Early influence of prior experience on face perception

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ABSTRACT

Inferring someone's personality from his or her photograph is a pervasive and automatic behavior that takes place even if no reliable information about one's character can be derived solely from facial features. This illustrates nicely the idea that perception is not a passive process, but rather an active combination of current sensory inputs with endogenous knowledge derived from prior experience. To understand how and when neural responses to faces can be modulated by prior experience, we recorded magneto-encephalographic (MEG) responses to new faces, before and after subjects were exposed for a short period of 15–20 min to an experimentally induced association between a facial feature (inter-eye distance) and a response (personality judgment). In spite of the absence of any observable response bias following such a short reinforcement phase, our experimental manipulation influenced neural responses to faces as early as 60–85 ms. Source localization of magneto-encephalographic signals, confirmed by intracranial recordings, suggests that prior experience modulates early neural processing along two initially independent neural routes, one initiated in an anterior system that includes the orbitofrontal cortex and the temporal poles, and the second one involving face-sensitive regions in the ventral visual pathway. The two routes are both active as early as 60 ms but engage in reciprocal interactions only later, between 135 and 160 ms. These experimental findings support recent models assuming the existence of a fast anterior pathway activated in parallel with the ventral visual system which would link prior experience with current sensory inputs.

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Introduction

We constantly, spontaneously and often unconsciously make inferences on encountered objects and persons (Barrett and Bar, 2009; Todorov et al., 2008; Uleman et al., 2008). For example, the man in blue overalls who is ringing at my door is likely to be the plumber I called this morning, although I never saw him before. Because the smile of the boy on the photograph reminds me of my nephew Joe, I assume this unknown boy to be as mischievous as Joe. In other words, even on a first encounter with someone never met before, we tend to spontaneously infer personality traits and social categories (Bar et al., 2006b; Hassin and Trope, 2000; Weisbuch et al., 2009; Willis and

Todorov, 2006; Zebrowitz, 1997). On a first encounter with someone's portrait, such inferences are bound to be based solely on a visual analysis of facial features, since no other information is available. Facial features tend to be associated to social categories or personality traits, on the basis of either shared social stereotypes (Zebrowitz and Montepare, 2005) or subject-dependent experience.

The association between facial features and some social judgment is flexible and can be manipulated experimentally. For instance, a face that has been presented along with the description of an emotionally positive (resp. negative) behavior is perceived as more positive (resp. negative) on the following encounter (Todorov et al., 2007). Moreover a hidden covariation between a facial feature and a personality trait may influence face evaluative judgment (Barker and Andrade, 2006; Lewicki, 1986). Inferences can also be influenced by the ongoing context: new faces are perceived as more male-looking after an experimentally induced adaptation to female faces (Webster et al., 2004). Thus, overall, behavioral data emphasize the importance of prior experience and knowledge in the formation of impression on faces. Moreover, they suggest a high degree of flexibility of the human brain which continuously adapts its response to incoming stimuli as a function of prior experience.

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What are the neural mechanisms involved in such flexibility? The last years have seen the development of influential theories (Friston et al., 2009; Kersten et al., 2004; Knill and Pouget, 2004; Kveraga et al., 2007a), which hold that visual perception is not a passive process aiming at creating a sensory representation corresponding to a faithful image of the environment, but rather an active combination of knowledge derived from prior experience with current sensory inputs. In the case of impression formation, knowledge about previously encountered faces and associations between physical features and personality traits may shape the neural response to newly encountered faces. The neuroanatomical basis for this combination of past and present experience is far from being well documented. It seems highly likely that some interplay between top-down and bottom-up pathways is involved. Imaging experiments have indeed suggested that prefrontal regions, particularly in their ventral part, exert top-down influences on sensory regions in object and face recognition tasks (Summerfield et al., 2006). Importantly, it has recently been suggested that high-level influences could occur at much earlier latencies than previously thought, namely in the 50–150 ms range (Bar et al., 2006a; Chaumon et al., 2008; Chaumon et al., 2009). However, to what extent these top-down influences may be associated with recent prior experience remains to be firmly established. Moreover, in the particular case of impression formation on persons, when and how structures of the social brain may be involved and interact with visual areas is far from clear (Barrett and Bar, 2009; Todorov et al., 2007; Todorov et al., 2008).

Here, we took advantage of the natural human tendency to automatically draw inferences from the visual appearance of others' face. We tested whether recent prior experience relative to an arbitrary association between a facial trait and a personality label would alter brain responses to new faces. Using magneto-encephalography (MEG), we examined whether the early stages of the neural re-

presentation of faces may be modified as a function of recent experience, and to what extent top-down influences may be involved. During the whole MEG recording session, subjects performed a face categorization task where they had to judge the person presented as either flexible or determined (Fig. 1). After an initial (pre-feedback) phase, subjects went on with the task but were now given a feedback on their performance on a trial-by-trial basis. Unknown to the subjects, this feedback was actually based on an association between inter-eye distance and personality trait. Half of the subjects were given positive feedback if they judged a person with small inter-eye distance as flexible and a person with large inter-eye distance as determined, while this association was reversed for the other half of the subjects. After this feedback phase of about 15 min, the subjects resumed exactly the same task as in the initial phase. Our hypothesis was that the reinforcement of the association between the physical feature (inter-eye distance) and the personality trait (flexible/determined) introduced during the feedback phase would induce a differentiation of the early visual responses to large and small inter-eye distance faces during the post-feedback phase.

Materials and methods

Participants

Eighteen participants took part in this study (11 female, mean age 25.2 ± 0.9 years). All participants were right-handed and had normal or corrected to normal vision. They provided informed written consent and were paid for their participation. All procedures were approved by the local ethics committee (CPP No. 07024). Two subjects were subsequently excluded from the analyses due to eye movement artifacts. Therefore, we analyzed the results of sixteen subjects.
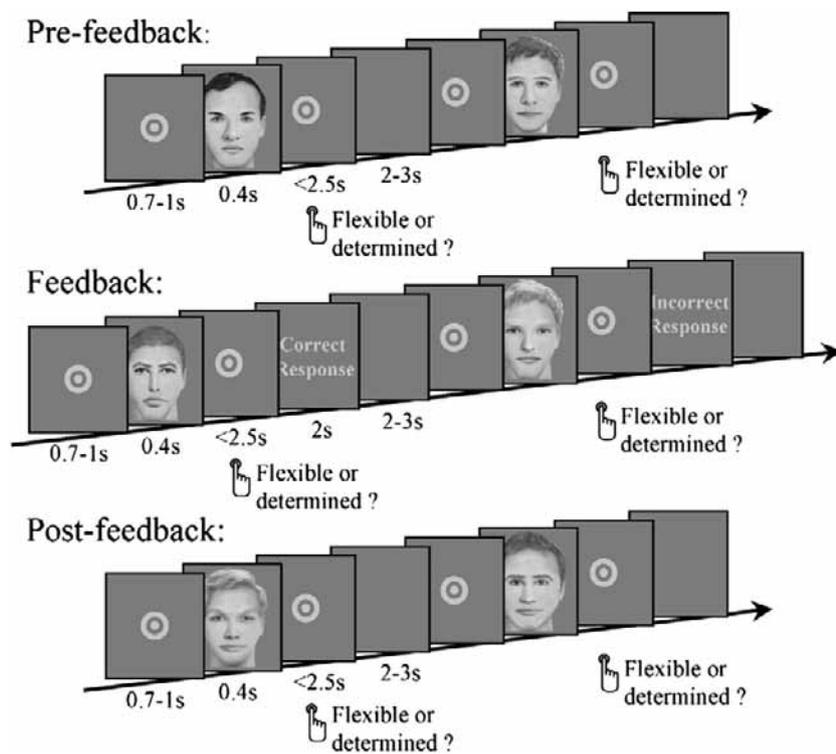
Fig. 1. Experimental design. Each trial started with a central fixation point, followed by a face that was presented for 400 ms and then replaced by the fixation point. Subjects were asked to rate the face as flexible or determined. In the feedback phase, subjects were given a feedback on the accuracy of this personality judgment, which – unknown to the subject – was based on the inter-eye distance of the face presented. We compared MEG responses to small and large inter-eye distance faces, with the hypothesis that differences should be observed in the post-feedback phase only. Note that there was no stimulus repetition across the successive phases of the study, so that every face and every face feature (including the eyes) were new for each phase.

