

The involvement of the “fusiform face area” in processing facial expression

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Abstract

We conducted an fMRI investigation to test the widely accepted notion that the fusiform face area (FFA) mediates the processing of facial identity but not expression. Participants attended either to the identity or to the expression of the same set of faces. If the processing of identity is neuroanatomically dissociable from that of expression, then one might expect the FFA to show higher activation when processing identity as opposed to expression. Contrary to this prediction, the FFA showed higher activation for judgments of expression. Furthermore, the FFA was sensitive to variations in expression even when attention was directed to identity. Finally, an independent observation showed higher activation in the FFA for passive viewing of faces when expression was varied as compared to when it remained constant. These findings suggest an interactive network for the processing of expression and identity, in which information about expression is computed from the unique structure of individual faces.

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1. Introduction

Face-recognition models have used behavioral and neuroanatomical data to argue that faces are processed in a distributed manner (Haxby, Hoffman, & Gobbini, 2000, 2002). The notion is that different attributes of the same face, such as identity, expression, or direction of gaze, are processed by separate brain regions. A crucial region for identity is thought to be the “fusiform face area” (FFA), a region within the lateral fusiform gyrus that shows robust activation for faces, mostly in the right hemisphere (Kanwisher, McDermott, & Chun, 1997). In contrast, the processing of expression is thought to be mediated by another set of brain regions, mainly in the superior temporal sulcus (STS) and the amygdala (Haxby et al., 2000).

Yet, although the role of the FFA in processing identity (Henson, Shallice, & Dolan, 2000; Henson, Goshen-

Gottstein, Ganel, Otten, Quayle, & Rugg, 2003) and the role of the STS and the amygdala in processing expression (Vuilleumier, Armony, Driver, & Dolan, 2003; Winston, Henson, Fine-Goulden, & Dolan, 2004) have been well established, it is less clear how dissociable these regions are (for recent reviews, see Pessoa & Ungerleider, 2004; Posamentier & Abdi, 2003). Of particular interest is the possible involvement of the FFA in the processing of expression. Although face-recognition models have speculated that this might be possible (Haxby et al., 2000, 2002; Pessoa & Ungerleider, 2004), the nature of the involvement has never been specified or directly addressed. In the current paper, we used fMRI to test whether or not such an involvement indeed exists.

We propose, on the basis of a broad range of behavioral studies (for a review, see Ganel & Goshen-Gottstein, 2004), that facial expressions can be best characterized as dynamic variations from the invariant structure of faces, i.e. their identity. In other words, the way an individual expresses emotion is always constrained by his or her identity. Differences between individuals should lead to systematic differences in the way they express emotions. We would predict, therefore, that

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to extract emotional expression from a specific face, it would be also necessary to process the identity of that face. Thus, the processing of facial expression should engage the same anatomical regions, such as the FFA, that have been traditionally associated with the processing of identity. Moreover, this involvement could be quite direct, and not just one of passively providing information about identity to other, more specialized “emotion-recognition” systems.

Recent imaging studies that showed stronger FFA activation to fearful as compared to neutral faces provide a preliminary support for a direct involvement of this region in processing of expressions (Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Vuilleumier, Armony, Driver, & Dolan, 2001). These findings, however, are limited by the fact that different sets of stimuli were used for the expressive and the neutral conditions. Such differences may have resulted in low-level visual differences between the images presented in the two conditions, differences that have already been found to have

robust effects on FFA activation (Vuilleumier et al., 2003). Furthermore, none of these studies controlled for differential attention to facial identity and expression, and therefore, could not isolate the effects of processing expression from those of processing identity within the FFA.

In the current study, we used a modified selective-attention task (Garner, 1974) that has been used in behavioral studies to test the functional relationship between the processing of different dimensions of objects (Felfoldy, 1974; Ganel & Goodale, 2003) and faces (Ganel & Goshen-Gottstein, 2002), including the relationship between the processing of identity and expression (Baudouin, Martin, Tiberghien, Verlut, & Franck, 2002; Ganel & Goshen-Gottstein, 2004; Schweinberger, Burton, & Kelly, 1999; Schweinberger & Soukup, 1998).

In this task, the same set of faces is presented for judgments of either identity or expression (Fig. 1), allowing us to compare the contributions of different brain regions to the

