that is otherwise unnoticed or denied.

Nevertheless, a definition of unconscious emotion remains hard to agree upon.

Kihlstrom (1987) proposed the concept of the *cognitive unconscious*, to comprehend those cognitive phenomena and responses that can be demonstrated not to have the characteristic of being conscious, like implicit memory, or implicit perception, as in the case of blindsight (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999). In blindsight paradigms, damages in the visual primary (striate) cortex cause the corresponding visual field to be blind. Nevertheless, patients can make accurate guesses about the attributes of stimuli presented to their blind field, of which they have no awareness.

Some years before, Gazzaniga and LeDoux (1978) had made some crucial experiments with split-brain patients. They presented some contents with emotional value to the right hemisphere, and while the patients were not able to report on the nature of the contents, they had no problem in reporting their emotional valence: good (*mom*) or bad (*gun*). Some years later, parallel to the idea of cognitive unconscious, Kihlstrom (1999; 2000) would also suggest *emotional unconscious* and *implicit emotion* for unconscious affective reactions, “changes in experience, thought, or action that are attributable to one’s emotional state, independent of his or her conscious awareness of that state” (1999, p. 432).

In 1995 Greenwald and Banaji applied the distinction conscious/unconscious also to attitudes. Attitudes can be regarded as affective dispositions in respect to certain groups or individuals, and are in fact usually expressed in terms of like/dislike, in favor or against, etc.

Wegner and Smart (1997) introduced the notion of “deep cognitive activation” as a mean to resolve the controversy aroused from the use of projective measures. Deep activation is “a tendency to think that does not carry with it the occurrence of the conscious thought”. Deep activation involves two key elements: the presence of an accessible thought in mind, and the absence of that in the conscious mind. An accessible thought is so quickly and easily brought to mind that it can influence a variety of mental processes before the conscious recognition of the thought's occurrence. When the thought is emotion-related, its effect can be an emotion that is not consciously experienced. An example is when the desire of "not to be sad" generates mental control by intentionally searching for happy thoughts (distracters). This generates an ironic process that monitors sad thoughts, which, in turn, induces surface activation of distracters and deep activation of sad thoughts. In the presence of mental load, the deep activated monitoring process would eventually fail, resulting in a sad mood (Wegner, 1994). In one study for instance, people instructed not to think of sex showed higher skin conductance levels than controls that were instead instructed to think of it (Wegner, Shortt, Blake, & Page, 1990).

Lately, Lacewing (2007) grouped different accounts in three families according to how they answered the question on feeling involved with unconscious emotions: whether they intended *unconscious* feeling be involved, or *conscious* feelings be involved – though the person *misunderstands* or is *unaware* of them, or *no* feeling at all be involved.

Weak instances of unconsciousness would be inaccurate labeling or errors of attention – as when people furiously fight any attempt to be calmed by affirming their not being angry. These are situations where consciousness of the emotion could be regained by directing extra attentional resources to the emotional aspect of the experience. However, a stronger definition of unconsciousness will be used in this study from now on: An emotion is to be considered unconscious whenever people will not be able to report (or point to an example of) it at the moment it is caused and, by extension, for other people's emotional expressions to be perceived unconsciously, an observer must be unaware that a, for example, sad facial expression was actually shown, i.e. the observer must not be able to report or label the emotion at the moment this was "seen." Yet, it is possible to demonstrate that the emotion is seen and categorized because it meaningfully affects subsequent decisions and behavior (Berridge & Winkielman, 2003; Zajonc, 2000).

New emotional evidence

Though complex emotions result from an extended sequence of cognitive appraisals (Ellsworth & Scherer, 2003), basic affective reactions may involve only minimal processing and be elicited by subliminal stimuli or priming (Bargh, Chen, & Burrows, 1996; Zajonc, 2000). These emotions can manifest themselves in decision-making or other observable affective reactions (Damasio, 1999; Zajonc, 2000), and they can occur unconsciously as "core" emotional responses (Berridge, 2003; Winkielman & Berridge, 2004). The states of pleasure and displeasure are called core affects because of the universal capacity to experience them (Mesquita & Walker, 2003), and because they are present at birth (Emde, Gaensbauer, & Harmon, 1976). They are measurable by means of peripheral nervous system activation (Bradley & Lang, 2000; Cacioppo, Berntson, Larsen, Poehlmann, & Ito, 2000), facial electromyographic activity (Dimberg, 1982; Dimberg, Thunberg, & Elmehed, 2000), vocal acoustics (Bachorowski, 1999), expressive behavior (Cacioppo & Gardner, 1999), and neural activations (Wager, Phan, Liberzon, & Taylor, 2003). For a review, see Barrett (2006).

A positive core emotional reaction has been the focus of a study by Winkielman, Berridge, and Wilbarger (2005). They explored the impact of affective priming on preference judgment and volitional behavior, by asking participants to specifically rate an unfamiliar beverage after being exposed to affective stimuli, either a happy or an angry face, presented subliminally. Their ratings of an identical, flavored, drink were respectively positively and negatively affected by the subliminal presentation. For such effects to take place, there must be a system in the brain that is capable to process an image very rapidly, so as to assign—at least unconsciously—a core emotional valence to the perceptual event before its perceptual/neural processing is interrupted by the masking stimulus (Kahneman, 1968; Kovacs, Vogels, & Orban, 1995; Macknik & Livingstone, 1998). One account is that there exist two parallel neural pathways or networks for emotional processing (LeDoux, 1996): a *high road* and a *low road*. The high road for emotional visual processing consists in a pathway that expands from the thalamus into a *cortical* network comprising the occipital and temporal lobes.

These cortical areas support fine-grained emotional processing, and perceptual categorization of the triggering stimulus (Haxby, Hoffman, & Gobbini, 2000), which implies a series of processing stages in feed-forward cortical areas (V1, V2, V4, inferior temporal cortex), with each stage adding processing time (cf. Rolls, Tovee, & Panzeri, 1999), and their analysis apparently requiring extensive attentional resources (Vuilleumier, Armony, Driver, & Dolan, 2001). In contrast, the low road would comprise a set of *subcortical* nuclei and *direct* connections from the thalamus to the amygdala (Morris, Ohman, & Dolan, 1999) that would be able to support rapid but rather coarse emotional processing.

The low road

Initial evidence of a low, subcortical fast route from sensory input to reaction came from animal studies with auditory fear conditioned stimuli (LeDoux, 1996), and, in humans, from lesion studies (blindsight) (de Gelder et al., 1999) and binocular rivalry studies (Pasley, Mayes, & Schultz, 2004). During binocular rivalry, the two eyes are presented with a different, incompatible image. The observer experiences alternating perceptual dominance of one image or the other. While one image is perceptually dominant, the other is completely suppressed, or unperceived.

Subjects in these studies were unaware of faces either presented in their blind field (blindsight) or that had been the suppressed stimulus (binocular rivalry). That notwithstanding, they were able to recognize fear expressions on those same faces they had not been able to report on. LeDoux (1996) proposed a direct path of projections from the thalamus to the amygdala that doesn't go through the cortex, a faster and coarser information circuit, not so very sensitive to nuances, but extremely fast: The low road would have ancestral origin, and an evolutionary advantage of such a faster pathway is obvious. Studies of living fish, amphibians, and reptile suggest that those projections were probably stronger relative to those to the rudimentary neocortex in primordial animals (Northcutt & Kaas, 1995). Consistent with LeDoux (1996), results by Ohman and Soares (1993; 1994), Morris, Ohman, and Dolan (1998), Morris, DeGelder, Weiskrantz, and

Dolan (2001), showed that conscious recognition of a fear stimulus is not necessary for activating fast responses to evolutionarily fear-relevant stimuli (but see Lipp, 2006, and Lipp, Derakshan, Waters, & Logies, 2004, for contrasting results). Hamm et al. (2003) reported the case of a patient with bilateral cortically blindness, due to infarction of both left and right posterior cerebral arteries, who could not detect any light change in the environment, nor was he able to orient to new stimuli or reach for grasping. Nevertheless, he could still learn normal fear conditioning to visual cues.

A fast route should imply subcortical response prior than (visual) cortex response. Such was found by Eimer and Holmes (2002), Eger, Jedynak, Iwaki, and Skrandies (2003), Pourtois, Dan, Grandjean, Sander, & Vuilleumier (2005), L. M. Williams, Palmer, Liddell, Song, and Gordon (2006), prior than and around 100-120 ms, i.e. prior the face-selective N170 component in EEG (or M170 in MEG), a negative response occurring 170 ms after stimulus onset, indexing the full perceptual analysis that differentiate faces form other objects (Bentin, Allison, Puce, Perez, & McCarthy, 1996); but see Rolls and Deco (2001), for response latencies of 40-50 ms in V1, and 80-100 ms in anterior inferior temporal cortex.