Stimuli

Three hundred and sixty face composites were created with FACES 4.0 software (IQ Biometrix). As described in Fig. 2, we selected 180 exemplars of each of the following face features: eyebrows, eyes, nose, mouth, and jaws as well as 30 haircuts repeated twice in 3 different colors. We then created 12 blocks of 30 faces out of the 180 exemplars of every feature. To build the 30 faces of a block, we first randomly selected 15 exemplars of each feature. By combining the facial features differently, two sets of faces were created, with the sole constraint that no face of the second set shared more than one feature with any face of the first set. Finally, the eyes of the first set of faces were moved away from each other resulting in the large inter-eye distance face pool (mean distance between the eyes = 1.41 ± 0.15° of visual angle). The eyes of the second set of faces were moved closer to each other to create the small inter-eye distance face pool (mean distance between the eyes = 1.21 ± 0.15° of visual angle). Thus, with this procedure for each block, we obtained two sets of faces made of exactly the same facial features, yet consisting in unique combinations of these features so that every face was different. Importantly, there was no low-level difference between the large and the small inter-eye distance face sets except the inter-eye distance per se. The procedure was repeated 12 times to create the 12 blocks of 30 faces used in the experiment. It is worth underlining that each face was seen only once during the experiment. Since influence of prior knowledge and top-down guidance may occur at an early latency (Bar et al., 2006a; Chaumon et al., 2008; Dambacher et al., 2009; George et al., 1997; Morel et al., 2009), we wanted to make sure that repetition effects could not interfere with the results. The faces were presented on a grey background (luminance: 44.5 cd/m²). They covered a visual angle of 5° vertically and 3.6° horizontally.

In addition, for the purpose of control analyses, two additional measures were taken on the stimulus set. Eye brightness was defined as the relative difference in mean gray level between the iris and pupil. Each stimulus could thus be classified as bright or dark-eyed according to a median split of eye brightness values. Face aspect ratio was defined according to Freiwald et al. (2009) definition as the eccentricity of a solid ellipse constituting the face outline (i.e. $\sqrt{1 - \left(\frac{b}{a}\right)^2}$ where b is the half-width of the face and a is its half-height). Each stimulus could thus be classified as large or elongated according to a median split of eccentricity values of our face set.

Procedure

Participants were comfortably seated in an electromagnetically shielded MEG room in front of a translucent screen placed at 85 cm from their eyes. Stimuli were back projected onto the screen through a video projector placed outside of the room and two mirrors inside the MEG room.

Before the recording session began, the participants performed a pseudo morpho-psychological test that was aimed at increasing their confidence in their ability to perform personality judgment based solely on facial traits. During this test, the participants had to choose among four personality traits which ones corresponded best – to their opinion – to presented faces. The flexible/determined labels were not used during this test. The same final score of 85% correct responses was attributed to every participant.

The recording session was divided into three phases, pre-feedback, feedback and post-feedback phases. In each phase, participants had to categorize the presented faces as either flexible or determined. A definition of these personality traits was provided beforehand, ensuring that for both traits, the descriptions contained similar amount of positively and negatively connoted terms, with both the pros and cons of flexible and determined personality.

In each trial, after a variable central fixation period of 0.7 to 1 s, a face stimulus was presented for 0.4 s. It was then replaced by the fixation point. The participant had to indicate whether the face looked
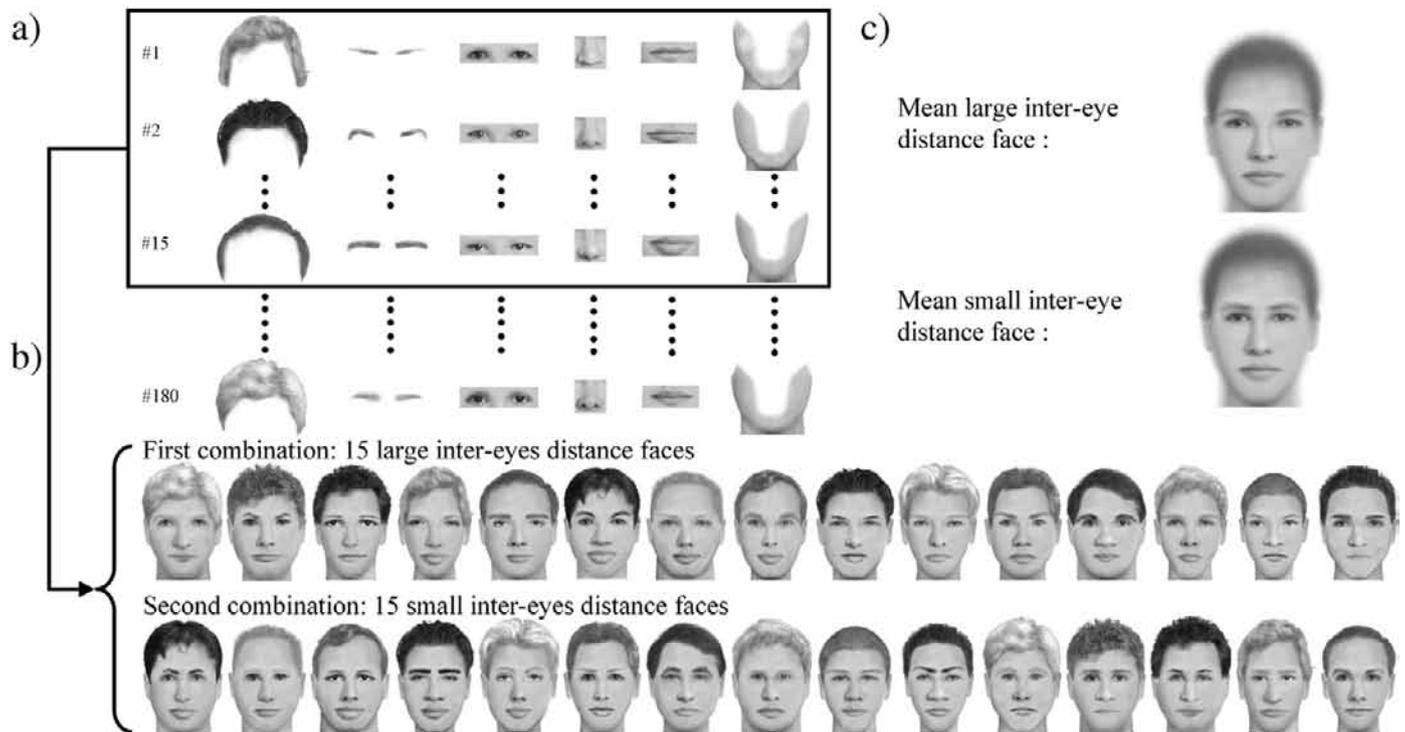
Fig. 2. Stimulus construction. a) Our face set was built out of a pool of 180 exemplars of different facial features. Each experimental block of 30 different faces was built from 15 exemplars of each feature. b) We drew two combinations of these facial features with the sole constraint that across the two subsets of 15 faces no stimulus shared more than one facial feature with any of the others. In this example, within each column, faces shared the same eyes (and only this feature). Inter-eye distance was decreased in the first subset, and increased in the second subset. This procedure was repeated 12 times so that all the 180 features were used once. c) Mean faces in the two conditions of inter-eye distance, showing that only this feature varied across the two conditions.