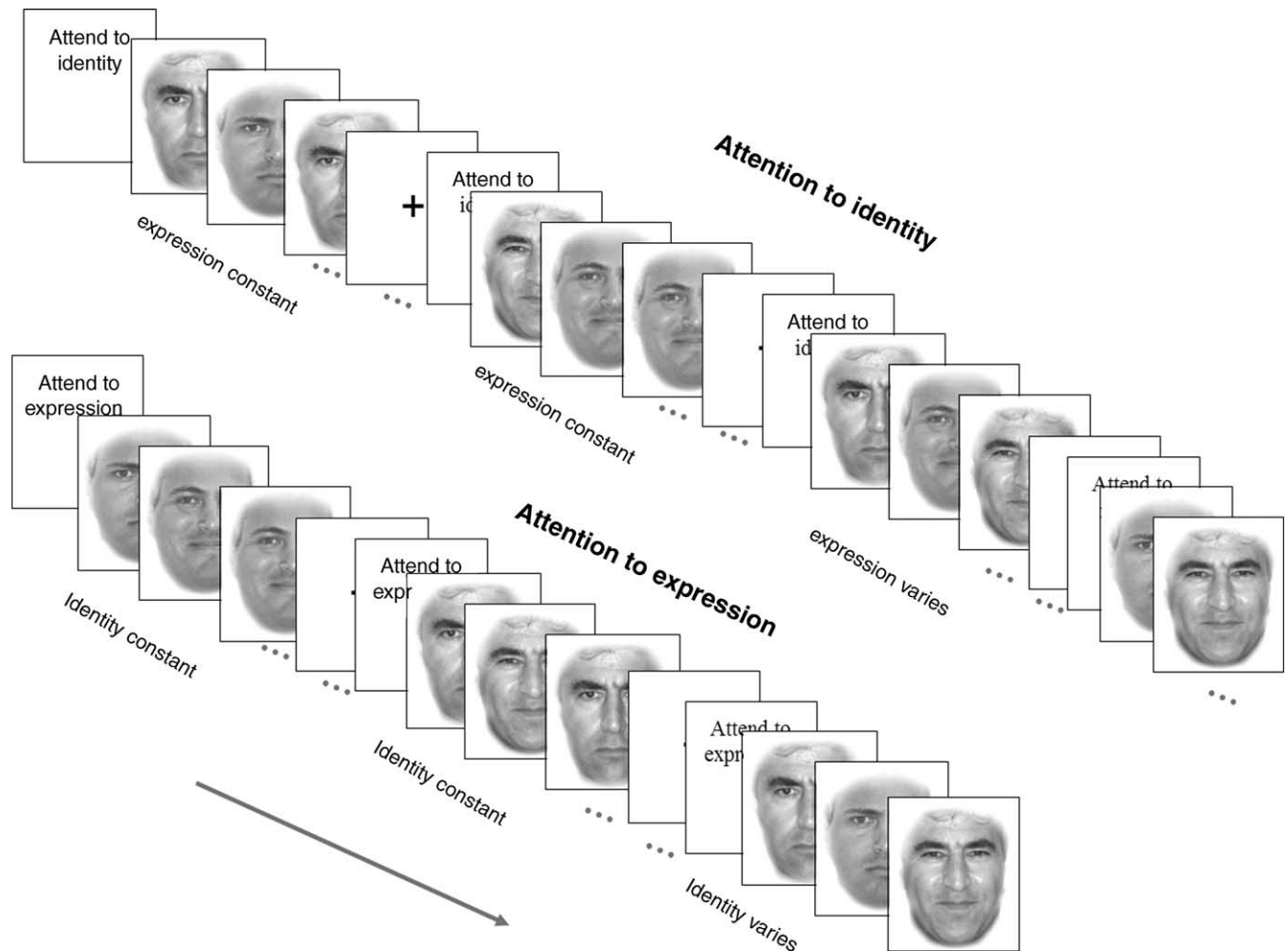


Fig. 1. Experimental design and examples of stimuli. The same set of faces was presented for speeded classification of identity (Person A/Person B) or of expression (happy/angry). Participants were asked to attend to one dimension while ignoring the other, while this irrelevant dimension either remained the same (baseline condition) or changed in value from trial to trial (filtering condition). Eight experimental runs were included, each containing all the experimental blocks. Order of experimental blocks was counterbalanced across runs.

processing of these facial attributes. Participants were asked to attend to either the identity or the expression of faces, while trying to ignore the other, irrelevant dimension. In some cases, the irrelevant dimension of identity (or expression) was held at a constant value (baseline condition) whereas in other cases the irrelevant dimension was randomly varied (filtering condition). (Note that the term “baseline” in this context refers to a task condition and should not be confused with the term “baseline activation” as it used in fMRI.)

It is well established that manipulating attention to different attributes of the same stimulus can be used to investigate the relative contribution of different brain regions to the processing of those attributes (O’Craven, Downing, & Kanwisher, 1999). In particular, larger activation was found in the FFA when attention was directed to the identity of a face as opposed to when it was directed to its direction of gaze (Hoffman & Haxby, 2000). This pattern of activation was used to suggest that the FFA is more heavily involved in the processing of identity than the direction of gaze. Using the same logic, we measured differences in activation in the FFA (and other regions) when attention was directed to the expression as compared to identity. If the FFA functions only as an “identity module”, as many face models propose, it should show higher activation when attention is directed to identity. If, on the other hand, the FFA does not actively involved in the processing of expression but instead simply provides information about identity to other more specialized systems (such as the STS and the amygdala), then activation in the FFA should be equivalent when attention is directed to identity or expression. But if, as we predict, the FFA is an integral part of the network that processes expression, then higher activation should be found in the FFA (as well as in other regions that are part of this network, such as the STS and the amygdala) when attention is directed to expression.

In addition to testing the effects of attention to identity and expression on activation in the FFA, STS and the amygdala, our design also allowed us to test whether or not these regions are also sensitive to expression even when attention is not directed to this attribute. This was achieved by comparing activation between the filtering and baseline conditions for each task (see Fig. 1). If, for example, a specific area is sensitive to variations in expression even when attention is explicitly directed to identity, activation in that area should be higher when expression varies than when it is constant. Thus, the task we used permitted us to test for both explicit and implicit processing of expression in the FFA.

2. Methods

2.1. Participants

Eleven right-handed subjects with normal or corrected-to-normal vision participated in the experiment. All subjects signed a consent form approved by the ethics committee at the University of Western Ontario.

2.2. Stimuli and apparatus

2.2.1. Selective attention task

The stimuli (Fig. 1) were taken from a database used in our recent behavioral study (Ganel & Goshen-Gottstein, 2004) and were created from a factorial combination of identity (Person A, Person B) \times expression (smiling, angry). An additional set of faces with two different identities (not shown in Fig. 1) was also presented to each subject.

Participants were asked to make speeded classifications of either the expression or the identity of a series of faces (one face at a time) while trying to ignore the irrelevant dimension. In the baseline blocks, participants judged one dimension (e.g., expression) while the other dimension was held at a constant value (e.g., Person A). In the filtering blocks, participants again judged only one dimension (e.g., expression) but this time the faces differed also in the irrelevant dimension (e.g., both Person A and Person B were presented). In all blocks, each photo was presented 16 times in random order, resulting in a total of 32 presentations for each baseline block and 64 presentations for the filtering blocks. To prevent difference between blocks as a result of different number of stimuli presentations within each block, the filtering blocks were divided into two equal parts (Ganel & Goodale, 2003), each containing 32 stimuli. Therefore, each baseline and filtering block included 32 stimuli presentations, with the first eight stimuli, which were used to acquaint participants with the experimental set (Ganel & Goshen-Gottstein, 2004), defined as practice and excluded from the analysis. Each face was presented for 800 ms and was followed by a 400-ms interval. A 19.2-s fixation period separated the different blocks. Eight runs were carried out, each run containing all the experimental blocks. The order of the experimental blocks was counterbalanced across runs. The order of the runs was counterbalanced across subjects.