A subcortical route from thalamus to amygdala has been specifically found in rats (Doron & LeDoux, 1999; Linke, De Lima, Schwegler, & Pape, 1999; Shi & Davis, 2001), partly in non-human primates (Jones & Burton, 1976; Stepniewska, Qi, & Kaas, 2000), and it's been detected in humans (Liddell et al., 2005; Morris et al., 2001; Morris et al., 1999). For a visual low road, the superior colliculus, located in the tectum, projects to the inferior aspect of the pulvinar nucleus of the thalamus, while there is some evidence that indicates that the medial aspect of the pulvinar projects to the amygdala. Necessity of pulvinar activation has been assessed also in humans (Ward, Calder, Parker, & Arend, 2007), though interconnections between the inferior and the medial nuclei of the pulvinar have not yet been described.

Moreover, this subcortical neural network, and especially the nucleus called amygdala[2], would apparently require minimal attentional resources in order to be engaged by an emotion-triggering stimulus (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Ohman, Esteves, & Soares, 1995; Ohman, Flykt, & Esteves, 2001; Vuilleumier et al., 2002; Vuilleumier et al., 2001; M. A. Williams, McGlone, Abbott, & Mattingley, 2005).

Weaknesses of previous studies

Quite a few neuroimaging studies have specifically used the *backward masking paradigm* to reveal which brain areas are involved when facial expressions can be processed only unconsciously (e.g., Morris, Ohman et al., 1998; Morris et al., 1999). These studies are generally concordant in indicating a key role of the amygdala in processing unconscious emotions (e.g., Dannlowski et al., 2007) and, in particular, fear (Liddell et al., 2005; Vuilleumier & Pourtois, 2007); but for a non-significant results see Phillips et al. (2004). In a typical experiment, two images of faces are rapidly presented in series, the first very briefly (i.e., a few tens of ms) and the second long enough to be acknowledged, so that the final image effectively erases the experience of having seen the initial face. If the first face shows an emotional expression and the second one a neutral expression and the second face effectively masks the perception of the first, then people must not be able to report having seen an emotional face at all. However, if the emotional face were unconsciously processed, the observer's subsequent behavior would be predictably influenced by the emotional content of the initial, subliminal, face. A good example is Whalen and colleagues' (1998) study. They showed for 33 ms fearful or happy facial expressions, followed for 167 ms by neutral facial expressions. Although subjects reported seeing only neutral faces,

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[2] Technically, the amygdala would be better referred to as the *amygdaloid complex* because it is composed of a number of nuclei, organized into several divisions that would have different functions and connections.

the activity in the amygdala was significantly higher when viewing masked fearful faces than when viewing masked happy faces.

Many of the original studies of unconscious emotional effects bore some weakness as they involved verbal stimuli. Nonverbal stimuli would be, though, more appropriate if emotions stem from a processing system evolutionarily much antecedent the cognitive one. This is why researchers started using faces as subliminal stimuli to elicit basic affective reactions measurable through physiology, facial expression, judging, and volitional behavior (Murphy & Zajonc, 1993; Rotteveel, de Groot, Geutskens, & Phaf, 2001). These studies were the first convincing evidence for unconscious emotional processing. Still, such studies involve either subliminal stimuli or backward masking paradigm. This means really short time periods, and a little amount of cognitive resources that can be dedicated to the processing task. Mostly important, not only the amount of information is minimal; it is also soon interrupted, i.e. cleared from memory and perception. This presents the disadvantage of introducing the respective confounds variables (cf. Kahneman, 1968; Rolls et al., 1999). See also Wiens (2006) for other possible weaknesses connected to masking technique, like, among others, different masking capacity of the same mask for different target categories.

Similarly, in affective blindsight experiments with cortically blind patients (de Gelder, Pourtois, & Weiskrantz, 2002), the processing of emotional stimuli by the primary visual pathway would be interrupted by the brain damage, and cortical responses (in striate, fusiform, and prefrontal areas) would necessarily be eliminated (Morris et al., 2001; Rolls & Tovee, 1994). When brain damage interferes with the deployment of attention, as in severe hemispatial neglect due to parietal damage, the reduced attentional processing to one side of space can lead, during bilateral presentations of two faces, to the "extinction" of an emotional face presented in the contralesional side of the visual field (M. A. Williams & Mattingley, 2004). However, the unattended emotional faces can still prime the emotional judgments (happy vs. sad) of a centrally located face that immediately followed the bilateral presented faces (Vuilleumier, 2000; M. A. Williams & Mattingley, 2004).

Another consideration is of importance when masking is used in a study. The bulk of the projections from the eye to the thalamus constitute the magnocellular (M), the parvocellular (P), and the koniocellular (K) pathways, substantially following the three fundamental dimensions of color vision: light/dark, red/green, and blue/yellow (Dobkins, 2000; Merigan & Maunsell, 1993). Neurons of the M pathway exhibit high luminance contrast (light/dark), i.e. sensitivity to low frequencies (LSF), yet low chromatic contrast sensitivity, while neurons of the P pathway exhibit the opposite, i.e., high chromatic, low luminance sensitivity, and sensitivity to high frequencies (HSF) (Dobkins, 2000; Lee, Pokorny, Smith, Martin, & Valberg, 1990). Studies on humans and nonhuman primates (Schneider, Richter, & Kastner, 2004) suggest that segregation of M and P at the lateral geniculate nucleus (LGN) continues in the extrastriate visual cortex, and that inputs relayed through those channels remain largely segregated through the highest levels of cortical processing, eventually dominating the activity of neurons in the motion pathway and the color and form pathway respectively (Maunsell, Nealey, & Depriest, 1990). Morris, Ohman, and Dolan (1999) have suggested that cortical parvocellular neurons might be more vulnerable to visual masking than the subcortical magnocellular neurons that provide their input to the superior colliculus or amygdala.

Hybrids: stimuli with no interruption

The method used in the experiments presented in this paper resolves those weaknesses by means of a kind of stimuli whose emotional component is not subliminal, is always present, and is nevertheless unconsciously processed. In a novel perceptual technique, originally developed by Schyns and Oliva (see Oliva & Schyns, 1997; Oliva, Torralba, & Schyns, 2006; Schyns, 1998; Schyns & Oliva, 1999), a facial image at a coarse spatial scale (LSF) is superimposed to a different facial image at the fine spatial scale (HSF). This creates a *hybrid* facial stimulus where different information is carried by the different spatial frequencies.

Similarly, in the present stimulus set, each face was composed of (1) an image of a female or male face digitally filtered so as to let pass only the lowest spatial frequencies (LSF, 1-6 cycles/image, low pass filter), showing one of five facial expressions (afraid, angry, happy, neutral, or sad); (2) the same individual's face, showing a neutral expression, digitally filtered with a high pass filter so as to let only finer, higher, spatial frequencies (HSF, 7-128 cycles/image) pass through. The two images were then combined together back into a single one. The rationale for generating these facial hybrids was based on fMRI evidence that the human amygdala responds just as strongly to low-pass filtered images of emotional fearful faces as it does to whole (unfiltered) images, whereas it remains unresponsive to the high-pass filtered version of the same facial expression (Vuilleumier et al., 2003).

Hybrid stimuli allow testing the hypothesis of unconscious processing in neural networks that are neither temporarily interfered with their operations nor permanently damaged. In contrast, pattern backward masking would result in subliminal effects by interfering with attentional processing so that the perceptual/neural processing of the emotional stimuli would be interrupted.

In contrast to the above evidence based on reduced sensory or attentional processing after neuronal damage, the low-passed emotional information of a hybrid image is a constituent part of the stimulus that is available at all times in the visual input (and supposedly visible to all visual areas) and can be attended together with the other image properties. Thus, revealing unconscious effects in intact brains with the present stimuli would strongly support the conclusion that the emotional visual information, which can be processed by subcortical areas like the amygdala only at these low spatial frequencies, simply cannot access consciousness and remains unconscious despite being uninterruptedly available in the visible image as well as embedded within the attentional focus.

The goal

The goal of the present study is to further test, with several emotions, the hypothesis that what is seen by the amygdala is indeed of an unconscious nature. Vuilleumier et al.'s (2003) study revealed that amygdala's activation to a low-pass image (< 6 cycles/image) of a fearful facial expression (i.e., showing fear) was greater than to a neutral facial expression, but no increase in activity to the same fearful facial expression was found when this was presented in higher spatial frequencies (> 24 cycles/image). In other words, the human amygdala appeared to be "blind" to most of the visible spatial frequency scale except the lowest. In contrast, the fusiform cortex was engaged more by the high-passed spatial frequency images than by the low-pass spatial frequency images, the latter evoking only a very weak response in fusiform cortex. Thus, the inferior temporal areas seemed predominantly influenced by fine-grained spatial frequency information. Vuilleumier et al.'s study found also that also fusiform showed greater activation to fearful LSF faces than to neutral LSF faces (despite greater responses to HSF components of faces, regardless of expression). The same was not the case for HSF faces. Their findings were then replicated by Winston et al. (2003).

Vuilleumier, Richardson, Armony, Driver, and Dolan (2004) compared 13 normal subjects (N), with 13 patients with damaged hippocampus and amygdala (AH) and 13 with lesions limited to hippocampus (H). Fusiform's response was higher to fearful stimuli as compared to neutral stimuli for all the subjects except AH.