flexible or determined as soon as possible after the face offset. The maximum response time was 2.5 s. The inter-trial interval (blank screen) varied randomly between 2 and 3 s, allowing time for the participant to blink. The task was the same throughout the three phases. However, in the feedback phase, participants received a 2 s feedback immediately after each of their responses which indicated "correct response" (in green) or "incorrect response" (in red). This feedback corresponded to an arbitrary association between the large or small inter-eye distance and the flexible or determined personality trait respectively. This association was constant for a given subject and counterbalanced across subjects so that for half of the participants, correct responses associated small inter-eye distance with "flexible" response and large inter-eye distance with "determined" response; the association was reversed for the other half. Half of the subjects responded "flexible" with their index finger and "determined" with their middle finger; this stimulus-response mapping pattern was reversed for the other half of the participants, and it was orthogonal to the association between inter-eye distance and personality label.

The pre-feedback, feedback and post-feedback phases were each divided into two runs and each run was composed of 2 (out of 12) blocks of 30 stimuli (15 large/15 small inter-eye distance faces). The blocks that composed the pre-feedback, feedback and post-feedback phases were counterbalanced across subjects. Within each block, the order of face presentation was randomized, so that a given facial trait was repeated (in a different face – see preceding discussion) with a minimum of three intervening stimuli. There was neither face nor face feature repetition across blocks.

At the end of the recording session, the participants went through a questionnaire. They were asked to rank five main face features (eyebrows, eyes, nose, mouth, and global face shape) from the least to the most important for both the flexible and determined judgments. Subjects were then asked to indicate which particular property (size, color, shape, thickness…) was relevant for the two topmost important features that they had chosen.

At the end of the experiment, the participants were informed of the main goal of the study. They were told that the morphological test was a false test and that it is not possible to accurately judge whether someone is flexible or determined based on facial appearance only. Participants were thus informed of the real aims of the study at the end of the experiment only. In that sense, the informed consent they gave at the beginning was only partially valid (Miller and Kaptchuk, 2008). Participants were therefore offered the opportunity to withdraw their data from the research — an opportunity that was not seized by any of the participants.

MEG recordings

Magneto-encephalographic signals were collected continuously on a whole-head MEG system with 151 axial gradiometers (CTF Systems, Port Coquitlam, British Columbia, Canada) at a sampling rate of 1250 Hz (band-pass: DC to 300 Hz). Seventeen external reference gradiometers and magnetometers were included to apply a synthetic third-gradient to all MEG signals for ambient field correction. Three small coils were attached to reference landmarks on the participant (left and right preauricular points, plus nasion) in order to monitor head position. Vertical and horizontal eye movements were monitored simultaneously to the MEG signal with an eye-tracker system (ISCAN ETL-400). The recording also included the signal of a photodiode that detected the actual appearance of the stimuli on the screen within the MEG room. This allowed correcting for the delay introduced by the video projector (20 ms) and averaging event-related magnetic fields (ERFs) precisely time-locked on the actual onset of the face stimulus.

For the purpose of evoked magnetic field analysis, MEG segments from 400 ms before to 400 ms after stimulus onset were extracted from the continuous MEG signal. Trials with saccades (rejection threshold: 1° of visual angle from fixation), eye blinks or muscle artifact were rejected upon visual inspection of the MEG and eye-tracking signals. Average MEG waveforms were then computed, digitally low-pass filtered at 30 Hz and baseline corrected with respect to the 300 ms preceding face onset. Averages were computed separately for each condition of inter-eye distance (small/large) for the pre-feedback and post-feedback phases respectively.

Data analysis

The evoked magnetic fields obtained for the small and large inter-eye distance faces during the pre- and post-feedback phases respectively were averaged across successive 25-ms time windows from 35 ms to 160 ms, to cover the 50–150 ms time range in which differences could be expected (Bar et al., 2006a; Chaumon et al., 2008, 2009). Any difference between evoked responses to small vs. large inter-eye distance faces that exceeded 20 fT was inspected. A difference of 20 fT corresponded to ~10% modulation of the maximal response, an effect size compatible with what is described in the literature. Only a single sensor occasionally exceeded this threshold in the pre-feedback phase. In the post-feedback phase, in addition to occasional isolated sensors, clusters of 5 or more neighboring sensors could be observed. Those clusters of at least 5 neighboring sensors exceeding 20 fT were thus measured and statistically tested.

Source localization and correlation

Cortical current source density mapping was obtained using a distributed source model consisting in 15,000 current dipoles in each subject and condition. Dipole locations and orientations were constrained to the cortical mantle of a generic brain model (Colin Homes) built from the standard brain of the Montreal Neurological Institute using the BrainSuite software package (http://neuroimage. usc.edu). This head model was then warped to the standard geometry of the MEG sensor cap. The warping procedure, all subsequent source analyses and visualization were performed with the BrainStorm software package (http://neuroimage.usc.edu/brainstorm). MEG forward modeling was computed with the overlapping-spheres analytical model. Cortical current maps were then computed from the MEG time series using a linear inverse estimator, the weighted minimum-norm current estimate. We computed the differences of cortical currents for large versus small inter-eye distance conditions and averaged these values for the 3 time windows of interest (60–80 ms, 110–135 ms and 135–160 ms). Only mean differential activities extending over at least 30 contiguous vertices with amplitudes above 60% of the maximal source amplitude were taken into account.