2.2.2. Passive viewing condition

In the passive viewing condition, which also served as a localizer for the regions of interest (ROIs), subjects viewed different classes of stimuli, separated into four different types of experimental blocks: faces with different identities and different emotions (happy, neutral, sad, angry, surprised), faces with different identity with a neutral emotion, objects, and scrambled faces. Photos of 180 different faces and 90 different objects were taken from various databases used in previous experiments in our laboratory. None of the faces used in our localizer was used in the experimental task. Each experimental run included three blocks of expressive faces, three blocks of neutral faces, and three blocks of objects, all separated by blocks of scrambled faces. Thirty stimuli were presented in each block. Each stimulus was presented for 460 ms and was followed by a 100-ms interval. Two different localizer runs with different order of blocks were used.

2.3. Imaging parameters and analysis

Imaging was done using a 4-T, whole-body MRI system (Varian/Siemens) and a quadrature radio-frequency head coil located at the Robarts Research Institute (London, Ont., Canada). Each imaging session consisted of 10 functional scans (two localizer and eight experimental), plus one high-resolution anatomical scan. Functional images were collected using a T2*-weighted, segmented (navigator-corrected), interleaved SPIRAL acquisition (TE = 150 ms, TR = 1200 ms, flip angle = 60°, two segments/plane) for oxygen-level-dependent (BOLD)-based imaging. The field of view was 19.2 cm × 19.2 cm × 10.5 cm, with an in-plane resolution of 64 × 64 pixels and 21 contiguous pseudo-axial scan plans per volume, resulting in a voxel size of 3.0 mm × 3.0 mm × 5.0 mm. Each volume required 2400 ms to acquire. High-resolution T1-weighted anatomical volumes were acquired using 3D magnetization-prepared FLASH acquisition (TI = 1300 ms, TE = 30 ms, TR = 50 ms, FA = 20°). The imaging data were preprocessed using the Brain Voyager 2D/3D data analysis tools. The anatomical volumes were transformed into a Talairach common space for all subjects (Talairach & Tournoux, 1998). Functional volumes for each subject underwent high-pass temporal frequency filtering in order to remove any linear drifts in the signal. Functional volumes were then aligned to the transformed anatomical volumes, thereby transforming the functional data into a common brain space across subjects.

The imaging data were analyzed using the Brain Voyager multi-study GLM (general linear model) procedure. This procedure allows the correlation of predictor variables or functions with the recorded activation data (criterion variables) across scanning sessions. Predictor functions were γ functions ($\Delta = 2.5$, $\tau = 1.25$), designed to estimate hemodynamic response properties (Boynton, Engel, Glover, & Heeger, 1996), spaced in time to coincide with the blocked stimulus paradigms. For each individual, the averaged functional volumes from localizer scans were used to identify the ROIs. The LO area was identified based on neuroanatomy and using its larger response to objects over scrambled faces. The FFA and the OFA were identified for each subject using the contrast, faces – objects (Kanwisher et al., 1997). Due to the fact that for a few subjects, distinct areas along the STS showed larger activation for faces as compared to objects, and given the established role of this area in processing facial expression (e.g., Winston et al., 2004), we limited our analysis to STS regions that were more responsive to emotional faces. Therefore, we used the contrast emotional – neutral faces to identify the STS. But to exclude the possibility that the pattern of activation that we found in the STS was due to the particular nature of the contrast that was used to identify this area, we conducted a further analysis, in which the STS was identified using the more general contrast, intact faces – scrambled faces, the same contrast that was used to identify the FFA. This analysis revealed the same pattern of results that was revealed using the emotional – neutral

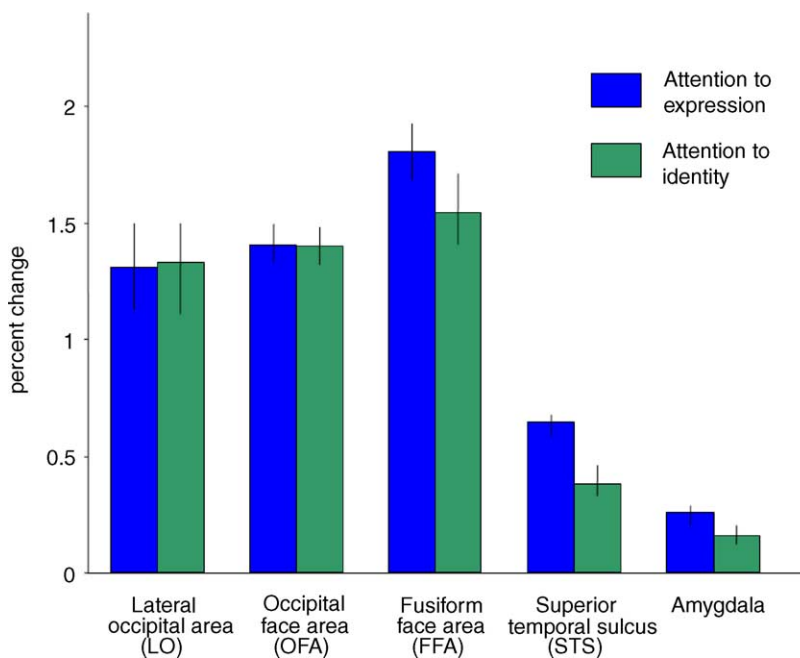


Fig. 2. fMRI activation when attending to expression and identity in the selective attention task. The regions of interest were defined independently for each of the subjects, the right LO ($x y z = 40 \pm 3$ (S.E.) $-79 \pm 2 -7 \pm 2$, 202 ± 10 voxels), right OFA ($x y z = 34 \pm 2 -72 \pm 1 -14 \pm 2$, 163 ± 12 voxels), right FFA ($x y z = 36 \pm 2 -51 \pm 2 -16 \pm 1$, 202 ± 15 voxels), right STS ($47 \pm 1 -42 \pm 3 9 \pm 2$, 133 ± 15 voxels) and right amygdala ($18 \pm 1 -7 \pm 1 -9 \pm 1$, 126 ± 9 voxels). The right FFA, the right STS, and the right amygdala showed higher activation for judgments of expression over identity. In the left hemisphere, none of the five ROI's showed differences between judgments of expression and identity.

faces ROI (see Fig. 2), with larger activation in the right STS ($x y z = 46 \pm 2$ (S.E.) $- 49 \pm 49 \pm 1$, 203 ± 19 voxels) for the expression task as compared to the identity task ($t(11) = 2.7$, $p < 0.05$).

