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Neural Representation of Faces in Human Visual Cortex: the Roles of Attention, Emotion, and Viewpoint

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1 Introduction

Faces constitute a special class of visual stimuli not only because we possess expert visual skills and specialized brain areas to recognize them, but also because we can extract a rich set of socially and affectively important information from them in a seemingly effortless manner. Abundant research conducted in cognitive psychology, neuroscience, and clinical neuropsychology has provided an elaborate model of the complex functional architecture underlying these different aspects of face processing, each presumably associated with specific neural substrates that are interconnected all together within a large-scale distributed network (Grüsser and Landis 1991). Thus, many influential neurocognitive models have proposed that face recognition may proceed along a series of distinct stages organized in a hierarchical stream of processing (Bruce and Young 1986; Haxby et al. 2000), from low-level visual analysis subserving the detection and organization of facial features, up to higher-level processes allowing the storage and retrieval of personal information and other associative functions (Fig. 1a). Furthermore, some dissociations in recognition performance in healthy subjects, as well as neuropsychological deficits observed in patients with focal brain lesions, have led to the idea that different processing pathways might be responsible for extracting identity-related information versus other facial features related to emotional expression, eye gaze direction, or speech lip motion, and that such pathways might operate in parallel (Bruce and Young 1986; Grüsser and Landis 1991). To what extent these different processing streams may interact to influence each other, and how the different kinds of information may eventually be unified in a single face percept, are two fundamental questions that still remain to be determined.

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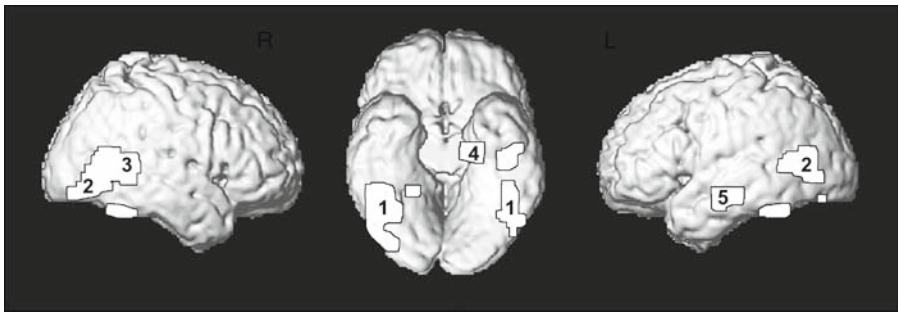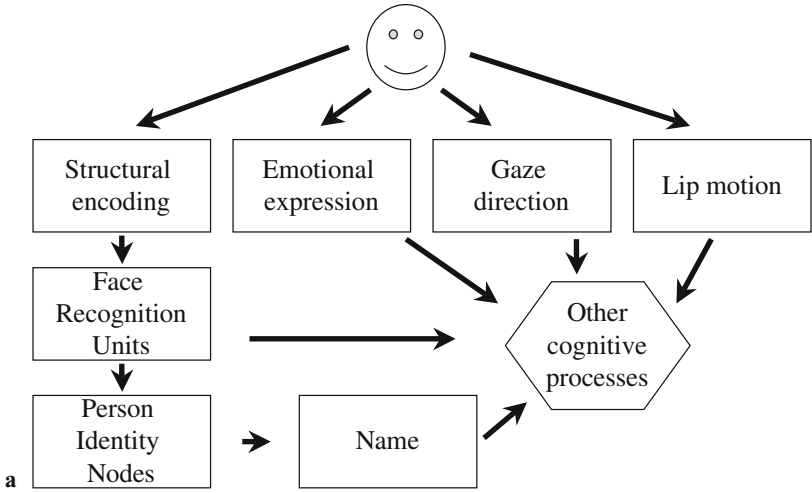
Fig. 1. **a** Traditional cognitive model of face processing derived from Bruce and Young (1986), in which identity and expression are processed along pathways of separate serial stages. **b** Network of brain areas typically activated by contrasting faces > other visual objects in fMRI, bilaterally but with variable hemispheric asymmetry, including (1) fusiform cortex, FFA; (2) lateral occipital cortex, OFA; (3) superior temporal sulcus, STS; (4) amygdala; (5) anterior lateral temporal cortex

Recent progress in functional brain imaging has allowed a tremendous refinement of our knowledge of the anatomy of the human face recognition system, and its operating properties. In particular, a cortical region in the human fusiform gyrus has been identified as critically implicated in face processing across a variety of studies using positron emission tomography (PET) (Sergent et al. 1992; Haxby et al. 1994) or functional resonance imaging (fMRI) (Kanwisher et al. 1997; McCarthy et al. 1997). This region is commonly referred to as the "fusiform face area" (FFA), and generally thought to play a major role in the detection as well as the discrimination of individual faces (Gauthier et al. 2000; Grill-Spector et al. 2004). The FFA is consistently activated by pictures or line-drawings of human faces more than by any other categories of visual objects or scenes, and its activation correlates with face perception during the presentation of ambigu-

ous stimuli, perceptual rivalry, or even mental imagery. However, several other brain regions, within and outside the visual system, are also differentially activated by faces relative to other visual objects (Sergent et al. 1992; Haxby et al. 2000). These regions include the lateral occipital face area (OFA), the superior temporal sulcus (STS), the amygdala, plus other areas in the temporal poles and ventromedial prefrontal cortex (Fig. 1b). In accord with previous cognitive models (Bruce and Young 1986), it has been proposed that the FFA might be crucially involved in processing visual features carrying face identity information, which should remain relatively invariant across changes due to expression, viewpoint, or pictorial format. Conversely, STS and amygdala might be more important for processing changing or dynamic features in faces, such as expression or gaze, which are socially and emotionally relevant and shared across many different identities (Haxby et al. 2000). The role of other brain regions still remains largely unsettled (for extended neuroanatomical model, see Gobbini and Haxby 2007).