For each region revealed by source localization, we selected the vertex showing the greatest differential activity and his 14 neighbors to define a region of interest (ROI). For each subject and condition, we computed the mean difference between small and large inter-eye distance faces in each ROI and time window of interest. We then computed Pearson correlation coefficients between each region in each time window across subjects.

Intracranial recordings

Two epileptic patients (one 25 years old male and one 43 years old female) gave their written informed consent to participate in the experiment. They both had normal or corrected to normal vision. The project was approved by the local ethics committee. The patients suffered from severe, pharmacoresistant partial epilepsy and were chronically implanted with depth electrodes with a view to surgical treatment (Ad-TechMedical Instruments, Racine, WI, US). Electrodes were composed of 4–10 contacts 2.3 mm long, 10 mm apart, mounted on a 1 mm wide flexible plastic probe. The cerebral structures

explored by intracerebral electrodes were defined according to the localization hypotheses derived from the non-invasive including electro-clinical and neuro-imaging (MRI, PET, SPECT) evaluations (Adam et al., 1996). Contacts located into the epileptogenic zone and/or displaying either spikes or abnormal rhythmic activity were not included in the data analysis. In Patient #1, the epileptic focus was located 1 to 2 cm ventrally and posteriorly to the contacts of interest described in Fig. 5. In Patient #2, the epileptic focus was in the right temporal lobe while the results were obtained in the left temporal lobe. Data were acquired with a Micromed System Plus (Micromed SpA, Mogliano Veneto, Italy) at a sampling rate of 1024 Hz (band-pass: 0.16 to 330 Hz) for Patient #1 and with a Nicolet 6000 (Nicolet-Viasys, Madison, WI, US) at a sampling rate of 400 Hz (band-pass: 0.05 to 150 Hz) for Patient #2, both with respect to a vertex scalp reference. Bipolar recordings between adjacent contacts were computed offline to minimize the influence of distant sources, and low-pass filtered at 30 Hz. A Z score of EEG activity was computed along time for each trial $Z(t) = (x(t) - \overline{BL})/\sigma_{BL}$ where $Z(t)$ is the Z-score value at time t, $x(t)$ is the raw data value at time t, $\overline{BL}$ is the mean baseline value from -300 to 0 ms and σ_{BL} is the standard deviation of the baseline. Evoked potentials were computed by averaging Z-score data across trials under small and large inter-eye distance conditions respectively (time courses on Figs. 5b and e). Z-score transformation allows normalizing the data according to baseline noise level on a trial-by-trial basis, thus avoiding a potential weighting bias toward noisier trials in the intracerebral ERP averages (see Chaumon et al., 2009 for a similar approach).

Statistical differences in evoked responses to small and large inter-eye distance faces in the post-feedback phase were estimated by a randomization procedure. The difference between the evoked responses in the two conditions was compared to an estimate of the expected difference distribution under the null hypothesis. The null distribution of the data was estimated using a randomization procedure repeated 1000 times: trials were randomly assigned to one of two groups of the same size as the actual experimental conditions, and the permuted difference was computed. At each time point, p values were the number of permuted differences reaching a higher level than the difference actually observed between conditions divided by the number of permutations, multiplied by 2 (two-sided randomization procedure).

Results

Behavior

Subjects responded "flexible" as often as "determined" throughout the blocks (mean number of trials per block = 28.1 ± 0.6 for the "flexible" response, 31.2 ± 0.6 for the "determined" response; χ^2 (15) = 14.3, $p = 0.50$) with a mean reaction time of 1095 ± 41 ms. The personality trait judgment was not affected by the feedback phase: the number of responses corresponding to the reinforced association did not increase in the post-feedback phase (mean number of responses corresponding to reinforced association in pre-feedback phase: 60.6 ± 1.3 and post-feedback phase: 60.5 ± 1.5, χ^2(15) = 6.44, $p = 0.97$). Reaction times were not affected by the feedback phase either (mean post-feedback reaction time for the reinforced association: 1070 ± 39 ms, for the non reinforced association: 1065 ± 40 ms; paired t-test: t(15) = 0.39, $p = 0.70$). Post-experiment questionnaires confirmed that the subjects did not report consciously using inter-eye distance for their judgments. Indeed, although 13 out of 16 subjects indicated the eyes as the most relevant feature for the task, only one of these 13 subjects chose inter-eye distance as the relevant property of the eyes, and he reported the wrong association between inter-eye distance and personality label.

The association between inter-eye distance and response introduced during feedback did not result in any observable behavioral bias in the personality judgment task. However, if the statistical regularity of the association between a personality trait and inter-eye distance induced during the feedback phase has been somehow registered, then differentiated neural responses to large versus small inter-eye distance faces might be observed during the post-feedback phase.
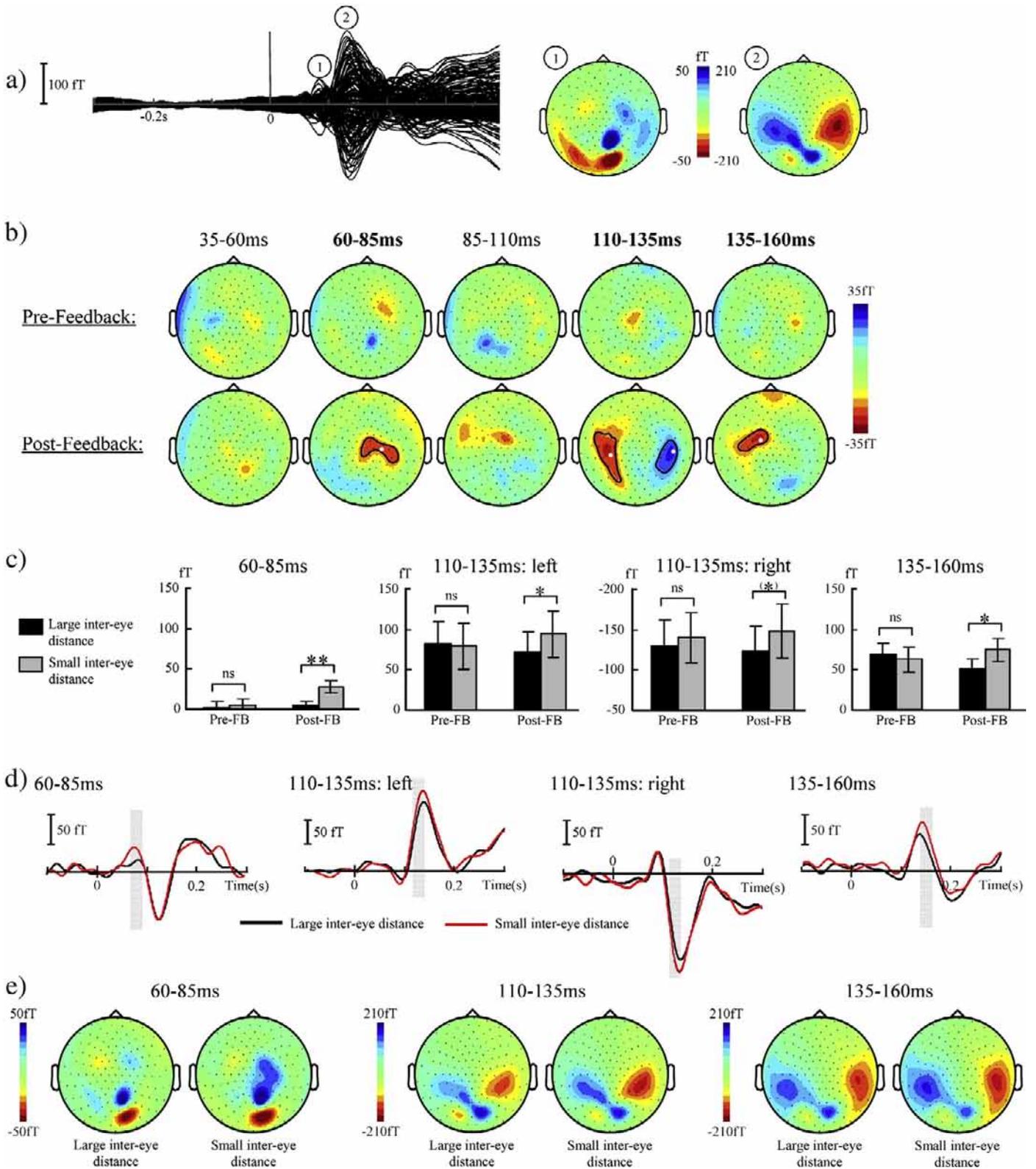
Event-related magnetic fields (ERFs)