Because the amygdala is relatively small and its size varies considerably from subject to subject, we identified it on the basis of both neuroanatomical location and the contrast between intact and scrambled faces. For all ROIs, the averaged time course of MR signal intensity during experimental scans was then extracted from each of these independently defined ROIs.

3. Results and discussion

3.1. fMRI activation in the selective attention task

Using a region-of-interest (ROI)-based approach, the lateral occipital area (LO), the occipital face area (OFA), the FFA, the STS, and the amygdala were identified independently for each subject in both hemispheres. As can be seen in Fig. 2, larger activation (averaged across the baseline and filtering blocks) for expression as compared to identity was found in the right STS (47 ± 1 (S.E.) $- 42 \pm 39 \pm 2$, 133 ± 15 voxels; $t(10) = 2.74$, $p < 0.05$), the right amygdala ($18 \pm 1 - 7 \pm 1 - 9 \pm 1$, 126 ± 9 voxels; $t(10) = 2.31$, $p < 0.05$), and most importantly, in the right FFA ($x y z = 36 \pm 2 - 51 \pm 2 - 16 \pm 1$, 202 ± 15 voxels; $t(10) = 2.61$, $p < 0.05$). These findings provide a first line of evidence in support for our hypothesis that the FFA is part of a network that processes facial expression.

Importantly, no activation differences between expression and identity were found either in the right LO ($x y z = 40 \pm 3 - 79 \pm 2 - 7 \pm 2$, 202 ± 10 voxels; $t(8) < 1$) or in the right OFA ($x y z = 34 \pm 2 - 72 \pm 1 - 14 \pm 2$, 163 ± 12 voxels; $t(10) < 1$), areas that are known to be involved in more general processing of objects and faces (Malach et al., 1995; Rossion, Seghier, Schuller, Lazeyras, & Mayer, 2003). In other words, the increased activation with expression found in the FFA, STS, and amygdala could not have been due to some sort of “general activation” effect related to possible differences in the attentional demands of expression and identity processing.

If the FFA is indeed involved in the processing of facial expression, then it should also be sensitive to variations in expression, even when attention is directed to identity. In order to test this prediction, we separately analyzed the results for each of the ROIs that showed larger activation for expression as compared to identity (see Fig. 3). Specific comparisons between the baseline and filtering blocks for the identity judgments in each ROI supported our second hypothesis, by showing higher activation in the filtering block, in which expression varied, as compared to the baseline blocks, in which expression was constant (for the FFA, $t(10) = 2.98$, $p < 0.05$; for the STS, $t(10) = 2.43$, $p < 0.05$; for the amygdala the difference was only marginally significant, probably due to rela-

tively higher variability in these regions, $t(10) = 1.86$, $p < 0.1$). As for the condition in which attention was directed to expression, only the FFA, as might be expected (given its established role in processing identity), showed sensitivity for variations in this dimension. This was indicated by higher activation in the FFA in the filtering as compared to the baseline condition when attention was directed to expression ($t(10) = 1.9$, $p < 0.05$, one-tailed). This last comparison was not significant for either the STS or the amygdala.

Overall, our findings from the selective attention task establish that the FFA is actively involved in processing facial expression, both when attention is explicitly directed to expression and when attention is directed to identity while sensitivity to variations in expression was used as a measure.

3.2. fMRI activation during passive viewing of faces

To provide converging evidence for the attentional effects that were presented in the previous section, subjects passively viewed, in a different set of trials, faces of different individuals portraying either a neutral emotion or a set of different emotions (happy, neutral, sad, angry, or surprised, see Fig. 4). In all three regions, higher activation was found for emotional than for neutral faces, in the right FFA, $t(10) = 2.72$, $p < 0.05$, the right STS, $t(10) = 3.49$, $p < 0.01$, and the right amygdala, $t(10) = 4.02$, $p < 0.01$. These results nicely complement the findings from our attentional manipulation (Figs. 2 and 3) and also converge with previous studies showing higher activation in the FFA and the amygdala for angry as compared to neutral faces (Pessoa et al., 2002; Vuilleumier et al., 2001). Overall, our fMRI results provide strong support for the notion that the FFA is an integral part of a distributed brain network that actively processes facial expression.

3.3. Behavioral results

Analysis of the behavioral results revealed better performance in baseline than in filtering both for judgments of identity (baseline: 465 ms, 94%; filtering: 500 ms, 94%) and for judgments of expression (baseline: 483 ms, 93%; filtering: 535 ms, 88%). The reaction times were analyzed in a 2 (identity judgments, expression judgments) \times 2 (baseline, filtering) repeated-measures ANOVA. This analysis showed significant main effects of task ($F(1, 10) = 14.5$, $p < 0.01$), block ($F(1, 10) = 66.8$, $p < 0.001$), and an interaction ($F(1, 10) = 11.8$, $p < 0.01$), which reflected a larger filtering – baseline difference in the expression task than in the identity task.