However, although there is now abundant evidence that face identity is processed in the FFA and that facial expression is processed in amygdala and STS, there is also increasing evidence that these two aspects of face recognition might not be entirely encapsulated and separately implemented in these different regions, as previously proposed by cognitive models. In particular, the present chapter will focus on two series of recent brain imaging studies showing that face representation in the FFA is not totally insensitive to emotional expression and not totally independent from viewpoint. By illustrating how different regions in the face recognition system may not carry out specialized processes alone but dynamically interact with each other, these findings call for a refinement of the current neurocognitive models of face recognition, which have considered only a serial feedforward mode of information processing but ignored the role of more interactive and re-entrant mechanisms.

2 Emotional Influences on Face Processing in Fusiform Cortex

A number of brain imaging studies have consistently shown that the activation of sensory cortical areas can be enhanced for emotionally relevant stimuli, including not only faces (Morris et al. 1998a; Vuilleumier et al. 2001) but also pictures (Lane et al. 1999; Sabatinelli et al. 2005) or voices (Grandjean et al. 2005). For instance, such increases may arise in the visual cortex with faces displaying fearful relative to neutral expressions, or with photographs containing aversive relative to more mundane scenes. A negative emotional content generally appears much more efficient in producing such increases, particularly for faces (Surguladze et al. 2003), although positive arousal can sometimes produce similar effects (Mourao-Miranda et al. 2003; Sabatinelli et al. 2005).

Such increases in response to emotional (e.g., fearful) faces have been observed in various regions such as the fusiform cortex, posterior inferior and lateral temporal cortex, as well as in very early occipital areas such as the primary striate

cortex (area V1) (Morris et al. 1998a; Vuilleumier et al. 2001; Pessoa et al. 2002b). However, these effects also exhibit a relative selectivity depending on the category of the emotional stimulus. For instance, in an fMRI study (Vuilleumier et al. 2001), where pictures of faces with either a fearful or neutral expression were presented together with pictures of houses, fear-related increases were found to arise selectively in the lateral fusiform region that also showed face-specific responses, corresponding to the FFA. However, a nearby region in the parahippocampal cortex showing house-specific responses (i.e., the parahippocampal place area, PPA) was not modulated by the emotional expression of faces seen with the houses (Fig. 2). This finding suggests that emotional signals received from faces can produce a selective influence on the cortical representation of faces in the FFA, and that face identity processing in fusiform cortex may not be purely encapsulated and immune to interactions with processes involved in face expression recognition.

Moreover, the modulation of the FFA by emotional expression of faces was found to arise in the same voxels in the cortex as the modulation produced by selective attention to faces (Fig. 2). In the same fMRI study using faces and houses presented together (Vuilleumier et al. 2001), we could compare the effect of expression and the effect of selective attention by manipulating attention and emotion orthogonally, while keeping the task identical across all conditions. While visual arrays always contained two faces (fearful or neutral expression) and two houses, the observers had to concentrate on two pictures only (either the vertical or horizontal pair) on each single trial, in order to make same/different judgments for these two pictures. Thus, we could measure the differential impact on neural responses due to fearful *vs* neutral emotional expressions when faces were either in the focus of attention, or outside the focus of attention. Three major results were found. First, the effects of emotion and attention on FFA responses were additive to each other, with a similar enhancement to fearful expression when faces were in the focus of attention (for a same/different judgment) and when they were outside the focus of attention (with a same/different judgment being made on houses instead). Second, the effect of emotion from ignored faces arose in the FFA despite a strong reduction in activity due to inattention when observers concentrated on the houses. Third, the peak of emotional effects in the FFA was exactly the same as the peak of attentional effects, and fully consistent with the location of face-selective areas reported in previous studies. This pattern of results has then been replicated in two further fMRI studies using the same paradigm in different subjects (Bentley et al. 2003; Vuilleumier et al. 2004).