These four pieces of evidence taken together – (1) the human amygdala appears to be "blind" to most of the visible spatial frequency scale except the lowest; (2) the fusiform intensifies its activity when the emotional expression is conveyed by LSF and not when it is conveyed by HSF; (3) the fusiform is otherwise engaged more by HSF than by LSF; (4) in absence of the amygdala, the fusiform reacts only to the presentation of the face irrespective of emotional expression – seem to indicate that information runs from the amygdala to the fusiform, and not vice versa, i.e. that in response to an emotion, the fusiform enhances its activity only through amygdala's feed forward. In other words, LSF through amygdala modulate fusiform's response. It remains to be seen whether amygdala's feed forward to the fusiform is enough to trigger awareness of an emotion conveyed exclusively by LSF, or if this must be also present in HSF.

I will present here three experiments (two of which divided in two phases), where (1) I tested whether people perceived these hybrids as neutral or they perceived the emotion conveyed by the LSF, (2) I tested whether the underlying emotion "hidden" in the LSF indeed would affect rating of friendliness for hybrids, (3) I simply executed a control condition for the first two tests, and (4) and (5) I repeated the same tests with a patient whose left amygdala (and the anterior part of left the temporal lobe) was resected.

Experiment 1A

The original broadband emotional pictures from the Karolinska Directed Emotional Faces set were mixed with their hybrid versions (that included low-passed emotional expressions), and a group of participants was asked to select the most appropriate emotional label for each picture.

The fusiform should react to the neutral face expression presented in HSF, while it should also react to the feed forward generated by the amygdala at the emotional face expression presented in LSF. In tachistoscopic tests, participants have been found to turn to LSF when the task at hand was to categorize different emotional face expressions (Schyns & Oliva, 1999), but to HSF when the time at their disposal for the perception or categorization task increased (Schyns & Oliva, 1994). Given that the task was the same as in Schyns and Oliva (1999), and that here there were no time constraints, it was difficult to predict the result of the present test. On the other end, a look at Figure 1 (bottom image) should convince the reader that when seeing the hybrid face, one is aware of seeing a neutral-looking face, although the image also shows a happy expression in its lowest spatial frequencies. In the initial phase of this experiment, the goal was thus to test whether the hybrid pictures (containing low-passed emotional expressions) are indeed consciously perceived as being neutral and not as explicitly expressing the specific emotions conveyed by the images' low spatial frequencies.

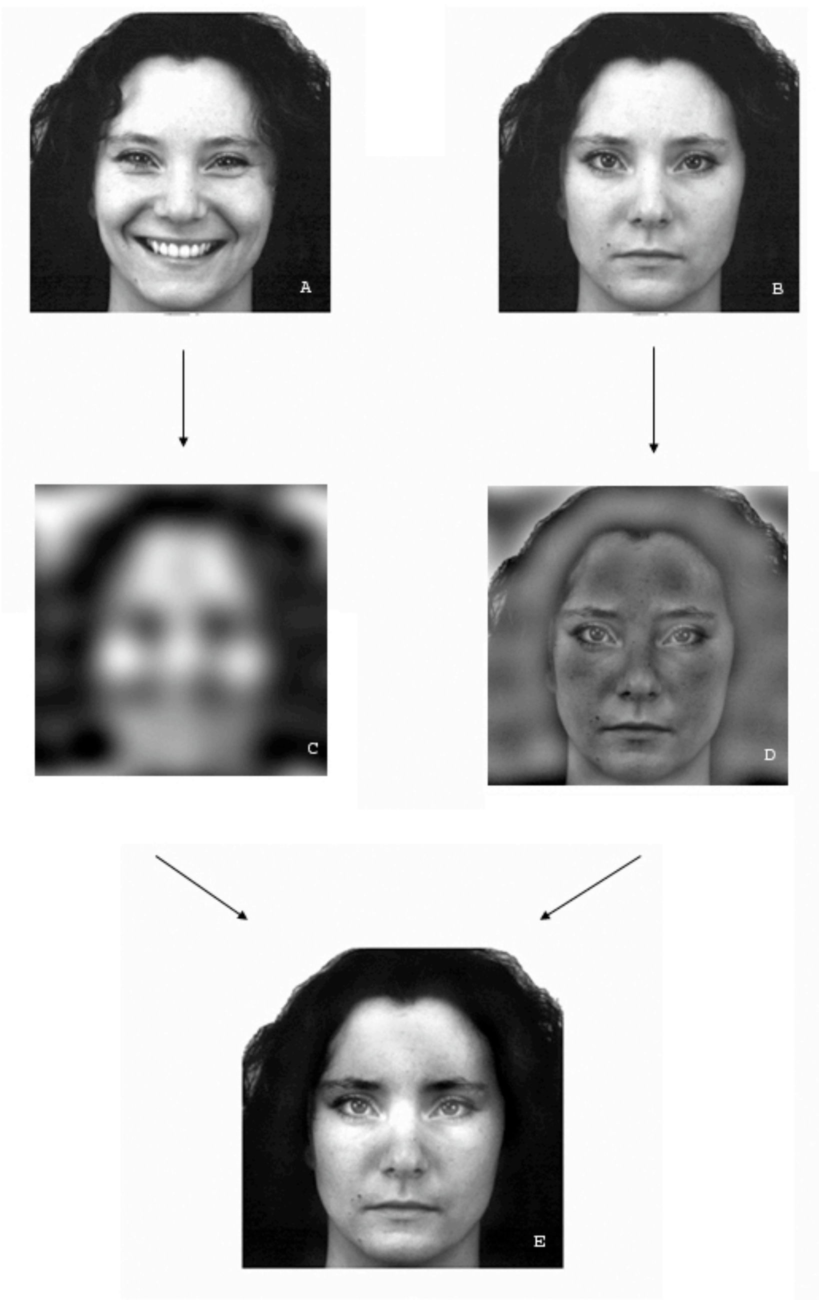

Figure 1. An example of the editing procedure used to obtain a hybrid expressive face: Image A and B are separate photographs of the same actress assuming a happy and neutral expression, respectively. Image C is the low-passed version (< 6 cycles/image) of Image A, whereas Image D is the high-passed version (> 7 cycles/image) of Image B. Image D is the hybrid picture or a combination of images C and D with a happy expression embedded exclusively in the lowest spatial frequencies.

Methods

Participants The participants were 14 female students (mean age = 22.5 years, SD = 1.7) at the University of Tromsø in Norway.

Stimuli The original stimuli consisted of 190, gray-scale, close-up photographs (198 x 252 pixels) of emotional and neutral faces selected from the Karolinska Directed Emotional Faces (Karolinska Hospital, Stockholm, Sweden, 1998; see http://www.facialstimuli.com/index_files/Page369.htm). The selected models were 19 females and 19 males. Each model displayed 4 different emotions (anger, fear, happiness, and sadness) plus one neutral expression. All of the selected photos showed full frontal or straight views of the head. From these original pictures, the spatial frequency content in each image was filtered (by use of MatLab® software). Specifically, each image was filtered using a low pass cut-off of 6 Hertz so as to obtain the low spatial frequency versions (1-6 cycles/image); whereas a high pass cut-off of 7 cycles was used on the neutral expression pictures so as to obtain the high-spatial frequency images (7-128 cycles/image). The neutral high-pass version of each model's face was then combined with each low-pass version of the same face, so as to obtain 5 final images of each face, 4 containing a different emotion (anger, fear, happiness, and sadness) which appeared only in the low spatial frequencies and one re-constituting the original broad band neutral expression of the same face (see Figure 1 for an illustration of the steps used in generating a test image). In addition, possible differences in apparent contrast were assessed (computed as the standard deviation of luminance for all pixels divided by the mean luminance) among the hybrid images. It is important to rule out that possible behavioral differences may be due to underlying (artifactual) differences in contrast between the different emotions. I did not find significant differences between the various emotional faces and these in relation to neutral faces, as confirmed by an ANOVA with emotion as the factor, $F < 1$, and apparent contrast as the dependent variable. Average values of apparent contrasts ranged from 4.5 (sad hybrids) to 5.5 (neutral hybrids). This new set of 190 (hybrid) images was added to the original pictures for a total set of 380 pictures.

Procedure Participants saw each image, one at a time, centered on a 17 inches computer screen and presented in full-screen mode. Each image remained on screen until the participant made a key press by selecting one of the digit keys on the keyboard labeled from 1 to 5, which led to the presentation of a new image. Participants were informed that each number would correspond to an emotional label (1 = Neutral; 2 = Happy; 3 = Afraid; 4 = Sad; 5 = Angry). They were also provided with a printed look-up table listing the numbers and corresponding labels that they could keep next to the keyboard and check at ease. Participants sat at a distance of 72 cm from the screen so that the size of the images would correspond to 6° of visual angle (so as to replicate the viewing conditions of Vuilleumier et al.'s study (2003). There were a total of 380 trials in the whole test, which took approximately half an hour to complete. Stimulus presentations were controlled by SuperLab© software, which also stored each key press. Each participant was only informed that they would see a series of faces to be labeled individually for their expressions, and it was not mentioned that some pictures contained "hidden" emotions.