The slower performance in the filtering, as compared to the baseline condition, indicates that while judging either one of the dimensions, identity or expression, participants could not avoid processing the irrelevant dimension. This interference of the irrelevant dimension on performance demonstrates the strong functional interdependence between the processing of identity and the processing of expression. This effect has been reported in many other behavioral experiments (Baudouin et al., 2002; Ganel & Goshen-Gottstein, 2004; Schweinberger

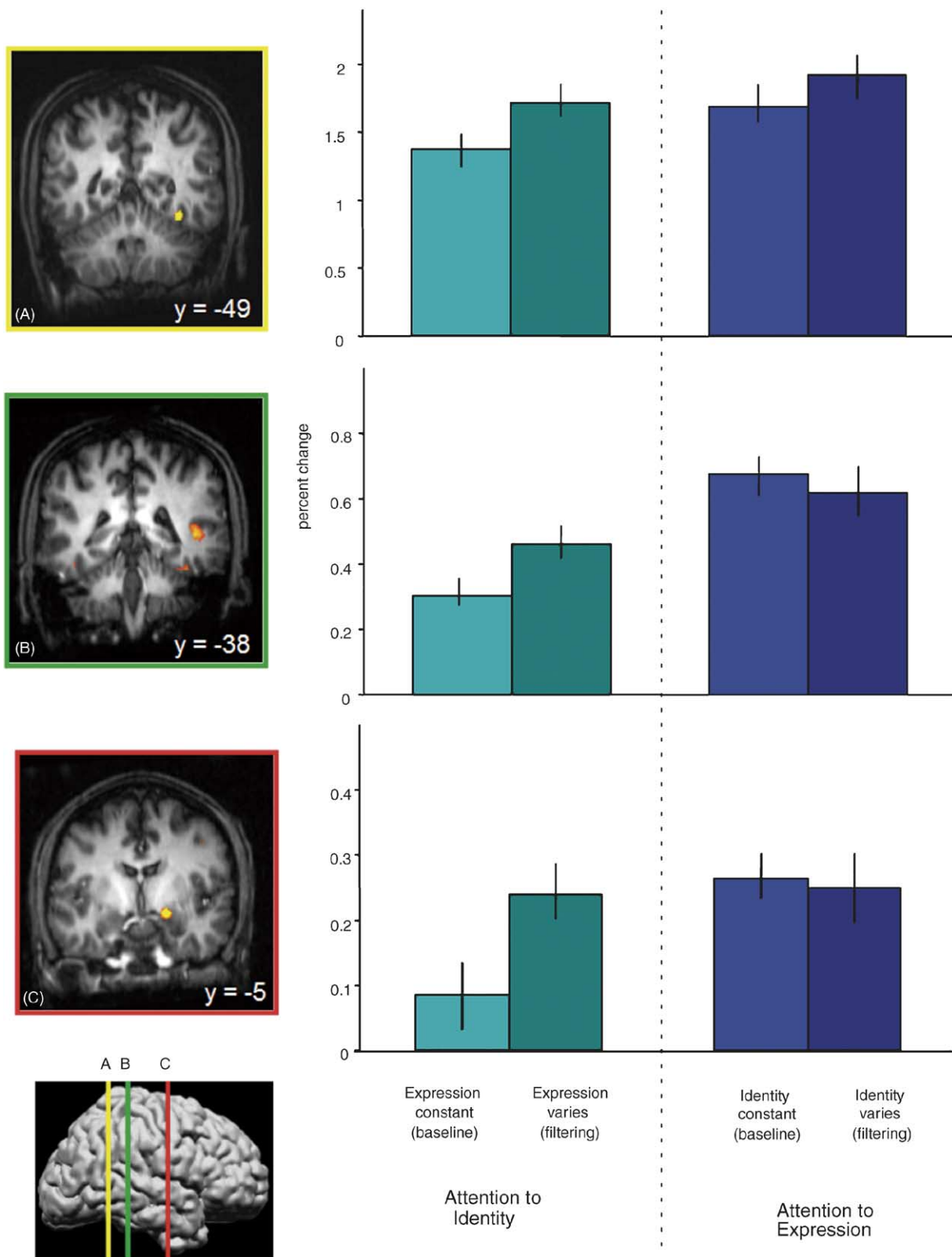


Fig. 3. fMRI activation in each of the experimental conditions of the selective attention task. The three regions of interest were defined the same regions presented in Fig. 2 which showed significantly higher activation for judgments of expression as compared to judgments of identity: the right FFA (upper), right STS (middle), and right amygdala (lower). All regions showed sensitivity to variations in expression even when attention was directed to identity.