Taken together, these findings suggest that FFA activity may be controlled by top-down influences imposed not only by attentional systems (presumably mediated by fronto-parietal cortical networks), based on current task demands (Wojciulik et al. 1998), but also by emotional systems extracting the potential affective or social value of faces even when these are not currently task-relevant or in the focus of attention. Such emotional effects on neural responses of the FFA might result in a more salient representation of faces with particular affec-
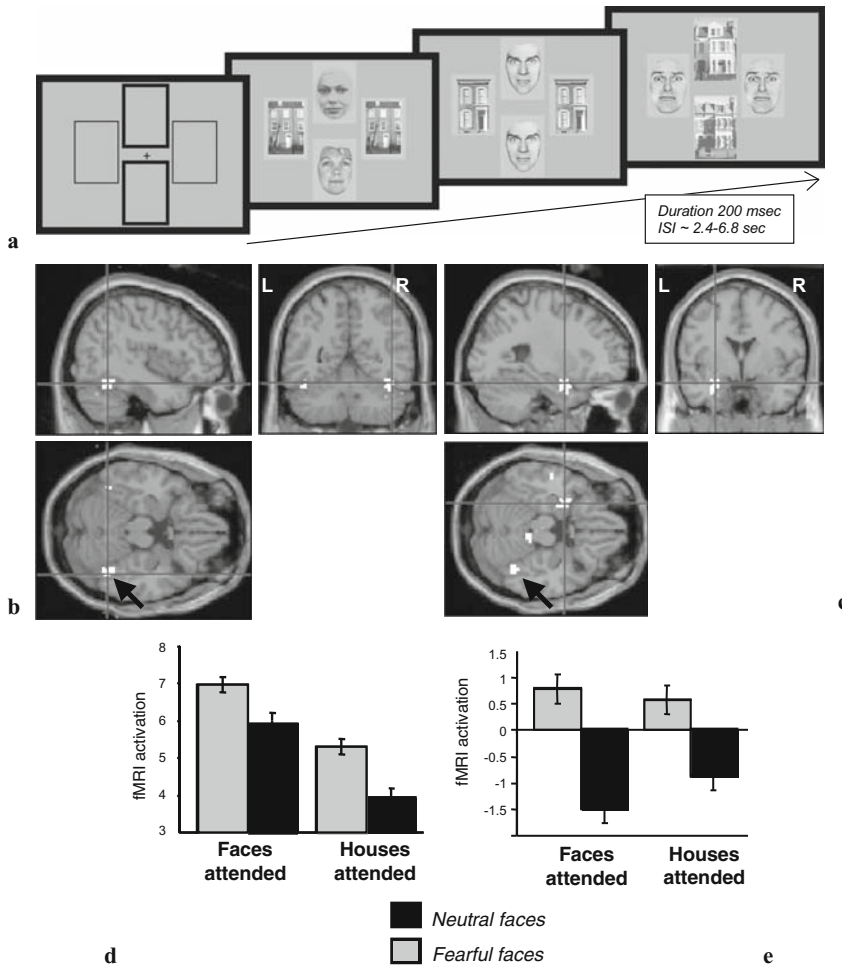
FIG. 2. **a** Paradigm used to compare the effects of emotion and attention in responses to faces. On each trial, two faces and two houses are presented together, aligned in either vertical or horizontal pair, while observers are instructed by an initial cue to concentrate only on one pair of locations (here vertical). Faces can be neutral or fearful. **b** Effect of attention to faces versus houses, resulting in an increased activation of both right and left FFA. **c** Effect of fearful versus neutral expression in faces, resulting in a similar increase in the FFA (bilaterally but stronger on the right, see arrow), in addition to an activation of the amygdala (bilaterally but stronger on the left as shown here). Average parameter estimates of activity (±SE) are shown across all conditions of attention and expression for (**d**) right FFA and (**e**) left amygdala

tive values, such as threat, and thus provide a plausible neural substrate for attentional biases towards emotional faces, as observed in several behavioral studies (Vuilleumier and Schwartz 2001a, b; Fox 2002; Vuilleumier 2005). For instance, as compared to neutral faces, faces with threat-related expressions tend to produce faster detection in visual search (Fox et al. 2000; Eastwood et al. 2001) or visual orienting paradigms (Mogg et al. 1994; Pourtois et al. 2004).

Our fMRI data also accord with neurophysiological recordings in the monkey showing that some face-selective neurons in temporal cortex may show enhanced responses to faces with particular expressions (Sugase et al. 1999). However, in neurophysiological recordings, other face-selective neurons in the same cortical area may also show enhanced responses to faces with a particular identity. Unfortunately, the spatial resolution of fMRI is still insufficient to determine whether distinct neuronal populations in the human FFA might be sensitive to facial expression or identity, and thus differentially modulated by emotion and attention. In the future, higher-field MRI and voxel-by-voxel analysis of activated regions within fusiform cortex might provide better insights into the fine cortical organization of distinct neuron clusters with different processing preferences. Some recordings in STS in the monkey have shown that identity-selective and emotion-selective neurons might be arranged in distinct clusters along the ventral and dorsal banks of STS, respectively (Hasselmo et al. 1989). However, it is still unclear what is the homology between these cortical visual areas in monkeys and humans.

3 Distant Sources of Emotional Signals from the Amygdala

Interestingly, neurophysiological data in the monkey suggest that an emotional modulation of face processing in visual cortex might occur only after some delay following the initial face-selective responses. Thus, the first neuronal activity (<100 ms) might primarily code for global stimulus category (face *vs* other object) whereas subsequent activity (100–150 ms) might code for finer information such as expression and/or identity (Sugase et al. 1999). This delayed modulation has therefore been attributed to some re-entrant influences from distant brain areas responsible for processing affective or familiarity information. In particular, emotional influences on visual cortex might be provided by the amygdala, which is known to be critically implicated in emotional processing, especially threat, and to give rise to feedback projections to all levels of the ventral visual cortical stream (Amaral et al. 2003). These anatomical connections might allow the amygdala to have substantial modulatory control over sensory processing at several stages along the visual pathways.