Did the feedback phase induce a sensitization to inter-eye distance at the neural level? To evaluate whether responses to large and small inter-eye distance faces differed in the post-feedback phase, we computed the mean amplitude of evoked magnetic fields over five successive 25-ms time windows covering the main peaks of activity (Fig. 3a) between 35 and 160 ms. In each time window, any difference between the magnetic responses to large and that to small inter-eye distance which exceeded 20 fT over 5 contiguous sensors was systematically tested. We averaged the ERF value over the sensors above threshold and computed a paired t-test on mean ERF amplitude for large versus small inter-eye distance conditions. This systematic measurement approach was first applied independently to both the pre- and the post-feedback phases to test for any difference in ERFs to large and small inter-eye distance faces in either phase (Fig. 3b).

This analysis revealed significant differences between small and large inter-eye distance faces during the post-feedback period only. During this phase, an early differential activity for small versus large inter-eye distance faces was observed as soon as between 60 and 85 ms (9 sensors above the 20 fT threshold). This early differential response was highly significant (t(15) = 3.31, $p < 0.005$). Later, ERFs to small and large inter-eye distance faces differed between 110 and 135 ms over the left temporal region (11 sensors, t(15) = −2.40, $p < 0.03$). The difference approached significance over the right temporal regions (5 sensors, t(15) = 2.07, $p = 0.056$). Finally, the difference in mean ERF amplitude was sustained between 135 and 160 ms on left anterior temporo-central sensors (7 sensors, t(15) = −2.26, $p < 0.04$). We further checked that these results were not dependent on the length of the time window of analysis: using shorter time windows (15 or 20 ms) did not alter the nature of the results.

Were these differential responses to large and small inter-eye distance faces due to the feedback phase, or could they be attributed to some pre-existing differential processing of faces with small versus large inter-eye distance? No group of 5 sensors exceeded, nor even approached, the 20 fT threshold during the pre-feedback phase, as can be seen in Fig. 3b. At most, only a single sensor exceeded the 20 fT threshold in the pre-feedback phase. In addition, to ensure that the post-feedback differential responses to large and small inter-eye distance were not present during the pre-feedback period, we measured the mean amplitude of pre-feedback ERFs over the same sensor sets as those selected on the basis of their post-feedback activity. This confirmed that there was not any trend toward a pre-existing differential response for large and small inter-eye distance over these sensors of interest (Fig. 3c), in either time window (all t (15) < 1.10, all $p > 0.32$). To conclude, there was not any significant difference between evoked responses to large and small inter-eye distance faces in the pre-feedback phase, whereas in the post-feedback phase, neural responses significantly differed as a function of inter-eye distance as early as from 60 to 85 ms.

A differential response to large and small inter-eye distance thus seemed to be induced by the feedback phase. Did this difference truly reflect the relevance of inter-eye distance for the task, or did it reflect a mere sensitization to the overall structure of our stimuli? Indeed, throughout the experiment, subjects were exposed to new faces that could be categorized as having small or large inter-eye distance, which is a salient configural feature of the faces. The difference observed could reflect an automatic sensitization to the intrinsic configural distribution of inter-eye distances in the stimulus set,

Fig. 3. Early dissociation along inter-eye distance. a) Left, superimposed time courses of the event-related magnetic fields (ERFs) over the 151 sensors, averaged across all faces in both pre- and post-feedback phases. Right, topography of ERFs at the two main peak latencies (83 ms and 132 ms). b) Mean ERF difference between large and small inter-eye distance faces in pre-feedback (top) and post-feedback (bottom) phases during five successive 25-ms time windows. The black contours delineate the regions of interest (ROI), which showed a difference of at least 20 fT over at least five contiguous sensors. c) Mean (and standard error of the mean) activity in identified ROIs for large and small inter-eye distance faces during pre- and post-feedback phases, for the three time windows of interest. (**$p < 0.01$; *$p < 0.05$; (*)$p < 0.1$; ns, non significant). d) ERFs to large (black) and small (red) inter-eye distance faces in the post-feedback phase, grand averaged across subjects, at the sensors of interest indicated by white dots on the topographical maps. e) Mean ERF topographical maps for large and small inter-eye distance conditions in each time windows of interest.

rather than an actual influence of the reinforced feature. Furthermore, it is also possible that our effect arose from an increased attention to the eye region favored by the feedback phase, yet non-specific to inter-eye distance per se. To rule out these hypotheses, we selected two other properties of the face: one that also concerned the eyes but was featural, namely eye brightness, and the other that concerned another important configural property of the faces and to which face neurons have been found to be highly sensitive (Freiwald et al., 2009; Tsao et al., 2008), namely face aspect ratio. We thus tested each previously identified time window of interest for differential post-feedback responses to eye brightness or face aspect ratio. There was not any post-feedback difference in the ERFs for dark versus bright eyes or for large vs. elongated faces which reached the 20 fT threshold over more than a single sensor in either time window: 60–85 ms, 110–135 ms, and 135–160 ms. In addition, we determined the threshold at which clusters of at least 5 neighboring sensors emerged in every time window of interest. We had to lower the threshold from 20 fT down to 12 fT (eye brightness) and 8 fT (face aspect ratio). Thus our post-feedback effects of inter-eye distance do not seem to be explained either by sensitization to the stimulus set structure or by increased unspecific attention to the eye region.