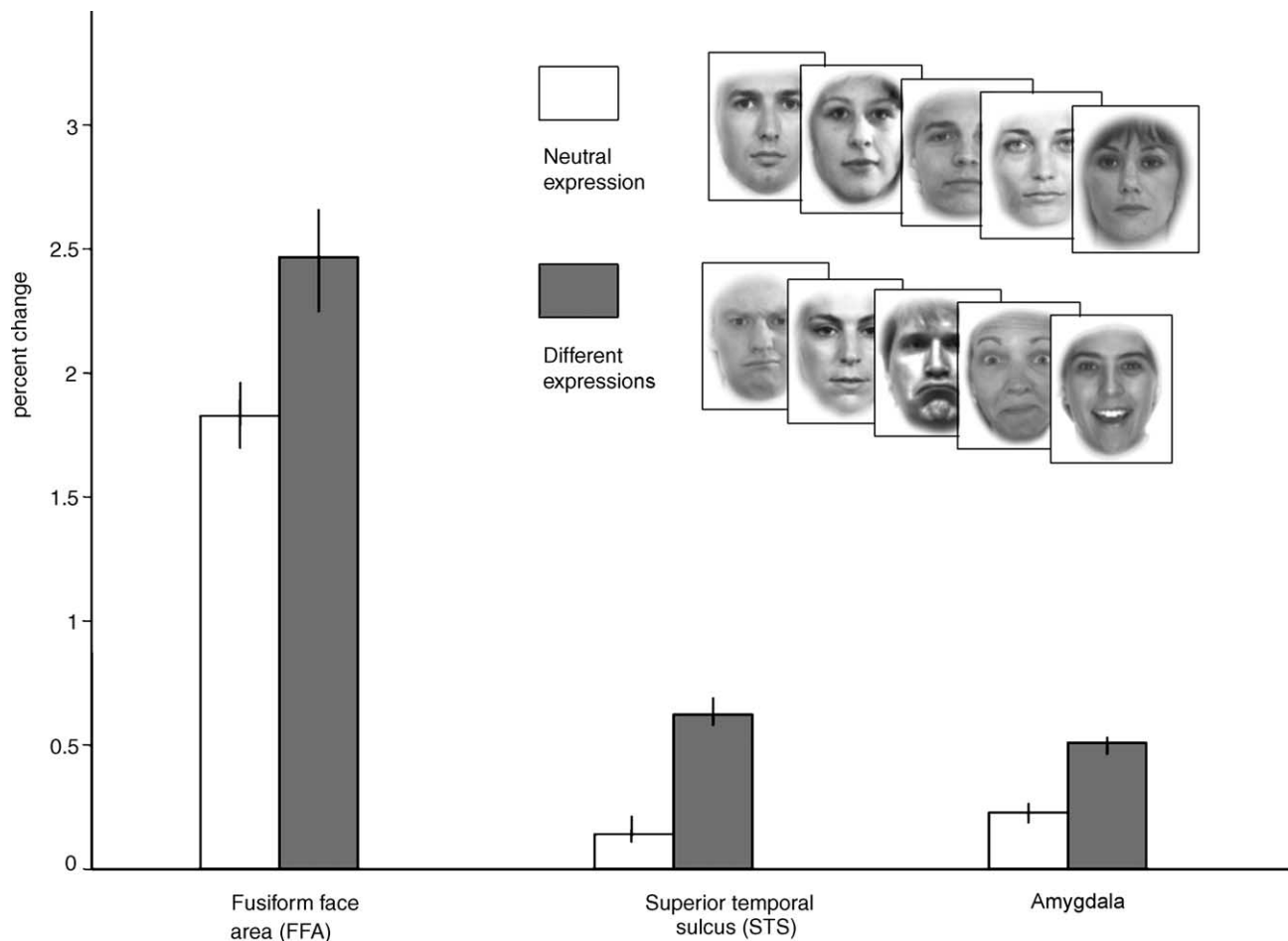


Fig. 4. Effects of face emotionality in the passive-viewing condition. Activation shown is in the same regions that are presented in Fig. 3. All regions showed higher activation for faces displaying different, as compared to neutral expressions.

et al., 1999; Schweinberger & Soukup, 1998) and provides a functional explanation for the pattern of fMRI activation we observed in the selective attention task. In other words, variations in the irrelevant dimension in each of the two filtering conditions engaged the networks that process that dimension, led both to an increase in reaction time and to a corresponding increase in BOLD activation in the FFA. Thus, the fact that this occurred when expression was the irrelevant dimension is further evidence that the FFA is part of a network that plays a critical role in the analysis of expression. As we shall see in the section below on correlational analyses, a robust relationship was found between the behavioral interference effects and the corresponding brain activation on a subject-by-subject basis.

The proposal that the identity of the face is used as a reference for processing expression is also supported by previous reports of larger effects of irrelevant variations in identity on the processing of expression as compared to the effects of irrelevant variations of expression on the processing of identity (see Baudouin et al., 2002; Ganel & Goshen-Gottstein, 2004; Schweinberger et al., 1999; Schweinberger & Soukup, 1998). The significant interaction between task and block in

our behavioral data provides a further replication of this robust effect and additional support for the notion that identity serves as a basic facial dimension from which information about expression can be extracted. Most importantly, this notion is also supported by our fMRI data in which higher activation was found in the FFA for expression, as compared to identity judgments.

3.4. Correlation between performance and fMRI activation

Although expression judgments were only 18 ms slower than identity judgments in the baseline condition, this difference was significant. The fact that the OFA region and the LO region did not show increased activation in the expression task as compared to the identity task (Fig. 2) provides a strong argument against the possibility that task difficulty by itself could account for the pattern of activation in the FFA, STS, and the amygdala. However, to provide further evidence against the possibility that task difficulty could account for the larger fMRI activation for expression in the FFA, we performed two additional sets of analysis.

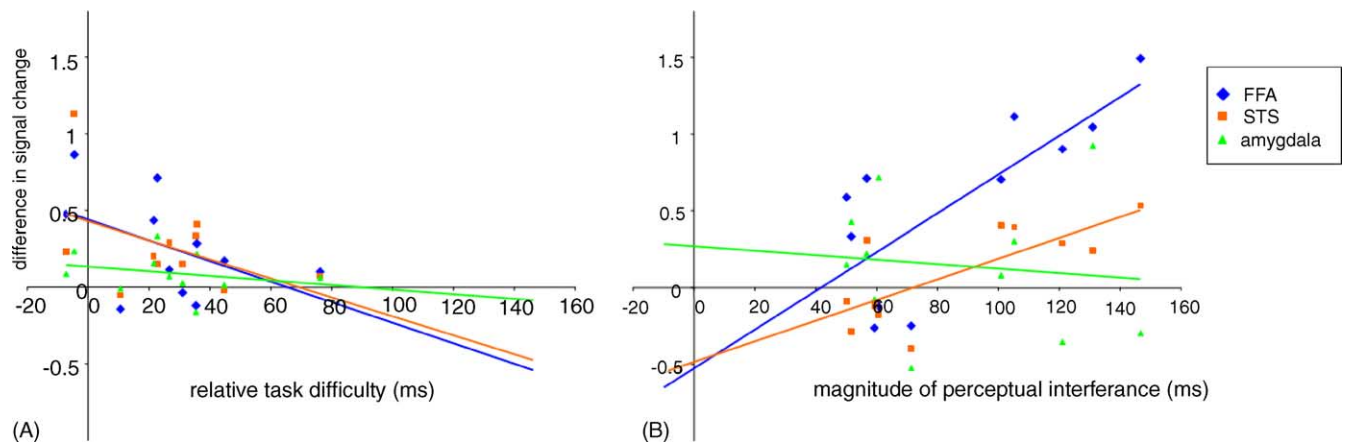


Fig. 5. Correlations between performance and brain activation. (A) No significant correlations were found in the FFA, STS, or the amygdala between task difficulty (reaction times for the expression task – reaction times for the identity task) and between fMRI activation (fMRI signal for the expression task – fMRI signal for the identity task) in each of the regions. (B) Significant positive correlations were found in the FFA and STS between the perceptual interference effects (average difference in reaction times between filtering and baseline blocks for identity and expression) and between the corresponding fMRI response (average activation difference between filtering and baseline blocks for identity and expression).