In agreement with this idea, our fMRI results revealed that the amygdala could respond to fearful faces irrespective of whether observers had to concentrate on faces or houses (Vuilleumier et al. 2001). Thus, amygdala activation was not significantly influenced by attention in this paradigm, despite the robust effect of attention on visual cortex (Fig. 2). These data suggest that emotional responses in the amygdala may not rely on face processing taking place in the fusiform

cortex, consistent with other findings that the amygdala can still be activated by threat cues in some conditions when observers are not aware of these cues (e.g., during masking (Morris et al. 1998b; Whalen et al. 1998), rivalry (Pasley et al. 2004; Williams et al. 2004), or blindsight (Morris et al. 2001; Pegna et al. 2005)). Yet it is possible that the amygdala responses can also be influenced by attention in other conditions (Pessoa et al. 2002a, b). More importantly, these results also suggest that amygdala activation to fearful expression might provide the primary source of emotional modulation on the FFA, leading to the persistent and additive enhancement regardless of the concomitant attentional modulation.

To test directly this idea of amygdala influences on the FFA, we conducted another fMRI study using the same paradigm with face-and-house pairs as above, but now in patients with amygdala lesions (Vuilleumier et al. 2004). In this study, two groups of patients with medial temporal lobe sclerosis were compared, half in whom the lesions affected both the amygdala and hippocampus, and the other half in whom the lesions affected the hippocampus only and spared the amygdala. Patients with hippocampus damage but intact amygdala showed a normal increased activation for fearful faces in fusiform and occipital cortex, whereas patients with additional amygdala damage showed no differential responses to fear in the FFA. In addition, parametric analyses revealed a linear inverse correlation between the severity of amygdala sclerosis and the enhancement of ipsilateral fusiform activity by fear, consistent with amygdala connections projecting mostly to ventral visual cortical pathways within the same hemisphere (Amaral et al. 2003). By contrast with this lack of emotional effects, both groups of patients showed a normal modulation of the FFA by attention to faces as compared to attention to houses. These findings therefore strongly support the idea that the amygdala can influence activity in distant visual areas and boost the representation of faces in the FFA based on their affective significance.

Face processing in the FFA is therefore likely to be partly controlled by "feedback" or re-entrant signals from the amygdala (Vuilleumier 2005), in addition to concomitant influences from other control systems in fronto-parietal attentional networks and probably still other sources yet to be identified. These modulatory influences from the amygdala may facilitate the detection of affectively significant information and enhance attention towards these salient stimuli, but also modify the establishment or retrieval of memory traces associated with emotional faces. In agreement with a role in detection and attention, previous behavioural results have shown that amygdala lesions in humans will abolish the typical attentional biases towards stimuli with threat versus neutral meaning. However, the functional consequences on memory still remain to be fully explored.

4 Distinct Visual Cues for Processing Faces in Fusiform Cortex and Amygdala

The fact that the amygdala might still respond to fearful faces presented outside the focus of attention (Vuilleumier et al. 2001), or sometimes even outside awareness (Morris et al. 1998b; Whalen et al. 1998; Pasley et al. 2004; Williams et al.

2004), has commonly been explained by the existence of distinct neural pathways for processing emotional cues. In particular, based on animal studies of fear-conditioning (LeDoux 2000) and studies of patients with blindsight after destruction of their primary visual cortex (Morris et al. 2001; Pegna et al. 2005), it has been hypothesized that the detection of threat-related stimuli might not depend on elaborate cortical analysis but rather implicate a fast subcortical pathway conveying only "quick and dirty" signals (Morris et al. 1999; LeDoux 2000). This subcortical pathway might involve direct visual inputs to the superior colliculus and/or pulvinar nucleus of the thalamus, bypassing early cortical stages of processing from geniculo-striate pathways to the ventral occipito-temporal stream (Morris et al. 1999, 2001). However, although this subcortical route might play an important role in blindsight or cortical blindness, its connections to the amygdala still remain controversial in humans (Pessoa 2005), and "quick and dirty" information might also reach the amygdala through a first volley of bottom-up inputs within the visual cortex prior to full perceptual analysis and attentional selection (Vuilleumier 2005).

In any case, a preservation of amygdala activation to stimuli perceived under poor conditions of visibility would make sense in order to afford rapid and efficient response to threat. Moreover, subcortical visual pathways are known to carry only crude visual information with low-spatial frequency, extracted from magnocellular pathways, whereas finer visual information in high-spatial frequency from parvocellular pathways project exclusively to cortical areas in the ventral occipito-temporal stream (Merigan and Maunsell 1993; Sahraie et al. 2002). Using fMRI in healthy subjects, we therefore tested for any differential sensitivity of amygdala and fusiform cortex to low-spatial frequency (LSF) and high-spatial frequency (HSF) (Vuilleumier et al. 2003a). Observers were presented with photographs of faces displaying either a neutral and fearful expression, and containing either low-pass, high-pass, or intact (broad-band) spatial frequency content (Fig. 3). Activation of the FFA was found to be generally reduced for LSF faces relative to intact or high-pass faces, irrespective of expression, consistent with an important role of fine edge and texture information in driving activity of temporal visual cortex. By contrast, amygdala responses to fearful expression were greater for both LSF and intact faces than for HSF faces, despite the reduced response to HSF in the FFA.

This dissociation suggests that amygdala and FFA may extract different spatial-frequency content in faces, which may play distinct roles in expression and identity processing, respectively (Vuilleumier et al. 2003a). This would be consistent with behavioral studies showing different perceptual biases to LSF and HSF cues when observers must categorize the identity and expression of "hybrid" stimuli, in which different faces with different content are superimposed (Schyns and Oliva 1999).