Results

Descriptive statistics for each participant were calculated, obtaining percent frequencies of each label for each picture type (broadband, hybrids) and expression. The results indicated than when looking at the (original) broadband pictures, participants selected, for 93.9% of the pictures, the labels that identified the "correct" emotion (i.e., corresponding to the emotion that the actors, who contributed to the Karolinska Directed Emotional Faces, were instructed to show) (see Table 1, top row). However, when these same emotional pictures were filtered and included within the low spatial frequencies of the hybrid images, while the rest of the spatial scale showed a neutral expression, participants selected the Neutral label for 88.9 % of the pictures. Hence, a conscious feeling of emotional neutrality clearly prevailed in these hybrid pictures (see Table 1, middle row). Interestingly, the correct emotional label (i.e., the one preferentially used for the broadband images) was not always the most likely alternative choice for the hybrid pictures (see Table 1, bottom row). A binomial test, with the hypothetical probability of choosing the correct label out of 5 set to equal (i.e., p = 0.2), confirmed that the likelihood of observing 7% or fewer choices of the correct label was much lower (0.03%) than that expected by chance. Most importantly, when seeing hybrids containing an expression of fear, the label Afraid was never chosen.

Table 1

Percentage of Label Chosen by Participants

	Expression				
Label chosen	Anger	Fear	Happiness	Neutrality	Sadness
Correct (broadband)	94.1	92.3	100	89.8	92.3
Neutral (hybrids)	88.4	90.9	85.9	85.9	93.4
Correct (hybrids)	6.6	0.0	6.6	85.9	2.2

Discussion

The hybrids were explicitly reported as showing a neutral expression. That is, the emotional expression, although being present in part of the spatial scale of the image and attended together with the other visible properties, was insufficient to trigger awareness that the hybrid face was showing any particular emotion. In other words, the emotion may have been processed, but unconsciously.

In their original 1994 study, Schyns and Oliva showed that both low and high frequencies were detected in scene recognition. In their 1999 study with face hybrids, they used a facial expression categorization task where two out of three different expressions (angry, happy, or neutral) were either low-passed (< 8 cycles/image) or high-passed (> 24 cycles/image) filtered images and then combined in a single face hybrid that was presented for 50 ms. On the basis of the participants' choice of expressions, they concluded that the participants categorized expressions by mainly attending to the low-passed component of the hybrid image. Similarly, in the present study, one could have expected participants to turn to LSF for the task at hand, and to recognize the emotions conveyed by those frequencies. Here participants seemed instead to have attended mainly to HFS, and hence their neutrality choices. This could be due to the fact that in this first part of the experiment, as in the following ones, there were no time constraints; thus, observers may preferentially attend to the low spatial frequency components only in data-limited (e.g., tachistoscopic) conditions. Another variable that could account for the results is that these hybrids were different from those used by Schyns and Oliva (1999) in that these always conveyed neutral expression in their HSF.

In Vuilleumier et al.’s (2003) study, the low-passed and high-passed images were shown separately and while the face-specific areas of the fusiform cortex were clearly engaged by the high-passed spatial frequency image, the low-passed spatial frequency image evoked very weak responses. Thus, if our conscious visual experience of a face and its expressions really depends on the activity of cortical (temporal) areas, as suggested by several researchers (e.g., Dolan et al., 1997), then the interpretation of the hybrid (Figure 1, Image E) as neutral instead of happy might reflect the preferred scale or bias in spatial frequency characteristic of neural networks supporting consciousness (e.g., temporal cortex specialized for facial processing). Interestingly, Moutoussis and Zeki (2002) showed in a binocular rivalry experiment, in which some stimuli (houses versus faces) were rendered “invisible” when combined together, that the invisible stimuli could activate their stimulus-specific areas in visual cortex but at much lower level than the visible stimuli; so that unconscious perception may be associated with a weak level of neural activation compared to conscious perception.

A look at Figure 1 will convince that the expression contained in the low spatial frequency image (Image C) can be readily and consciously apprehended when presented alone, but once this image is blended with a neutral expression shown in the rest of the visible spatial frequencies (Image D), the emotional nuance seems to vanish from sight (Image E). One might suspect that this phenomenon simply reflects the fact that only a minor proportion (a few cycles/image) of all the available spatial frequencies in these images carries emotional content, whereas the rest of the image is preponderantly consistent with a neutral expression. This asymmetry in informational content may force the perceptual system to settle for one of two possible interpretations of the image in a winner-take-all process.

Moreover, Schyns and Oliva (1994) have proposed that visual recognition occurs at both coarse and fine spatial scales but, by attending first to the coarse scale, the visual system can get a quick and rough estimate of the input so as to initially activate schemas in memory, while attending to fine information allows subsequent refinement, or refutation of the raw estimate (Hochstein & Ahissar, 2002). Thus, the different informational contents at different levels of the spatial frequencies scale may compete for attention (Navon, 1977), so that the disappearance of the emotion in the present hybrids could reflect a simultaneous (instead of backward) form of visual masking, where the spatial channels carrying the neutral image would effectively mask or attenuate (perhaps due to wired-in cortical biases) the lowest spatial channels and, ultimately, narrow the perceptual/neural processing to the higher range of the spatial scale.

However, as it will become clearer later, the above accounts have explanatory power only by assuming that the winner-take-all effect of the higher range of the spatial scale is confined to the processing localized in the cortical areas. In fact, in light of Vuilleumier et al.’s (2003) results, one should not expect such a competition to take place in the amygdala, since it appears to be insensitive to the information contained in the higher scales. Besides, in 1997, Oliva and Schyns specifically showed that subject who explicitly categorized a scene based on one of the two scales that was functional to the task, nonetheless unconsciously registered the irrelevant one, as this subsequently influenced an explicit recognition test. Indeed, as shown in the next phase (1B) of this experiment, despite the fact that the low-passed emotions are not acknowledged and they do not determine the participants’ choice of emotional labels, they do have clear influences on the observers’ behavior and judgments. Hence, the lowest spatial channels are not masked or filtered out of perception, yet they fail to reach consciousness.

Experiment 1B

In the second phase of the first experiment, I put to test the main hypothesis that hybrid faces, although consciously experienced as having a neutral expression, can at the same time unconsciously influence social judgments of the persons portrayed in these hybrid images. Specifically, as in Berridge and Winkielman's (2003) study, I expected the unconscious emotional expressions to influence a core sense of liking/disliking of each facial stimulus. Thus, I predicted that (1) filtered negative expressions like anger, fear, and sadness would result in ratings towards the *unfriendly* range of the scale, (2) a filtered positive expression like happiness would result in ratings towards the *friendly* range of the scale, and (3) ratings of the fully neutral expression should lie somewhere in the middle of those for the emotional hybrids.

Methods

Participants Thirty-two students (22 females) at the University of Bergen volunteered to participate in a study on facial perception. They were all native Norwegian speakers; mean age = 23.1 (SD = 2.6).

Stimuli Only the hybrid pictures were used. As described above, these included four emotional expressions (anger, fear, happiness, and sadness) for each face, only present in the low spatial frequencies of the image, while the rest of the bandwidth showed a neutral expression, plus one re-constituted broadband neutral expression.

Procedure Participants saw each image, one at a time, centered on a 17 inches computer screen and presented in full-screen mode at a distance of 72 cm so that the size of the images corresponded to 6° of visual angle. Each image remained on screen until the participant made a key press by selecting one of the digit keys on the keyboard labeled from 1 to 5, which led to the presentation of a new image. The task was to indicate "how friendly" each person appeared to the participant (1 being *most unfriendly* and 5 *most friendly*, 3 representing the neutrality point). Stimulus presentations were controlled by SuperLab© software, which also stored each key press. There were two versions of the tests (A and B) so as to keep the session relatively short (i.e., 95 trials). The different expressions were distributed across the two tests in a counterbalanced manner so that every participant saw an equal amount of the same expressions. Sixteen participants were administered the A set of pictures and the rest saw the B set. Each participant was only informed that they would see a series of faces to be rated individually. Nothing was mentioned about the underlying, "hidden," expressions.

Results

Descriptive statistics for each participant were calculated, obtaining mean ratings for each low-passed expression and then performed a repeated-measures analysis of variance on mean ratings as the dependent variable, with expressions (anger, fear, happiness, neutrality, and sadness) as the within-subject variable and sex (female, male) as a between-subjects factor. Preliminary analyses had shown no effect of picture set (A, B) or any interaction with the other factors.

The ANOVA revealed a main effect of expressions, $F(4,120) = 20.8$, $p <.0001$ (Lambda = 83.1; Power = 1.0). As shown in Figure 2, neutral faces were rated close to, but slightly lower (mean = 2.88, SD = .32), than the neutral midpoint. However, as the bars representing 95% confidence intervals indicate, happy faces were significantly rated friendlier than neutral faces and faces with other expressions. In contrast, angry faces were significantly rated less friendly than neutral and afraid faces. Finally, although afraid and sad faces obtained lower friendliness ratings than neutral faces, the differences between these means failed to reach significance. The analysis also revealed a significant interaction of sex and expressions, $F(4,120) = 2.4$, $p = .05$. This was mainly due to differences in women and men's ratings for the happy and angry faces. Men showed the highest mean value for the happy emotion, whereas women gave the lowest ratings for the angry emotion. In general, men tended to give higher friendliness ratings to all of the emotional pictures; however, there was no significant main effect of sex on ratings, $F(4,120) = 0.8$ $p<.38$.