First, we conducted a correlation analysis across subjects between the difference in performance (mean reaction time for the expression task in the filtering and the baseline blocks – mean reaction time for identity task in the filtering and the baseline blocks) and the difference in fMRI activation (mean fMRI signal for the expression task – mean fMRI signal for the identity task). If the higher activation in the FFA, STS, and the amygdala for expression as compared to identity a simple consequence of task difficulty then there should be a positive correlation between these two measures. As can be seen in Fig. 5A, no such correlation was found. Indeed, the correlations between task difficulty and activation were negative and non-significant for all three regions (Pearson correlation; for the FFA, $r = -0.47$; for the STS, $r = -0.45$; for the amygdala, $r = -0.26$; all p -values > 0.1).

Notice that although the correlation analysis provides one line of support against the task difficulty account, the fact that the argument relies on null findings reduces its power to some extent. Nevertheless, it is important to note that, although there were no correlations between brain activation and task difficulty, there were significant correlations between brain activation and a different measure of performance. In particular, when we correlated the behavioral interference between identity and expression (mean difference in reaction time between the filtering and baseline blocks for identity and for expression) and the corresponding fMRI activation (mean difference in BOLD signal between the filtering and baseline blocks for identity and for expression), we found a significant positive correlation between these measures. As can be seen in Fig. 5B, these positive correlations were found for the FFA ($r = 0.76$, $p < 0.01$) and for the STS ($r = 0.74$, $p < 0.01$), but not for the amygdala ($r = -0.12$, $p > 0.1$). Taken together with the absence of a correlation between activation and task difficulty, these findings support our contention that the functional interdependence between the processing of identity and the processing of expression is mediated by

face-selective regions, and in particular by the FFA (see also Ganel & Goshen-Gottstein, 2004). The lack of correlation between performance and fMRI activation in the amygdala may reflect the fact that the amygdala is not so specifically “visual” as the other two regions (for a discussion, see Stark & Squire, 2001).

To further explore the relationship between activation in our ROIs, we performed an additional analysis, in which we correlated the pattern of activation (mean fMRI signal for the expression task – mean fMRI signal for the identity task) in the FFA, STS, and the amygdala. This analysis revealed significant positive correlations between fMRI activation in the FFA and the STS ($r = 0.61$, $p < 0.05$), and fMRI activation in the FFA and the amygdala ($r = 0.84$, $p < 0.01$). These results provide further support for the idea that these regions are part of an integrated network for processing expression. The correlation between the pattern of activation in the STS and the amygdala did not achieve significance ($r = 0.37$, $p > 0.1$).

A final argument against a task-difficulty-based explanation for our findings comes from a separate analysis that we carried out on the data from the two subjects who did not show greater difficulty for expression judgments as compared to identity judgments. In fact, both subjects show a slight trend in the opposite direction: for subject bm, identity judgments, 468 ms, 96% accuracy; expression judgments, 461 ms, 98% accuracy; for subject kv, identity judgments, 556 ms, 95% accuracy; expression judgments, 551 ms, 94% accuracy. If the higher activation found in the FFA for expression as compared to identity was simply the result of the fact that subjects found the expression task harder, then these two subjects should not show this pattern of activation. Yet, both subjects showed higher activation in the FFA for judgments of expression as compared to judgments of identity (for subject bm, overall percent change in the identity task, 2.75%, in the expression task, 3.22%; for subject kv, percent change in the identity task, 2.35%, in the expression task, 3.21%).

Indeed, the pattern of activation for these two subjects was essentially identical to that seen in the averaged data presented in Figs. 2 and 3.

3.5. An adaptation-based interpretation of the results

In recent years, fMRI adaptation has been used to test specificity in the processing of different dimensions of objects and faces (Grill-Spector & Malach, 2001; Epstein, Graham, & Downing, 2003; Winston et al., 2004). The logic behind this technique is that a brain area that is involved in processing a specific dimension (i.e., expression) should show adaptation to this dimension. Adaptation is commonly associated with a reduction in BOLD activity when subjects are presented with stimuli in which the value of the dimension of interest is kept constant (e.g., faces with the same expression) as compared to when the values of that same dimension are changed (e.g., faces with different expressions). Thus, if an area is involved in the processing of expression, it should maintain high activation when expression is changed from trial to trial. This is exactly what we found in the FFA, STS, and amygdala, in our passive viewing condition. In other words, activity was higher in all three areas during the block of trials in which facial expression varied as compared to the block in which expression did not change (neutral faces throughout the block).

Adaptation effects could also account, in part, for the pattern of activation that we observed in our selective attention paradigm. Note that during the baseline blocks, attention was directed towards a particular facial dimension (e.g. expression) while the other dimension (e.g. identity) was always held constant. In the filtering blocks, however, both the relevant and the irrelevant dimensions were varied. Thus, the higher activation in the filtering as compared to the baseline blocks could reflect adaptation in the baseline block to the unchanging irrelevant dimension. Such an adaptation-based explanation, however, is in perfect agreement with our theoretical model because all three regions, the FFA, STS, and the amygdala, showed adaptation to expression (higher activation when expression varied as compared to when it was constant, see Fig. 3). Note that this also suggests that among the three “principal ROIs”, the FFA was the only region that showed sensitivity to identity, by showing significant adaptation to this dimension (higher activation when identity varied as compared to when it was constant, see Fig. 3). At the same time, within all three ROIs, the higher activation associated with the expression baseline blocks (where identity was held constant) compared to that associated with the identity baseline blocks (where expression was held constant) reflects a more robust adaptation effect to expression as compared to identity. Again, this pattern is consistent with our argument that the FFA plays a critical role in the processing of facial expression. However, given that explicit attention was always directed towards one dimension or the other these sorts of strictly adaptation-based accounts are likely to be over simplistic. Indeed, very little is known about the role of explicit attention in fMRI adaptation or about the possible

interaction effects between adaptation and selective attention (but see, Eger, Henson, Driver, & Dolan, 2004; Murray & Wojciulik, 2004). But in any case, our proposal that the FFA plays an important role in the processing of expression can accommodate either a selective attention account or an adaptation-based account. Finally, it should be pointed out that a selective attention account, but not an adaptation-based account, can explain why there was higher activation for expression judgments than identity judgments in both the filtering blocks (where the same stimuli were used and only selective attention was manipulated) and the baseline blocks.