Remarkably, however, we found that the FFA was increased by fearful relative to neutral expression only with LSF (and intact) faces, but not with HSF, even though the FFA was generally less sensitive to HSF than LSF cues (Vuilleumier et al. 2003a). This pattern provides further support to the idea that such
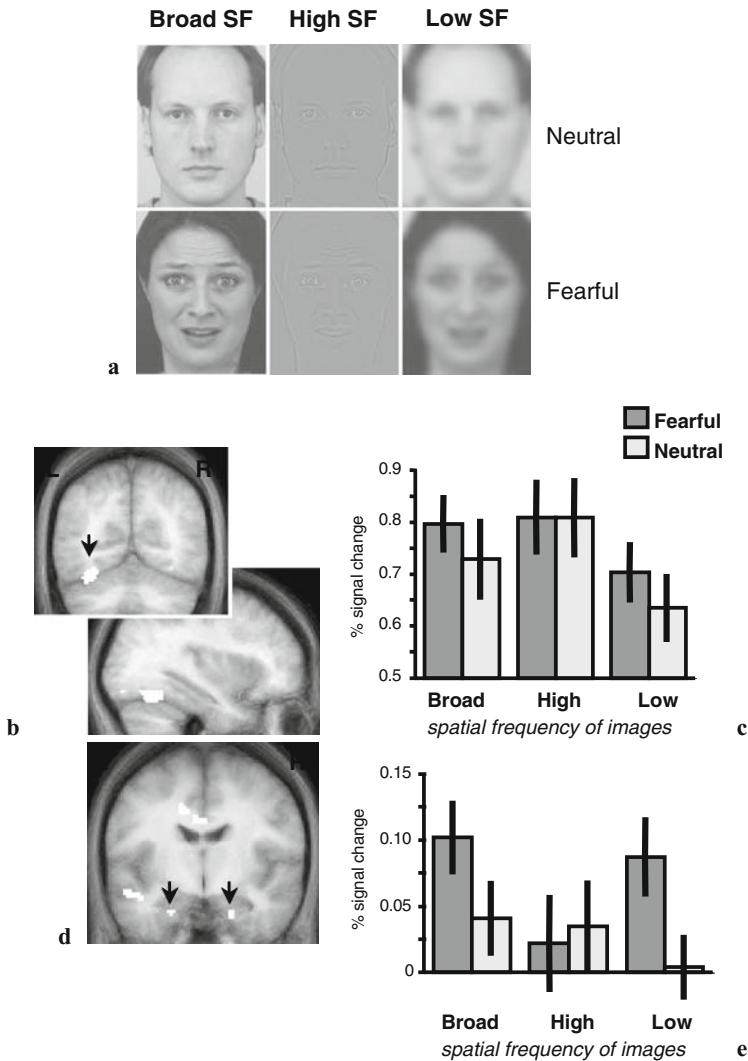
Fig. 3. **a** Stimuli used to compare face processing based on the low-spatial frequency (LSF) and high-spatial frequency (HSF) content of images, relative to normal (broad-band) images. **b** Posterior fusiform cortex was activated by the presence of HSF in face stimuli, but not by LSF. **c** Average parameter estimates of activity (±SE) in FFA. Note however that an enhancement by fearful expression was driven by the presence of LSF. **d** Amygdala was activated by fearful expression in the LSF of face stimuli, but not by HSF. **e** Average parameter estimates of activity (±SE) in amygdala

emotional effect in FFA may depend on inputs from the amygdala, rather than on intrinsic cortical processing. The same pattern was observed in two subsequent imaging studies where "hybrid" faces were used. Both in fMRI (Winston et al. 2003) and ERPs (Pourtois et al. 2005a), we found that differential cortical responses to fearful *vs* neutral faces were evoked only when fearful expression was presented within the LSF content of pictures, irrespective of the expression of another superimposed face presented in HSF. This critical role of LSF information seems consistent not only with several recent studies showing that amygdala processing of fearful expression in faces may be highly sensitive to the large eye features that are typically present in these faces (Morris et al. 2002; Whalen et al. 2004; Adolphs et al. 2005), but also with some psychophysical results showing an important role of configural information for the recognition of face expression (rather than just local features) (Calder et al. 2000).

Conversely, our fMRI study (Vuilleumier et al. 2003a) also suggested that face identity processing in the FFA was established from HSF more reliably than from LSF cues. Because each individual face identity was repeated once during the whole course of the fMRI experiment, we could test for any repetition-priming effects induced by different visual images of the same face identity. Repetition-priming effects correspond to a selective decrease in the activation of cortical areas processing a particular stimulus type when this stimulus is repeated, relative to its first exposure, and such effects can thus reveal the specific attributes extracted by neurons in that particular area (Grill-Spector and Malach 2001; Naccache and Dehaene 2001). Here, by comparing repetition-priming effects for HSF and LSF faces relative to those for intact faces, we found that only faces first seen in HSF produced subsequent decrease when repeated later in a different format (Fig. 4), whereas faces first seen in LSF produced no decrease when repeated (Vuilleumier et al. 2003a). These data suggest that a long-term representation of identity in the FFA was more efficiently established and more efficiently generalized to other images when derived from HSF than from LSF information. Moreover, repetition-priming effects for identity across different images were found to predominate in more anterior regions of the fusiform cortex, whereas the peak of frequency-selectivity for HSF *vs* LSF was found in a more posterior fusiform region. Other imaging findings have also shown that the FFA might code for face identity irrespective of spatial frequency (Eger et al. 2004) or contrast polarity (George et al. 1999).