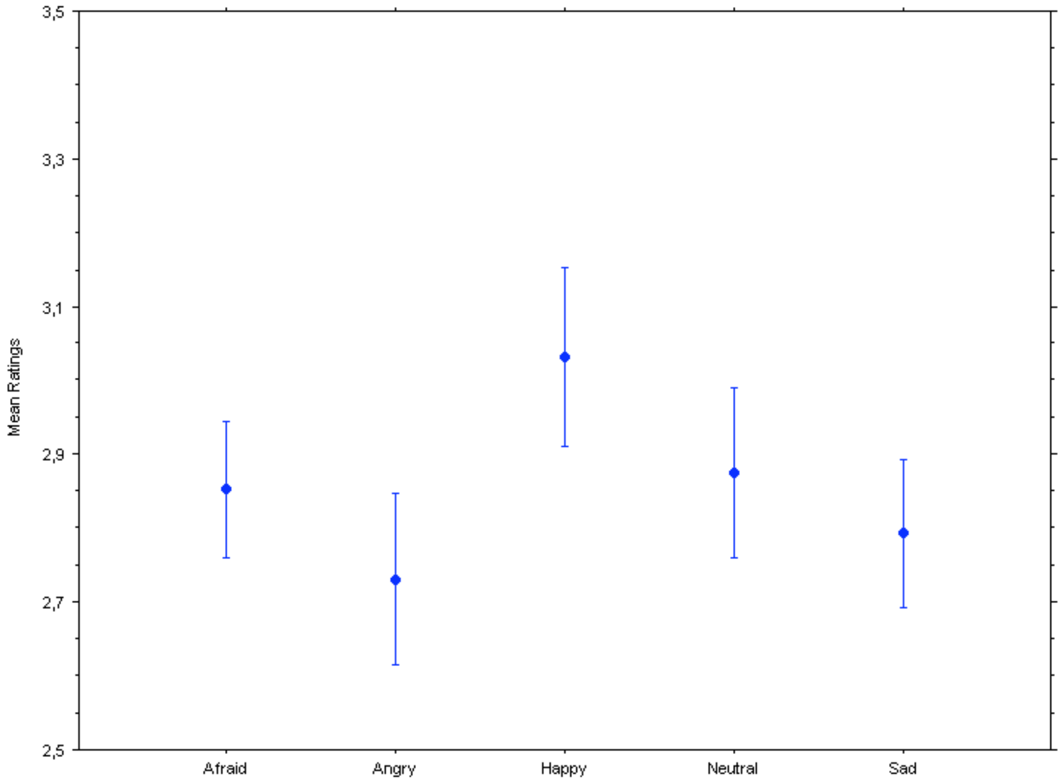

Figure 2. Mean ratings (circles; bars represent 95% confidence intervals) of face hybrids, with emotions in low frequencies only, on the friendliness scale (1-5).

Discussion

Filtered negative expressions of anger led participants to judge these faces as unfriendly. Faces that showed fear or sadness resulted in only slightly lowered judgment of friendliness, whereas filtered positive expressions of happiness resulted in judgments that these faces were friendlier than any other emotional face or than the neutral expression. As expected the neutral expression lay somewhere in the middle of those for the emotional hybrids.

Vuilleumier and colleagues (2003) have shown that the human amygdala is essentially "blind" to most of the visible spatial frequency scale except the lowest (< 6 cycles/image). Given that the hybrid face stimuli used here showed emotions in the same range of low spatial frequencies of Vuilleumier et al.'s (2003) study, I conclude that the hybrids optimally stimulated the amygdala but could only weakly stimulate cortical areas specialized in face perception (e.g., fusiform areas). Indeed, the results of Experiment 1A had shown that the same emotional hybrids used in the present Experiment 1B were consistently judged as neutral or having no clear emotional expression. Following Berridge and Winkielman's (2003) account, I interpret the present results as supportive of the hypothesis that unconscious, emotional expressions influenced a core sense of liking/disliking.

A somewhat expected result of the experiment was that sad and afraid expressions did not reliably differ in their friendliness ratings from neutral faces, and that also neutral rating lay (slightly) under the neutrality point.

Previous research has shown that the amygdala is especially tuned to process expressions of fear (Adolphs et al., 2005; Adolphs, Tranel, Damasio, & Damasio, 1995; Anderson et al., 2003; Das et al., 2005; Johnstone et al., 2005; Morris, Ohman et al., 1998; Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005; Vuilleumier et al., 2003; Whalen et al., 2004; Whalen et al., 1998) but there is also evidence that the amygdala plays a role in the response to expressions of sadness (Adolphs & Tranel, 2004; Blair, Morris, Frith, Perrett, & Dolan, 1999; Wang, McCarthy, Song, & LaBar, 2005), or even to any expression of emotion (Fitzgerald, Angstadt, Jelsone, Nathan, & Phan, 2006; Yang et al., 2002).

The present results would be in line with Vuilleumier et al.'s (2002) following the idea that neutral faces, since ambiguous, should actually be regarded – from an evolutionistic point of view – as much dangerous as both sad and fearful expressions, inasmuch in nature false alarm have less ominous consequences than misses (Whalen, 1998). Thus the three expressions could well have activated a similar "negative" response in the subjects, even though less evident than the fourth expression (anger), which is more directly a sign of threat. However, neither sad nor afraid expressions may be unconditionally judged as unfriendly, since these expressions do not necessarily signal any imminent threat to the observer and, in fact, they could also elicit prosocial responses towards compassion or help (Marsh & Ambady, 2007; Marsh, Kozak, & Ambady, 2007). Consistently, the angry faces, which should always signal threat, caused here a clear shift towards the unfriendly range of the scale.

Women gave overall more negative ratings than men. Differences between the sexes in processing emotional stimuli have often been reported in the literature. Several studies have found that women are generally superior at decoding others' emotions (Montagne, Kessels, Frigerio, de Haan, & Perrett, 2005; Thayer & Johnsen, 2000). It is possible that the women's greater sensitivity to emotional stimuli may have influenced the ratings of the hybrids and that this became particularly clear for some emotions like anger, happiness, and sadness.

Experiment 2

As previously argued, since a neutral expression was always present in the range of spatial frequencies that are invisible to the amygdala, cortical areas might have been biased to perceive only the neutral expression. Thus, as a control condition for the previous experiments, I showed both the low-passed images alone and the high-passed version of each emotion as well. I expected that each emotional expression would be clearly seen in such high-passed images and labeled correctly, but not necessarily so for the low-passed images.

Methods

Participants The participants were 15 female students (mean age = 21.6 years, SD = 2.6) at the University of Tromsø in Norway.

Stimuli The stimuli consisted of the filtered, grey-scale, images of the faces and emotions of the same models seen in the previous experiments. Both the low spatial frequency versions (1-6 cycles/image) alone and the high-spatial frequency images (7-128 cycles/image) alone were used as stimuli. There were a total of 380 trials (190 showing low-passed face images).

Procedure This was the same used in experiment 1A.

Results

Descriptive statistics for each participant were calculated, obtaining percent frequencies of each label for each picture type (high-passed, low-passed) and expression. When looking at the high-passed pictures, participants selected the labels that identified the emotion for 88.9 % (SD= 4.1) of the pictures (range= 73-93 %). However, when these same emotional pictures were low-passed participants selected the correct label only for 36.9 % (SD= 3.3) of the pictures. Hence, the emotion was clearly seen only when emotional information was seen in the higher spatial frequencies.

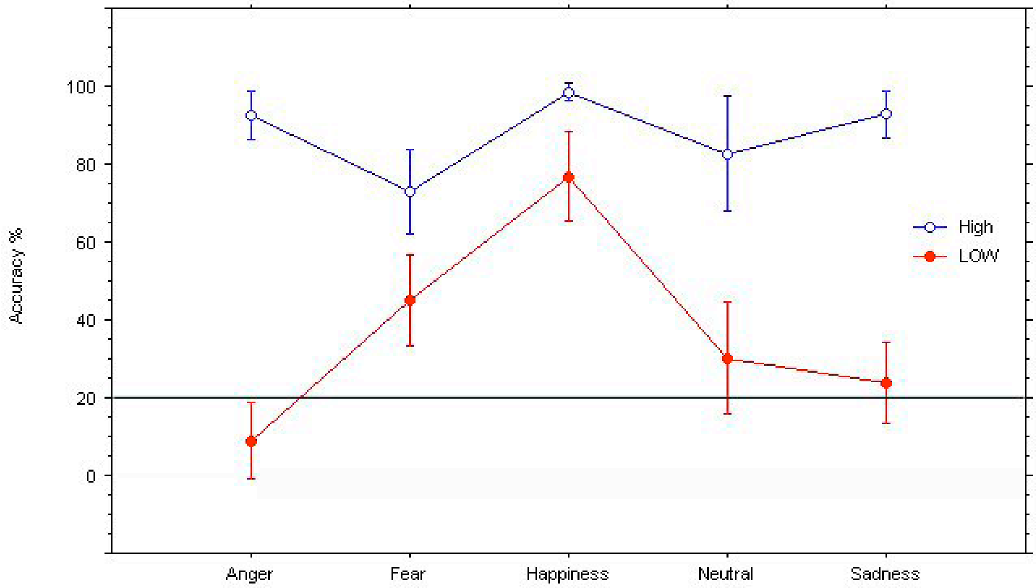

Figure 3. Percent choice of emotional labels consistent with the facial emotion shown in the stimuli from the Karolinska Directed Emotional Faces (filled circles = low-passed images; empty circles = high-passed images; bars represent 95% confidence intervals).