Finally, in order to further examine whether sensitization to inter-eye distance per se but independent of the feedback phase could account for our results, we examined whether there was some hint for such sensitization developing over the experiment. In other words, if sensitization to inter-eye distance occurred, there should be some hint of this sensitization when comparing the 1st and 2nd blocks of the pre-feedback period as well as greater effects in the 6th than the 5th blocks during the post-feedback phase. We therefore compared the amplitude of ERF difference between small and large inter-eye distance faces in the 1st and 2nd blocks of the pre-feedback period. There was no trend to an emergence of a difference (sum of ERF differences, over all sensors and time windows of interest = 1.74 fT in the 1st block, 0.3 fT in the 2nd block; $p > 0.70$ in both blocks). We also examined the ERF differences between small and large inter-eye distance in the 5th and 6th blocks (i.e. post-feedback blocks). If anything, the inter-eye distance effect observed in the 5th block, just after the feedback period, tended to be more marked, with a sum of ERF differences over the sensors and time windows of interest of 29.5 fT in the 5th block ($p < 0.01$), and of 14.9 fT in the 6th block ($p = 0.11$). Note that the statistical power of these analyses per run was inevitably limited, since signal-to-noise ratio was lower in this block-by-block analysis, and p values are only reported here descriptively.

In sum, the difference of magnetic responses to large and small inter-eye distance faces found in the post-feedback phase did not seem attributable either to a mere sensitization to the intrinsic structure of the stimulus set or to a non-specific increase of attention toward the eye region. Rather it seemed that the regular association between inter-eye distance and the subject's response introduced during the feedback phase resulted in sensitized brain responses to inter-eye distance, with differentiated responses to large and small inter-eye distance faces as early as between 60 and 85 ms.

Source localization and correlation analysis

To confirm our findings and determine the regions that encoded differentially inter-eye distance, we estimated the cortical sources activated by small and large inter-eye distance faces in the post-feedback phase, and computed the mean source amplitude difference in the three time windows of interest, 60–85 ms, 110–135 ms and 135–160 ms. This revealed a spatially and temporally structured network of activated regions (Fig. 4). Differential encoding of inter-eye distance begun in the orbitofrontal area and temporal pole, as well as in a lateral inferotemporal region between 60 and 85 ms. Then, the activity from the lateral inferotemporal region spreads into the
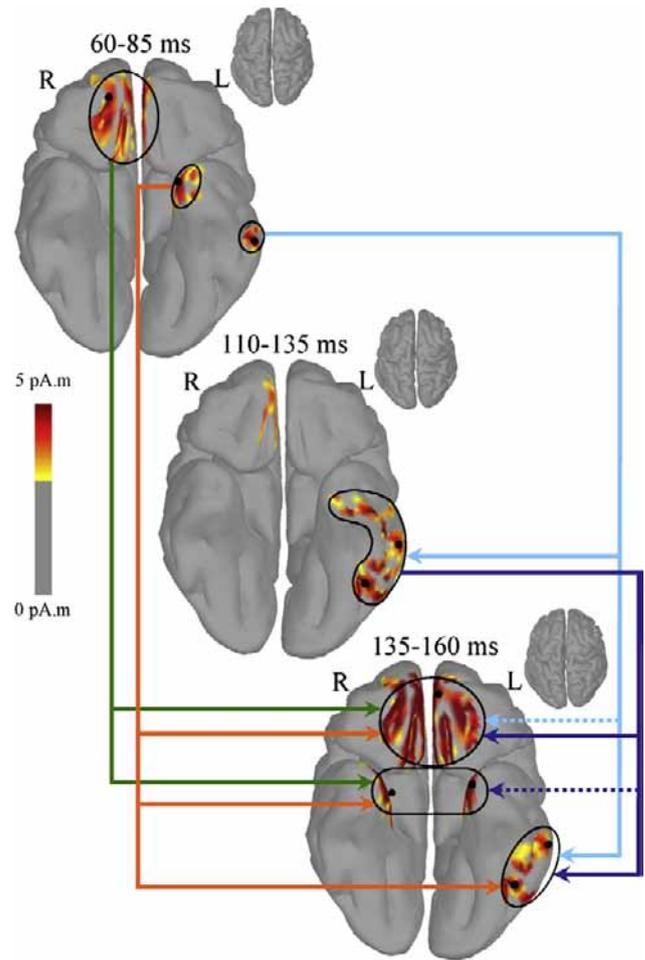
Fig. 4. Regions differentially activated by small and large inter-eye distance faces in the post-feedback phase. Results are presented in the three windows of interest (60–85 ms, 110–135 ms and 135–160 ms), on a ventral view of the brain. The dorsal view is also presented as a small inset. Only regions that show the 60% topmost difference over at least 30 contiguous vertices are displayed. Black dots indicate the vertices showing the largest differences in each region. Black contours delineate regions that respond in a similar manner and that display similar correlations with other areas. Colored arrows indicate the significant correlations between regions across the time windows and doted arrows show near significant correlations. The complete list of correlation values can be found in Table 1. R: right hemisphere; L: left hemisphere.

ventral visual pathway, toward both more anterior and more posterior regions of the ventral inferotemporal cortex, between 110 and 135 ms. Finally, between 135 and 160 ms, the lateral and posterior parts of the inferotemporal regions remained differentially activated while a re-activation of orbitofrontal and temporopolar regions was observed bilaterally. There was not any other differentially activated region.

In order to ensure that the differential activity located in the orbitofrontal areas could not be related to uncontrolled eye movement differences, we averaged eye-tracker signals for the two conditions of inter-eye distance in the post-feedback phase. The analysis of this signal over the two time windows (60–85 ms and 135–160 ms) where orbitofrontal sources were found did not reveal any significant effect of eye movements either in the vertical or in the horizontal directions (all t(15) < 1.4, all $p > 0.15$).

We then sought to determine whether the clusters of differentially activated brain sources were independent from each other, or whether they were functionally coupled. Specifically, we tested if neural activity in a given region and in a given time window would influence the activity of another brain region in the same or a later

time window. To that aim, we selected the maximally activated vertex and its 14 neighboring vertices for each region identified in every time window of interest and we computed the Pearson correlation coefficient between the mean amplitudes of these source clusters across subjects (Table 1 and Fig. 4). The early (60–85 ms) source activation in orbitofrontal and temporopolar regions significantly correlated with the late (135–160 ms) re-activation within these regions, but also and more interestingly with the 135–160 ms activity in the inferotemporal regions (significant correlation between the 60–85 ms activity in the left temporal pole and the 135–160 ms activity in the ventral inferotemporal cortex). By contrast, correlations between the early sources in the orbito-temporopolar regions and the 60–85 ms or 110–135 ms sources in the inferotemporal regions were weak and did not reach significance. This pattern of results suggest that the anterior areas and the ventral visual regions were initially activated in parallel, and interacted at a later stage, between 135 and 160 ms. In line with this idea, source activation in the inferotemporal regions between 110 and 135 ms correlated with the late (135–160 ms) source activations in the orbitofrontal region – and to lesser extent – in the temporopolar regions. There was also a trend to a correlation between the early (60–85 ms) activity in the lateral inferotemporal region and the late orbitofrontal activation. Furthermore, the early (60–85 ms) source activation in the lateral inferotemporal region correlated with the source activation in inferotemporal regions between 110 and 135 ms and between 135 and 160 ms.