Taken together, these data suggest that face processing may not only take place in different brain pathways for different purposes (e.g., identity recognition in FFA and expression recognition in amygdala), but also exploit different information (e.g., LSF or HSF, global *vs* local cues) and probably proceed at different time-scale in different brain areas (with expression processed earlier in amygdala and then fed back to FFA). Thus, models of face processing should not only incorporate a "dual-route" framework for identity and emotion information (Bruce and Young 1986; Haxby et al. 2000), but also a "dual-stage" framework.
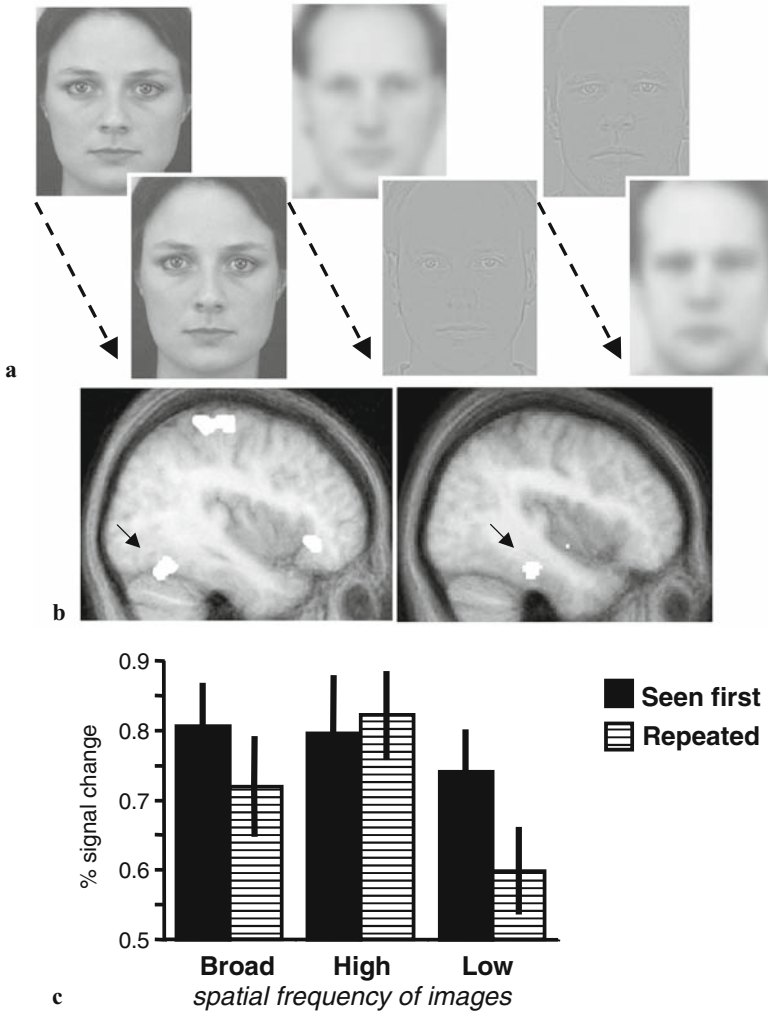
Fig. 4. **a** Stimuli used to test for repetition-priming effects when face identity is repeated, either in the same picture format or across different picture formats (e.g., first seen in LSF and later repeated in HSF, or vice versa). **b** Repetition-priming effects in posterior (left) and anterior (right) fusiform cortex, where responses showed a selective decrease when face identity was repeated irrespective of whether the repetition was with the same or with different images. **c** Average parameter estimates of activity (±SE) in anterior fusiform cortex, where repetition-priming were the strongest when the face identity was first seen in HSF and repeated in LSF (as opposed to the reverse order)

5 View-Selectivity and Invariance

If the FFA can encode faces irrespective of format and process identity across different spatial-frequency cues, what is the degree of invariance to other changes in visual inputs during identity recognition? A critical issue in visual perception in general has concerned how objects and faces can be identified despite changes in their visual appearance across different encounters (Biederman and Kalocsai 1997; Tarr and Bulthoff 1998; Biederman and Bar 2000; Vuilleumier et al. 2002). Thus, the identity of an individual face can usually be recognized across substantial visual changes due to different expressions, age, or viewpoint. In fact, we probably never see the same face twice with exactly the same view, yet we can readily identify a person across two meetings, or an old friend who has not been seen for several years. However, still little is known about how the visual system may achieve such efficient recognition abilities across very different visual inputs. Although the FFA has consistently been shown to process face identity cues (Gauthier et al. 2000; Grill-Spector et al. 2004), it remains unclear how face identity is represented in the FFA.

According to classic models of face recognition (Bruce and Young 1986), after some initial structural encoding stage, view-invariant traits might be extracted and stored into a long-term visual representation of a given individual face (e.g., "face recognition unit"), which may then allow a generalization of recognition from a particular view to another view of the same face. However, few studies have systematically examined whether the neural substrates of such "face recognition units" might correspond to the FFA and code for a particular face identity across different views (Grill-Spector et al. 1999). We have addressed this question in two recent brain imaging studies (Pourtois et al. 2005b, c) by using a repetition-priming paradigm in which different views of the same faces were presented twice, with an intervening delay of several minutes. As mentioned above, repetition-priming leads to a decreased activation for repeated stimuli as compared with their initial presentation, reflecting a selective adaptation of neurons tuned to particular stimulus attributes when these attributes are repeated (Grill-Spector and Malach 2001; Naccache and Dehaene 2001). This provides a useful method for probing the critical properties to which neurons respond, even when the different populations overlap in the same cortical region, since adaptation should occur for a repeated stimulus if the same neuronal population represents this stimulus across various appearances; whereas a lack of adaptation for a given stimulus repeated with a different appearance indicates the recruitment of a new population of neurons. Several studies found repetition-priming decreases in the FFA when faces were repeated but most have used the same photograph (Grill-Spector et al. 1999; Gauthier et al. 2000; Henson et al. 2000; Huettel and McCarthy 2001; Henson et al. 2002) or the same view with different renderings (George et al. 1999; Vuilleumier et al. 2003a; Eger et al. 2004).