As illustrated in Figure 3, when seeing low-passed images, only the expression of happiness was labeled correctly most of the time (76.8 %; SD = 11.5) and at a rate comparable to those of the high-passed images, where all expressions were correctly matched for at least 73% of the stimuli. However, low-passed expressions of fear were poorly processed (44.9 % correct; SD = 11.6), although the label was correctly selected above chance (i.e., above 20%). Most remarkably, when the low-passed images showed a sad or neutral expression, participants' choices of the respective labels Sad (23.7 % correct; SD = 10.4) or Neutral (30.1 % correct; SD = 14.4) did not differ from chance (in Figure 3: the chance level, represented by the horizontal line at 20% performance, lies within each mean's 95% confidence intervals). The least visible emotion was anger, since participants' choices were actually significantly below chance level (8.9 % correct; SD = 9.8).

Discussion

Emotions in the present low-passed facial images were perceived (at a conscious level) very poorly. Indeed, it appeared that anger was not visible at all to the observers and sad and neutral expressions were reported at a rate that was no more likely than guessing. Only the expression of happiness was reported at a rate within the range of emotions reported for high-passed images, which in turn did not differ from that of the original, broadband, pictures (see Table 1). Remarkably, the expression of fear was correctly labeled less than half of the time when shown in low-passed facial images.

Experiment 3A

A well-established method for proving the role played by a particular brain area in a specific type of processing is to assess the effect of damage to that area (Lurìa, 1966). If the amygdala is implicated in the implicit perception of the low spatial frequency content in the hybrid faces, then damage to the amygdala, should impair the observed unconscious effects of these stimuli.

Hence, a young, female patient (S.S.) was recruited, whom had the anterior part of the left temporal lobe surgically removed as a treatment for a brain tumor, which resulted in a complete resection of the left amygdala. One might expect that only bilateral lesions would result in changes in emotional processing (Adolphs et al., 1995). Yet, there are suggestions from both clinical (Anderson & Phelps, 2001) and neuroimaging studies (Adams, Gordon, Baird, Ambady, & Kleck, 2003; Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Hardee, Thompson, & Puce, 2008; Morris, Friston et al., 1998; Pasley et al., 2004; Phelps et al., 2001) that, compared to its right-sided mirror structure, the left amygdala plays the major role in the processing of some emotions (in particular of fear), and especially so for female individuals (Cahill et al., 2001; Cahill, Uncapher, Kilpatrick, Alkire, & Turner, 2004; Cahill & van Stegeren, 2003; but see Sergerie, Chochol, & Armony, 2008 for a review and for the limitations of such contrasts). I therefore predicted that S.S. would judge the friendliness of the hybrids in a rather different manner than her matched control subjects. Specifically, I predicted that the brain lesion would eliminate the previously described unconscious emotional effects.

Methods

Participants S.S. is a 22.5 years old, female, patient that, in October 2000, at the age of 15, was hospitalized due to tonic-clonic seizures. A CT scan of the brain revealed a hypodense lesion, 2 x 2 cm, located in the left temporal region. A MR scan performed at the Neurology Department of the University Hospital of Northern Norway showed an expansive tumor, which was located anterior and medially in the left temporal lobe. She went through surgery with macroscopic extirpation of the tumor. Histological diagnosis confirmed a pilocystic astrocytoma. A post-operative MR-scan showed no tumor remnants. A relapse was suspected in July 2001 and she was re-operated with resection of the tumor remnants, the remaining part of amygdala, uncus, hippocampus and the corresponding part of gyrus parahippocampalis as well as a modest resection of the lateral cortex. A preoperative Wada test had demonstrated left-sided linguistic dominance and bilateral capacity of memory. In June 2005, the anti-epileptic treatment was ceased. At this time, she worked fulltime as a shop assistant. Due to relapse of epilepsy in September 2005, treatment with carbamazepine was started. In February 2006, a striking impairment of memory function was noticed. A MR-scan in 2007 showed no signs of tumor relapse (Figure 4).

S.S. was subjected to standard neuropsychological examinations at the University Hospital of Northern Norway. These included the Wechsler Memory Scale Revised (WMS-R) (Wechsler, 1987), the Wechsler Adult Intelligence Scale – Third Edition (WAIS-III) (Wechsler, Nyman, & Nordvik, 2003) and the Halstead Reitan Battery (HRB) (Reitan, 1974). On the WAIS-III her test performance was within the normal age range based on Norwegian norms. She achieved the following IQ-scores: Verbal IQ = 86, Performance IQ = 106 and Total IQ score = 94. She achieved the lowest test performance on Verbal subtests (age scaled scores Information = 6, Vocabulary = 7, Similarities = 4, and Comprehension = 6), while Performance subtests were better (Picture Completion = 8, Block Design = 12, Matrix Reasoning = 10, and Picture Reasoning = 17), thus producing no scores on the Performance subtests that could be categorized as impaired. Her long-term memory from daily life seems not to be affected. On WMS-R she achieved a General Memory Index of 78. The Attention/Concentration Index was 112. She achieved better performance on Visual Memory Index (103), than Verbal Memory Index (75). However her percentile scores on delayed memory tests were significantly impaired, with the lowest score on Logical Memory II subtest (1 % raw score = 0) and the highest on the Visual Reproduction II subtest (8 % raw score = 21). On the HRB, S.S. had no scores categorized as impaired, except for the Memory component of the Tactual Performance Test (T-score 35). The overall pattern of scores indicates that S.S. has retained normal attentional functions, psychomotor speed, problem-solving and executive functions, while being severely impaired on tests of delayed memory, especially verbal delayed recall. Fourteen of the female participants that matched S.S. in age (± 3 years) and who were originally recruited at the University of Bergen for Experiment 1B were selected as age- and sex-matched control subjects for S.S.

Stimuli These were the same stimuli used in Experiment 1B.

Procedure This was also the same used in Experiment 1B, with the only difference that S.S. viewed all hybrids in one session whereas the control participants were equally split between those who saw picture set A or B. Again, nothing was mentioned about the "hidden" emotional expressions.

Results

Descriptive statistics were calculated, obtaining mean ratings for each low-passed expression. Control participants' mean performance was averaged for each condition and 95% confidence intervals were computed. When S.S.'s mean performance was compared to that of the controls, as illustrated in Figure 5, it appeared that the patient's ratings of hybrids containing fear or sadness were placed at exactly the neutrality midpoint of the scale. In contrast, S.S.'s ratings for the other emotions were within the confidence intervals' range of the controls.