Our findings are relevant to a current debate in the face-recognition literature. Some have argued that the processing of identity by the FFA depends on quite different inputs than the processing of expression in the amygdala (Vuilleumier et al., 2003; Winston et al., 2004). Others argue that the information about facial structure is sent directly from the FFA to the amygdala (as well as to other face-specific regions, such as the STS) for the processing of expression (Pessoa et al., 2002; Pessoa & Ungerleider, 2004). Our results suggest that the role of FFA is not limited to providing information to the amygdala and other brain regions about facial structure alone. Indeed, we would suggest that the FFA is not simply an “identity-specific” module, as has been widely assumed, but is also directly involved in processing facial expression.

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References

- Baudouin, J. Y., Martin, F., Tiberghien, G., Verlut, I., & Franck, N. (2002). Selective attention to facial identity and emotion in schizophrenia. *Neuropsychologia*, *40*, 503–511.
- Boynton, G. M., Engel, S. A., Glover, G. H., & Heeger, D. J. S. (1996). Linear systems analysis of functional magnetic resonance imaging in human V1. *Journal of Neuroscience*, *16*, 4207–4221.
- Eger, E., Henson, R. N., Driver, J., & Dolan, R. J. (2004). BOLD repetition decreases in object-responsive ventral visual areas depend on spatial attention. *Journal of Neurophysiology*, *92*, 1241–1247.
- Epstein, R., Graham, K. S., & Downing, P. E. (2003). Viewpoint-specific scene representations in human parahippocampal cortex. *Neuron*, *37*, 865–876.
- Felfoldy, G. L. (1974). Repetition effects in choice reaction time to multidimensional stimuli. *Perception & Psychophysics*, *15*, 453–459.
- Ganel, T., & Goodale, M. A. (2003). Visual control of action but not perception requires analytical processing of object shape. *Nature*, *426*, 664–669.
- Ganel, T., & Goshen-Gottstein, Y. (2002). The perceptual integrality of sex & identity of faces: Further evidence for the single-route hypothesis. *Journal of Experimental Psychology: Human Perception and Performance*, *28*, 854–867.

- Ganel, T., & Goshen-Gottstein, Y. (2004). Effects of familiarity on the perceptual integrity of the identity & expression of faces: The parallel-route hypothesis revisited. *Journal of Experimental Psychology: Human Perception and Performance*, *30*, 583–597.
- Garner, W. R. (1974). *The processing of information and structure*. Potomac, MD: Lawrence Erlbaum.
- Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychologica (Amsterdam)*, *107*, 293–321.
- Haxby, J. C., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*, 223–233.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2002). Human neural systems for face recognition and social Communication. *Biological Psychiatry*, *51*, 59–67.
- Henson, R., Shallice, T., & Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science*, *287*, 1269–1272.
- Henson, R. N. A., Goshen-Gottstein, Y., Ganel, T., Otten, L. J., Quayle, A., & Rugg, M. D. (2003). Electrophysiological and haemodynamic correlates of face perception, recognition and priming. *Cerebral Cortex*, *13*, 793–805.
- Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience*, *3*, 80–84.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R., & Tootell, R. B. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. In *Proceedings of the National Academy of Sciences (USA)*, vol. 92 (pp. 8135–8139).
- Murray, S. O., & Wojciulik, E. (2004). Attention increases neural selectivity in the human lateral occipital complex. *Nature Neuroscience*, *7*, 70–74.
- O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature*, *401*, 584–587.
- Pessoa, L., McKenna, M., Gutierrez, E., & Ungerleider, L. G. (2002). Neural processing of emotional faces requires attention. In *Proceedings of the National Academy of Sciences (USA)*, vol. 99 (pp. 11458–11463).
- Pessoa, L., & Ungerleider, L. G. (2004). Neuroimaging studies of attention and the processing of emotion-laden stimuli. *Progress in Brain Research*, *144*, 171–182.
- Posamentier, M. T., & Abdi, H. (2003). Processing faces and facial expressions. *Neuropsychology Review*, *13*, 113–143.
- Rossion, B., Caldara, R., Seghier, M., Schuller, A. M., Lazeyras, F., & Mayer, E. (2003). A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain*, *126*, 2381–2395.
- Schweinberger, S. R., Burton, A. M., & Kelly, S. W. (1999). Asymmetric dependencies in perceiving identity & emotion: Experiments with morphed faces. *Perception & Psychophysics*, *61*, 1102–1115.
- Schweinberger, S. R., & Soukup, G. R. (1998). Asymmetric relationships among perceptions of facial identity, emotion, and facial speech. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 1748–1765.
- Stark, C. E., & Squire, L. R. (2001). When zero is not zero: the problem of ambiguous baseline conditions in fMRI. In *Proceedings of the National Academy of Sciences (USA)*, vol. 98 (pp. 12760–12766).
- Talairach, J., & Tournoux, P. (1998). *Co-Planar stereotaxic atlas of the human brain. Three-dimensional proportional system: An Approach to imaging*. New York: Thieme.
- Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of attention and emotion on face processing in the human brain: An event-related fMRI study. *Neuron*, *30*, 829–841.
- Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience*, *6*, 624–631.
- Winston, J. S., Henson, R. N., Fine-Goulden, M. R., & Dolan, R. J. (2004). fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. *Journal of Neurophysiology*, *92*, 1830–1839.