In a first study (Pourtois et al. 2005b), unfamiliar faces were first shown in front-views or three-quarter views, and later repeated either with the same view (using different photographic shot) or with a different view. We found that the

FFA in both hemispheres showed view-sensitive repetition effects, with only a partial generalization from three-quarter to front views (Fig. 5). This indicates that face representation in the FFA is not view-invariant, and does not form a truly abstract and three-dimensional trace of faces after a single encounter. However, the asymmetrical pattern of repetition-priming effects (with some adaptation from three-quarter to front views but not vice versa) suggests that three-quarter views may provide more critical features to derive another view later, or provide better tridimensional cues relative to incomplete or inaccurate information in front-views. By contrast, we found that more medial regions in fusiform cortex showed repetition effects across all types of viewpoint changes, but these regions were outside face-selective areas and may contribute to higher-level processing stages related to associative processes related to semantic information or more abstract person-identity representations. Moreover, this generalization across viewpoints arose selectively in the left hemisphere. This hemispheric asymmetry might be consistent with other results showing that view-invariant priming effects for man-made objects were also selectively present in the left but not right anterior fusiform cortex (Vuilleumier et al. 2002).

A second fMRI study (Pourtois et al. 2005c) has recently confirmed that representation of faces in the FFA does not generalize across different views of the same identity, now using faces from both unfamiliar and famous people. We reasoned that famous faces would be more likely to give rise to a robust view-invariance in long-term representations as compared with unfamiliar faces viewed only once as in our previous study (Pourtois et al. 2005b). In this new experiment (Pourtois et al. 2005c), each individual face identity was first shown in a given view and then repeated in a different view after a varying delay (counterbalanced across subjects). Again, the FFA showed priming effects only when faces were repeated with the same view. There was no priming whatsoever in the FFA when the same face identity was repeated from one view to another, even for faces of famous people or actors that have repeatedly been seen under different appearance. All repetition effects for these well-known faces arose in left temporal and frontal cortex only, suggesting that they implicated more semantic information about person-identity rather than abstract visual representation of faces (Rhodes 1985; Damasio et al. 1990; Vuilleumier et al. 2003b).

This study also showed that a region in the medial fusiform gyrus, outside the FFA, showed some priming-realated decreases when unfamiliar faces were repeated with a slightly different viewpoint but still a similar appearance (Fig. 6). Unlike the previous study, this medial fusiform region was now found in the right but not left hemisphere. Thus, our results point to distinct subregions within fusiform cortex that may show a different sensitivity to viewpoint or visual similarity.