A

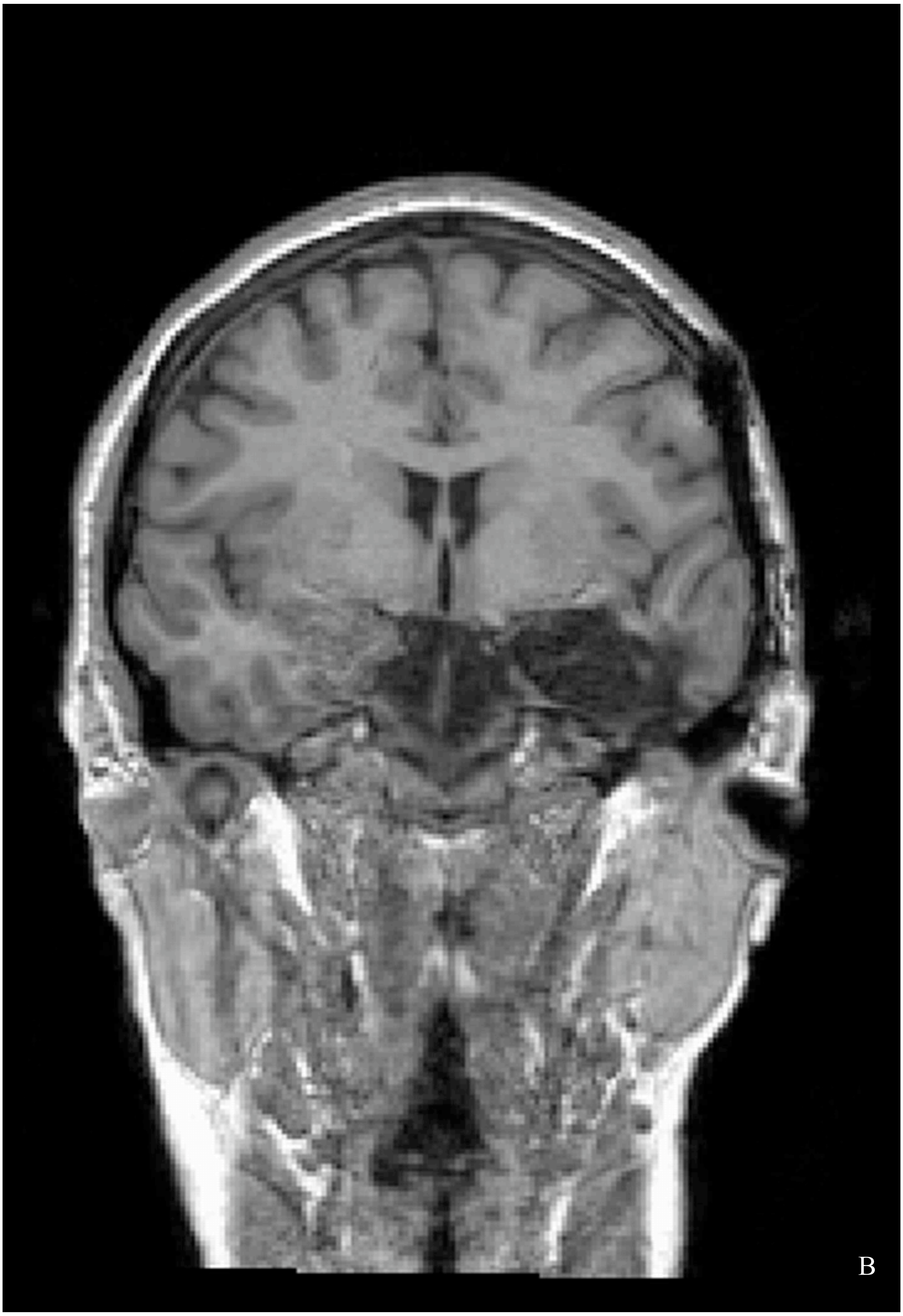

Figure 4. Sagittal (A) and coronal (B) T1W MRI shows the resected area of left temporal lobe > 4 cm from anterior pole.

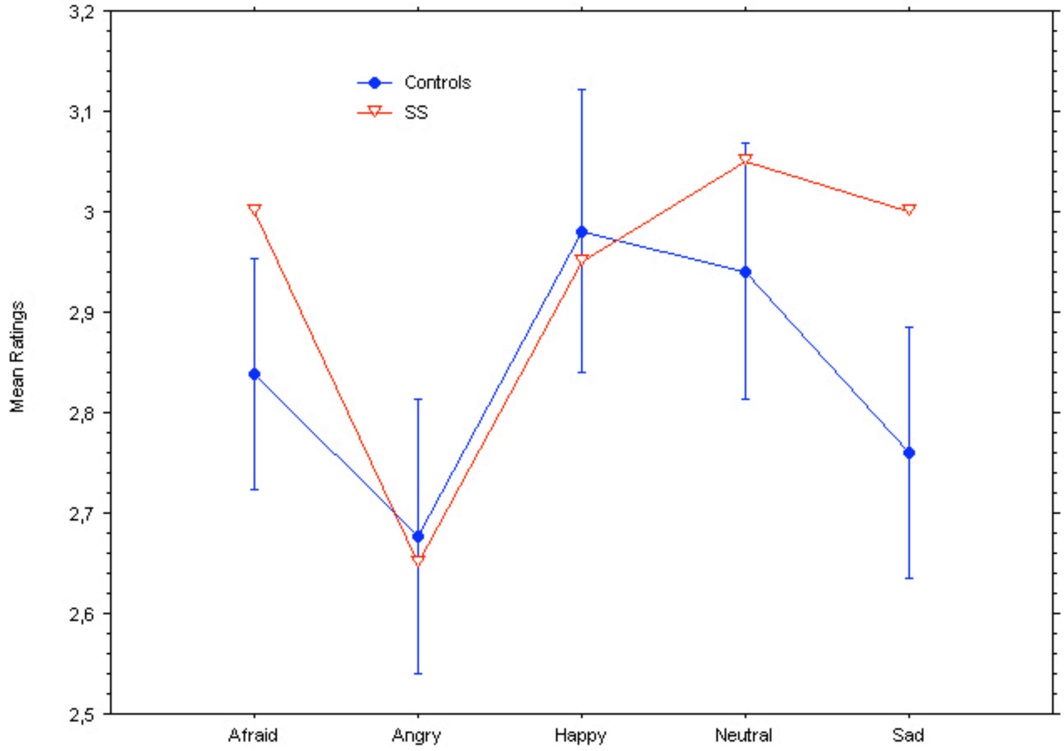

Figure 5. Mean ratings of face hybrids, with emotions in low frequencies only, on the friendliness scale (1-5). S.S. (triangles) is a patient with a left temporal lobe resection that included the amygdala, and Controls (circles; bars represent 95% confidence intervals) are 14 women matched by age to S.S.

Discussion

As predicted, S.S.'s judgments of the hybrids' friendliness were not the same as those of her matched control subjects. Specifically, two of the low-passed negative emotions (i.e., fear and sadness) that had triggered a clear unconscious emotional response in the control participants, as reflected in their negative (unfriendly) ratings, had no effect on S.S., who instead judged these faces as neither friendly nor unfriendly. Thus, it would seem that the left anterior temporal lobe resection had also eliminated a normal, albeit unconscious, response to the emotional information contained in the low spatial frequencies. Since the left amygdala was completely removed by the surgery and given that the hybrid stimuli carry information that would optimally stimulate the amygdala but only weakly the cortical areas, I suggest that the present findings are consistent with a role of the left amygdala in the implicit perception of some negative emotions. In the next experiment, I assessed whether S.S.'s explicit emotional labeling of broadband (unfiltered) facial expressions also differed from her matched controls.

Experiment 3B

The evidence that lesions to the amygdala can result in deficit also in the conscious judgment of emotions has been inconsistent, either in terms of establishing the presence of such impairment or in identifying the compromised emotions.

Some of the clinical studies of patients with bilateral damage (Adolphs & Tranel, 2003; Adolphs, Tranel, Damasio, & Damasio, 1994; Calder et al., 1996; Graham, Devinsky, & LaBar, 2007) have indicated that explicit recognition of facial expressions can be impaired in some of these patients. Some degree of impairment has also been found in some patients with unilateral lesions of the amygdala (Adolphs, Baron-Cohen, & Tranel, 2002; Anderson, Spencer, Fulbright, & Phelps, 2000; Fowler et al., 2006), as well as possible changes in these patients' subjective feeling and expression of fear (Sprengelmeyer et al., 1999).

At the same time, patients with apparently very similar brain lesion profiles can either show or fail to show impairment in the explicit recognition of emotion in face stimuli (Hamann et al., 1996). Response deficit can even vary across testing sessions within a given patient. For example, patient S.P. consecutively showed impaired (Adolphs et al., 1999) and unimpaired (Anderson & Phelps, 2000) recognition of anger across two occasions a few months in time from each other, where the only difference between the two tasks was the number of stimulus repetitions. In contrast, patients with amygdala lesions do not seem to have problems in recognizing positive expressions of happiness (Adolphs & Tranel, 2004; Adolphs et al., 1994; Calder et al., 1996).

Evidently, the explicit recognition of facial emotion does not seem to have an absolute dependence on the amygdala. However, Hamann and colleagues (1996) also pointed out that whether the damage occurred early in life could play a crucial role in the emergence of an emotional deficit. Another variable to consider is that of patients' gender, since some studies have suggested that the amygdala's functional role in emotion may be more left lateralized in women than in men (Cahill et al., 2001; Cahill et al., 2004; Cahill & van Stegeren, 2003).

Thus, based on the above evidence, it is difficult to predict whether patient S.S., who showed decreases in the unconscious effects of facial expressions of fear and sadness, would also show abnormality in conscious judgments of the same emotions. However, I was led to predict that S.S. would be impaired in conscious judgments of emotion, based on (1) the fact that the tumor revealed itself in adolescence and it had probably already been developing during childhood; and (2) the suggestion that the role of the left amygdala in emotional processing is particularly expressed in women.

Methods

Participants S.S. and 10 female control participants, matched by age to S.S. (± 3 years) and recruited among students at the University of Tromsø.

Stimuli These were the original (broadband) stimuli selected from the Karolinska Directed Emotional Faces, also used in Experiment 1A, consisting of 190, gray-scale, close-up photographs of emotional and neutral faces.

Procedure This was the same as in Experiment 1A, where participants matched, by pressing a key indicating an emotional label (1 = Neutral; 2 = Happy; 3 = Afraid; 4 = Sad; 5 = Angry) to each of the 190 images.

Results

Descriptive statistics for the participants were calculated, obtaining percent frequencies of each label for each pictured emotion as well as 95% confidence intervals around the means of the control group. Comparisons between consistencies in label choice of S.S. and her matched controls are illustrated in Figure 6. This shows that the normal participants selected the labels that identify the target emotions (according to the Karolinska Directed Emotional Faces system) for more than 90% of the pictures within each emotional category.