Overall, these results suggest two distinct routes by which prior experience influenced early neural responses to the faces in the post-feedback phase. The first one originates in the lateral inferotemporal cortex between 60 and 85 ms and spreads its influence along the ventral inferotemporal regions. The second one stems from the orbitofrontal cortex and temporal pole as early as 60–85 ms. At 135–160 ms, there is reciprocal influence between the orbito-temporopolar route and the inferotemporal regions. This suggests that at 135–160 ms, information from the two routes is fully integrated in a distributed and recurrent network comprising the orbitofrontal cortex and temporal poles on the one hand and the lateral and ventral inferotemporal regions on the other hand.

Intracranial data

We had the opportunity to confirm the anatomical localization of the early differential effects in intracranial recordings in 2 patients. This is all the more important that source localization of MEG data was obtained on an anatomical template, not on individual MRIs. One patient's implantation schema included an electrode in the orbitofrontal cortex (Fig. 5a). We systematically tested the difference between small and large inter-eye distance faces during the post-feedback phase by computing mean amplitude of EEG signal in sliding 10-ms time window from −300 ms to +400 ms, for every trial. The only significant differences ($p<0.05$, two-sided randomization procedure) were observed from 61 to 82 ms as well as later on, between 288 and 309 ms (Fig. 5b), in the post-feedback phase. No significant difference was observed in the pre-feedback phase. We then checked (Fig. 5c) that the mean 61–82 ms EEG amplitude significantly differed between small and large inter-eye distance faces during the post-feedback phase ($p<0.03$) but not during the pre-feedback phase ($p = 0.32$, two-sided randomization procedure).

In addition, the posterior inferotemporal region was investigated in another patient (Figs. 5d, e and f). The same procedure revealed a significant difference in electrical response to small and large inter-eye distance stimuli during the post-feedback phase from 112 to 125 ms ($p<0.05$, two-sided randomization procedure).No significant difference was observed in the pre-feedback phase. We further checked that the mean 112–125 ms EEG amplitude differed significantly for small versus large inter-eye distance during the post-feedback phase only ($p<0.04$), whereas it was nonsignificant in the pre-feedback phase ($p = 0.15$).

Discussion

We show that when attempting to infer one's personality from his/her photograph, a short exposure to an unconscious association rule between a facial feature and a personality trait influences the neural responses to newly encountered faces at surprisingly early latencies. Differential responses that were specific to the manipulated facial feature, namely inter-eye distance, emerged as early as around 70 ms. Source localization, confirmed by intracranial recordings, suggests that the early differential response, around 70 ms, stems from the orbitofrontal cortex and temporal poles on the one hand, and from the lateral convexity of the temporal lobe on the other hand. The latter activity spreads around 120 ms in the ventral visual pathway. Last, correlation measures suggest that these two routes are initially independent but influence each other around 150 ms.

Reinforcing the association between inter-eye distance and the subject's response induced a differential neural activity to small and large inter-eye distance faces which was not present in the pre-feedback phase. Because the onset latency of the effect was very early, around 70 ms, it is worth examining whether it could be due to another parameter than the associative reinforcement between inter-eye distance and personality judgment. Low-level differences between stimuli other than related to inter-eye distance can in principle be ruled out, since stimuli were counterbalanced between subjects and small and large inter-eye distance faces did not differ on average apart from their inter-eye distance. Mere repetition effects cannot have influenced the results since each face was presented only once during the experiment. Moreover, although each facial feature was seen twice, it was always within the same phase and therefore cannot account for any difference between pre- and post-feedback phases. However, subjects could have become sensitized on inter-eye

Table 1
Pearson correlation coefficients between each region in each time window.

	Regions	60–85 ms			110–135 ms		135–160 ms				
		Orbitofrontal	Left TP	Lateral IT	Lateral IT	Ventral IT	Orbitofrontal	Left TP	Right TP	Lateral IT	Ventral IT
60–85 ms	Orbitofrontal	—	**0.88*****	0.12	0.07	0.13	**0.74****	**0.81*****	**0.82*****	0.13	0.33
	Left TP		—	0.28	0.25	0.31	**0.73****	**0.80*****	**0.85*****	0.35	**0.57***
	Lateral IT			—	**0.80*****	**0.83*****	**0.50**(*)	0.29	0.35	**0.74****	**0.81*****
110–135 ms	Lateral IT				—	**0.94*****	**0.54***	**0.42**(*)	**0.43**(*)	**0.94*****	**0.84*****
	Ventral IT					—	**0.59***	**0.46**(*)	**0.43**(*)	**0.86*****	**0.88*****
	Orbitofrontal						—	**0.92*****	**0.91*****	**0.57***	**0.73****
135–160 ms	Left TP							—	**0.95*****	**0.47**(*)	**0.64****
	Right TP								—	**0.50***	**0.62****
	Lateral IT									—	**0.87*****
	Ventral IT										—

Note. Significant and near significant correlations ((*)$p \leq 0.1$; *$p<0.05$; **$p<0.01$; ***$p<0.001$) are highlighted in bold font. TP: temporal pole; IT: inferotemporal.
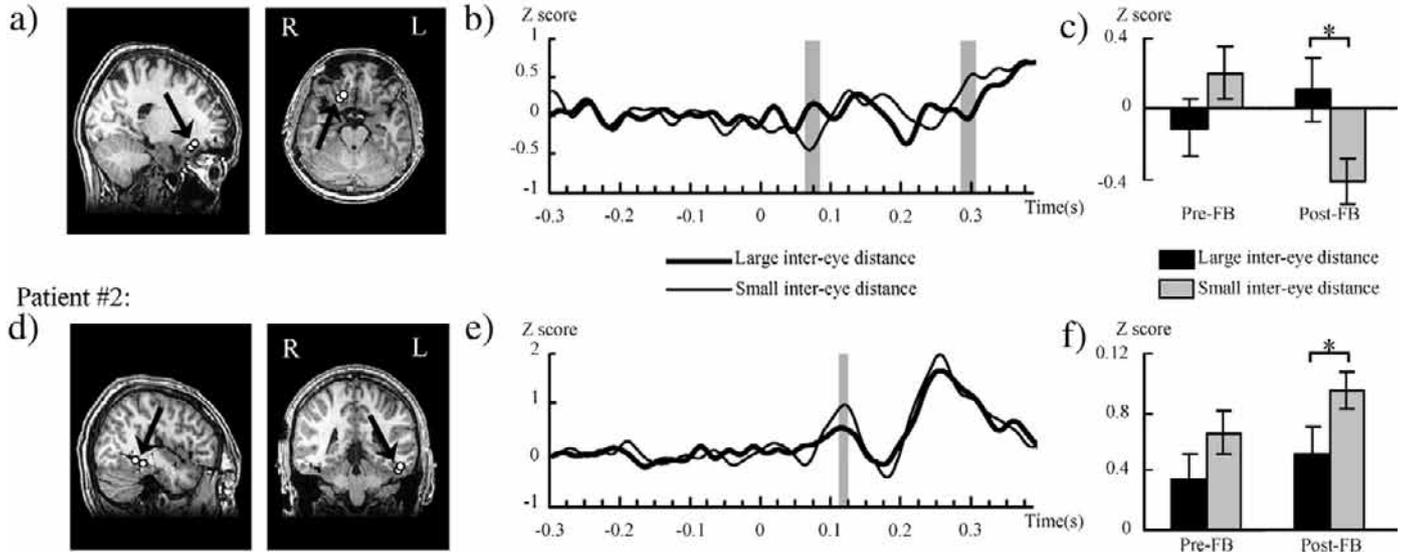
Fig. 5. Intracranial recordings. a) and d) Anatomical MRIs showing the recording sites. R: right hemisphere; L: left hemisphere. b) and e) Time course of the Z-transformed bipolar intracranial evoked potentials, in response to small (thin line) and large (thick line) inter-eye distance faces, during the post-feedback phase. The time windows revealing significant differences are highlighted in gray. c) Mean 61–82 ms response (and standard error of the mean) in the orbitofrontal cortex for small (gray bar) and large (black bar) inter-eye distance faces, in the pre- and post-feedback phases (*$p<0.05$). f) Mean 112–125 ms response (and standard error of the mean) in the posterior inferotemporal region for small (gray bar) and large (black bar) inter-eye distance faces, in the pre- and post-feedback phases (*$p<0.05$).