Taken together, our data do not support the hypothesis that the FFA may hold "face recognition units" representing faces in a view-independent format. Rather, face identity appears to be coded in a view-sensitive manner in the FFA, but it can generalize across different image renderings when these show the same viewpoint. Thus, memory traces of a given face identity might be represented in more distributed networks linking visual cortex with other distant brain areas
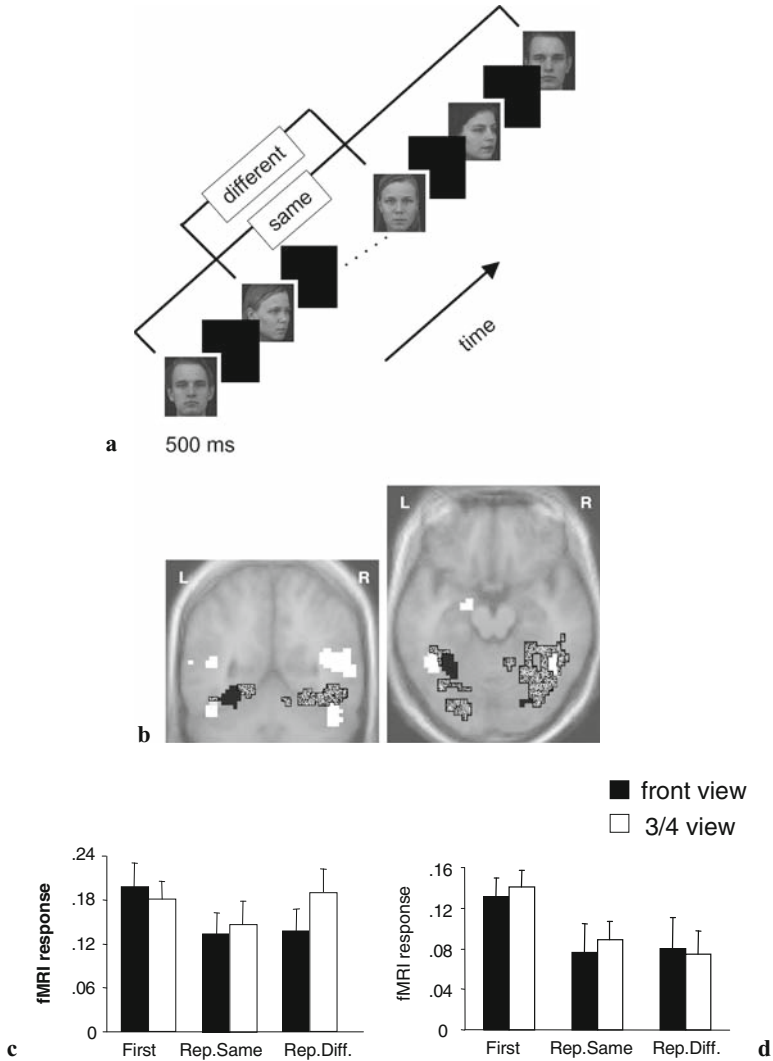
FIG. 5. **a** Stimuli used to test for repetition-priming effects when face identity is repeated either with the same viewpoint (*front-view* or *three-quarter*) or with a different viewpoint (e.g., first seen in front-view and later repeated in three-quarter, or vice versa). **b** Activation pattern across the different experimental conditions, overlaid on the mean anatomical scan of participants. White-colored areas show brain regions with face-selective responses, including FFA, STS, and amygdala. Gray-speckled areas show repetition-priming effects for faces repeated with the same view condition, involving extensive bilateral ventral temporal regions including FFA on both sides. Black-colored areas show repetition-priming effects for faces repeated with a different view, relative to faces seen for the fist time, involving the left medial fusiform cortex outside the FFA. Average parameter estimates of activity (±SE) are plotted for (**c**) the right FFA (red area) and (**d**) left medial fusiform cortex (blue area)
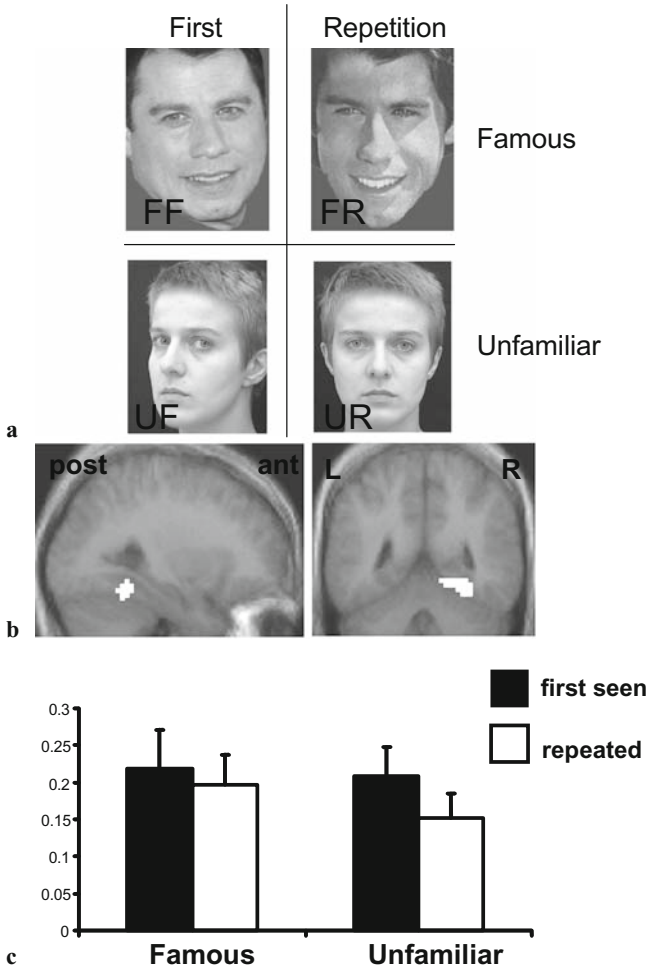
FIG. 6. **a** Stimuli used to test for repetition-priming effects when identity is repeated with the same or different viewpoint for either well-known or unknown faces. **b** Repetition-priming effects arose in a medial region of right fusiform cortex when identity was repeated across different views, but only for unknown faces which were visually more similar to each other, as compared to different views of famous faces which were visually more different. **c** Average parameter estimates of activity (±SE) in right fusiform cortex

(Bruce 1982; Damasio et al. 1990; Vuilleumier et al. 2003b), rather than being supported by in a single neuronal populations in a single brain area.

6 Conclusions

Recent brain imaging studies have highlighted the distributed and interactive nature of face perception in the human brain (Haxby et al. 2000, p. 256). The present chapter has focused on the processing of two major facial attributes (identity and expression) in the main brain regions associated with face recognition, i.e., the fusiform cortex (FFA), as well as the amygdala. Our findings reveal that although the FFA is critically implicated in face identity processing, repetition-priming effects may arise when the same face is seen across different picture formats but not when the same identity is seen across different viewpoint, suggesting that representations of faces in the FFA are not view-invariant and do not maintain a fully abstract 3D memory trace for previously encountered faces, even when these are from well-known people. In addition, face processing in the FFA is not totally independent of emotional expression, as predicted by traditional cognitive models proposing a strict segregation between processing pathways for expression and those for identity. However, emotional effects in the FFA are essentially generated by amygdala feedback on extrastriate cortex, which may arise during a second stage of processing after a first sweep of coarse visual inputs into the visual system. Future research still needs to elucidate the nature of visual information and computations taking place in different brain regions, and their dynamic interactions over time. Despite our impression that faces can be recognized effortlessly in a single glance, face recognition clearly involves more than a single brain process triggered in a single instant.

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