S.S. showed more inconsistent choices than her matched controls, since she chose the same label significantly less frequently for the facial expressions of fear and anger. Most impressively, S.S. used the label Afraid in only 74.5% of the cases for faces where actors intended to express fear, whereas the control group chose this label on average 93.3% of the time. Also impressively, both S.S. and normal participants chose the label Happy in 100% of the occasions for the faces where actors intended to show a happy expression.

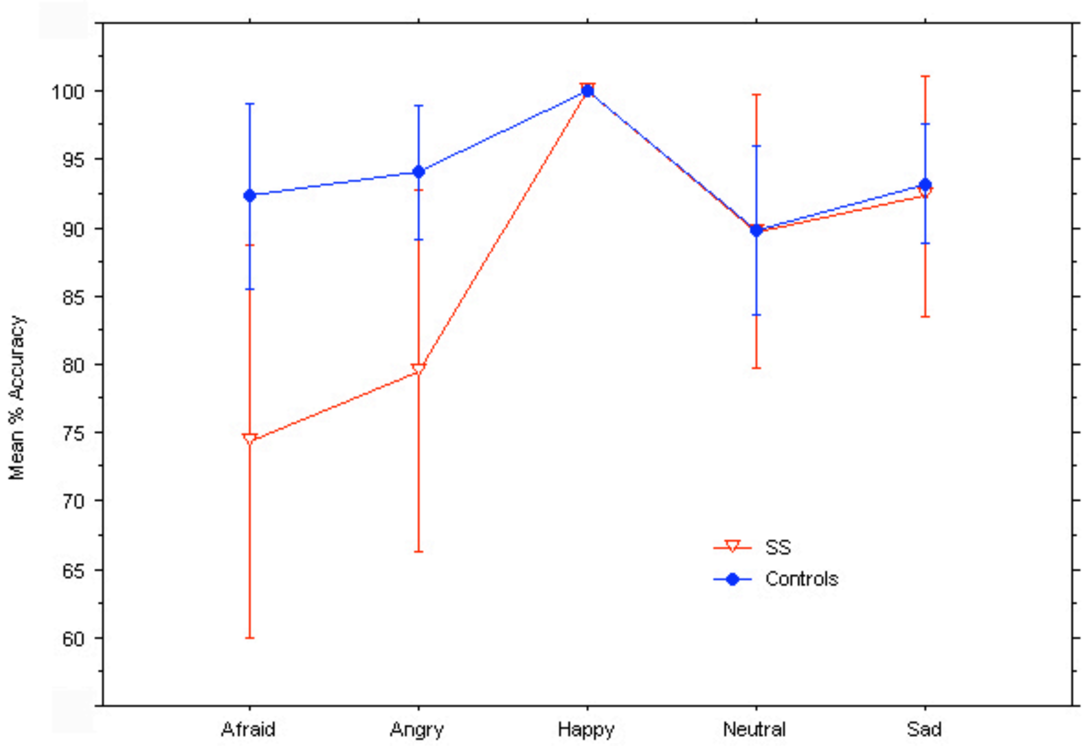

Figure 6. Percent of choice of emotional labels consistent with the facial emotion shown in the stimuli from the Karolinska Directed Emotional Faces (broadband pictures). S.S.'s choices (triangles) are compared to those of 10 female control participants (circles; bars represent 95% confidence intervals).

Discussion

Consistent with these tentative predictions, S.S. showed more variable conscious judgments of facial emotions, showing less accuracy in the choice of Angry or Afraid labels. Thus, effects of a tumor developing early in life, combined with a special role of the left amygdala in supporting representation of fear in a female patient, might all have contributed in the significantly different response of the patients compared to other girls of her own age.

One should note that in the present experiment the unfiltered photos were exclusively used and that the broadband information was consistent with a single emotional interpretation. Hence, the patient's attenuated ability to recognize expressions of anger or fear cannot be attributed to the absence of emotional information that could stimulate cortical areas associated with the conscious appraisal of emotions. On the contrary, it would seem that the absence of the perceptual constraint normally exerted by the unconscious processing has made the rest of the system unable to settle in a consistent manner for a conscious interpretation of the seen stimuli.

Finally, one should note that the patient's lesion included several cerebral structures beside the left amygdala like part of the hippocampus, uncus, and parahippocampal gyrus. Hence, one should have caution in concluding that the present findings with S.S. are the direct result of the absence of just the left amygdala. However, we know from animal studies (LeDoux, 1996) that of all the areas included in the lesion, damage to the amygdala is the likely cause of a deficit in the recognition of emotions (in particular, fear). Moreover, the fMRI study by Vuilleumier et al. (2003) clearly showed that of the above named structures only the amygdala showed significant activations for low-passed images of facial expressions of fear. Thus, we can conclude that the present findings with expression of fear most likely reflect the loss of functions that are dependent on the (left) amygdala.

While these results were clearly in line with a role of the amygdala in the unconscious processing of fear, the performance of S.S. showed dissociated conscious and unconscious responses to the expressions of anger and sadness. In particular, S.S. responded unconsciously to angry facial expressions as the normal participants did but, differently from these, she was unable to select correctly the Angry emotional label to the broadband pictures. In contrast, S.S. correctly matched the Sad emotional label to the broadband pictures but her unconscious response to sad facial expressions (i.e., in judgment of friendliness) was absent.

The present pattern of dissociations between conscious and unconscious effects of specific emotions rather than indicate an equivalently complex pattern of the amygdala's role for the *unconscious* and *conscious* response to the same emotions, more plausibly seems to indicate an idiosyncratic combination of additional damage outside the amygdala, together with the different age at which the damage was sustained (Hamann & Adolphs, 1999), the functionality of the remaining contralateral amygdala, and the personal compensatory mechanisms developed by the patient. Patients with damaged amygdala may use compensatory cognitive mechanisms (heuristics) such as facial feature analysis, or quantity of eye white for instance, as an aid to facial expression recognition. This would be possible especially whenever the time at their disposal is quite long, or even unlimited as in the case of these experiments. This could give rise to the inconsistencies in behavioral measures seen both within and between patients (Graham et al., 2007).

General Discussion

Our mental life is colored and enlivened by conscious, "felt", emotions that we call feelings. However, just like perception, decisions, and reasoning involve a great deal of cerebral activity that we are not able to access consciously, also felt emotions might be the end-product of a great deal of physiological activity that takes place at an unconscious level. What remains unclear is the fate of such emotional processes when they fail to reach awareness: Are they necessarily excluded from the causality of our behavior, ideas, and choices? Or may they subtly affect the way we interact with the physical and social world?

The evidence presented here with healthy participant and one brain-damaged patient, with the use of hybrids, suggests that amygdala is involved in the unconscious emotional processing that influences in predictable ways participants' social judgments as well as their explicit interpretation of facial expressions.

While Vuilleumier et al. (2003) showed that the human amygdala appears to be "blind" to most of the visible spatial frequency scale except the lowest, Vuilleumier et al. (2004) showed that in absence of the amygdala, the fusiform reacts to faces irrespectively of emotional expression. Hybrid stimuli would seem to neither interfere nor rule out the influence of other parts of the neural system. In fact, in these stimuli, the low-passed emotional information is a constituent part of the image, fully available at all times and (apparently) to all visual areas as well as included in the focus of attention. Hence, revealing unconscious influences of the present stimuli would strongly support the conclusion that the emotional visual information simply cannot access consciousness. In the present study, when presented with a hybrid stimulus, the unconscious system would register what is within its visible bandwidth (for instance, the expression of fear) but – paradoxically – the conscious system would be alerted to process what, in its visible bandwidth, is a neutral expression. Consequently, the hybrids can result in simultaneous but differing implicit and explicit perceptions. Remarkably, such a dissociation and unawareness of the emotional content can occur despite each hybrid face is fully attended.

People presented with pictures of emotional faces containing only the low spatial frequency constituent, labeled the expression of fear less than half of the times, and were not able at all to "see" the expression of anger. Moreover, people judged[3] the hybrid pictures as neutral. Nevertheless, these same stimuli influenced predictably social judgments about the friendliness of the faces. This unconscious influence was eliminated for fear and sadness in a patient where the anterior portion of the temporal lobe (which includes the amygdala) had been surgically

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[3] Pessoa, Japee, and Ungerleider (2005) have come with some challenge to the subjective criterion for the determination of unconsciousness described above and used in this study as percentage correct measures can be skewed by response bias. They made use of a more objective algorithm from signal detection theory. According to this paradigm, a signal is considered undetected if it lies in the area under the line corresponding to the ratio between the number of hits and the number of misses.

removed. Finally, the same patient had also reduced consistency in her attributions of fear or anger towards wholly (unfiltered) emotional faces. Even though S.S. showed some inconsistent relationship between the damage in the left anterior temporal lobe and conscious versus unconscious processing of some emotion, for the emotion that mostly and most strongly has been connected to the amygdala, fear, the results were clearly in line with this structure having a role in unconscious processing.

Based on these results, this study suggests that the amygdala processes facial emotional information present in the low spatial frequency bandwidth and that this remains unconscious; however, this unconscious information, these "unfelt" emotions, influence behavior and, normally, modulate how emotional information is perceived and categorized explicitly.

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