distance in a task-independent manner. If this were the case, then 1) subjects should become sensitized on other facial features that are not relevant for the task and 2) differences between small and large inter-eye distance faces should develop gradually during the experiment, not appear abruptly after the feedback phase. We first checked that no differential response emerged for task-irrelevant features such as eye brightness (which is another salient feature of the eyes) or face aspect ratio (which is another configural facial feature to which inferotemporal neurons are sensitive (Freiwald et al., 2009). No differentiated magnetic responses could be observed in the post-feedback phase for these face features at which the participants were not trained at and that were not relevant for the task. Second, differences between small and large inter-eye distance faces were more pronounced immediately after the feedback phase. The emergence of a difference in the visual processing of large and small inter-eye distance faces therefore appears to be due to the reinforcement rule based on inter-eye distance.

Despite the influence of the reinforcement rule on neural activity, it did not produce any observable bias in personality judgment. Thus, the early neural processes described here, in the first 150 ms of activity, appear to be well upstream from decision making and personality judgment that occurred on average at 1095 ms. Several explanations might account for this surprising dissociation between behavioral performance and neural activity. First, judging someone's personality from his photograph is bound to be influenced by multiple sources of knowledge, some of them highly subject-dependent. For instance one person may look like your former supervisor who was highly determined. The large number of variables that can be involved in social judgments may explain the lack of consistency in behavioral results of previous studies, which reported biased judgments with longer (Lewicki, 1986) or faster (Barker and Andrade, 2006) reaction times as well as weak or negative findings (Bos and Bonke, 1998; Hendrickx et al., 1997). Thus, our experimental manipulation of a single variable among the vast amount of information gathered through life-long experience may not have been sufficient to directly influence the final decision. Second, the feedback phase was quite short, about 15 min. It is possible that a longer feedback phase might have led to a measurable behavioral effect. Third, the behavioral

measure we used may not have been sensitive enough to reveal such behavioral effect. Confidence ratings or wagering for instance might be better suited to capture a subtle behavioral difference in the post-feedback phase (Persaud et al., 2007). Here, the manipulated variable clearly affected early neural responses, showing that the brain evaluates the relevant feature at early processing stages although this piece of information did not influence significantly later decisional stages. This brain/behavior dissociation is reminiscent of previous findings in patients with ventral prefrontal lesions whose behavioral impairment could be assessed experimentally only using an especially designed gambling task (Bechara et al., 2000; Damasio, 1994).

The first hint of a differential processing of large and small inter-eye distance faces in the post-feedback phase occurs surprisingly early, around 70 ms. This result is in line with a growing body of evidence showing that visual categorization mechanisms could be much faster than previously thought (Liu et al., 2002; Meeren et al., 2008; Thorpe et al., 1996). Thus several studies have shown that visual responses can be modulated even before 100 ms by various cognitive factors. Such modulations have been reported for attention (Kelly et al., 2008; Poghosyan and Ioannides, 2008), perceptual learning (Pourtois et al., 2008), implicit categorization (Meeren et al., 2008; Mouchetant-Rostaing and Giard, 2003; Pourtois et al., 2005; Thorpe et al., 1983), as well as prior knowledge on words (Dambacher et al., 2009) or abstract visual scenes (Chaumon et al., 2008), and for the combination of experience- and emotion-related factors (Morel et al., 2009; Stolarova et al., 2006). Our results extend on previous findings on fast visual mechanisms in two respects. First, we show that such mechanisms can operate flexibly, depending on recent reinforcement history since the implicit categorization rule introduced through simple feedback altered MEG responses to faces after only 15–20 min of training. Second, we confirm that these mechanisms can operate totally unconsciously as subjects had no explicit knowledge about the underlying task's structure (Chaumon et al., 2008, 2009). Moreover, our results provide a detailed spatial and temporal characterization of the very first steps of neural categorization. Two initially independent routes were differentially activated by different values of the relevant feature around 70 ms. The first

route involves the lateral and ventral inferotemporal lobe, and the other originates in the orbitofrontal and temporopolar regions.

The temporal route showed differential responses as early as 70 ms on the lateral convexity, with this differential activity then spreading to the ventral inferotemporal cortex both posteriorly and anteriorly. The location of these source clusters are in line with the face-responsive regions typically observed in humans, along the lateral convexity (Allison et al., 1999; Puce et al., 1998), the posterior fusiform gyrus (Hadjikhani et al., 2009; Kanwisher et al., 1997) and more anteriorly in the vicinity of the human homologue of the anterior face patch (Kriegeskorte et al., 2007; Rajimehr et al., 2009). Face-responsive regions typically contain neurons that are sensitive to inter-eye distance (Freiwald et al., 2009; Tsao and Livingstone, 2008). Prior experience might affect either the sensitivity of these neurons or foster their spatial segregation, the two alternatives being not mutually exclusive. Thus, we show that face (and eye) responsive regions in the ventral and lateral temporal lobe are altered by training, in line with previous findings showing that experience alters the brain regions that were already responsive to the manipulated stimulus properties before training (Gauthier and Tarr, 1997; Li et al., 2009; Op de Beeck et al., 2006; Sigala and Logothetis, 2002). As for the temporal dynamics of these brain regions, the influence of training in the ventral inferotemporal cortex, around 120 ms, is consistent with electrophysiological data in monkeys (Sigala and Logothetis, 2002; Vogels, 1999), although pioneer work in humans suggested slightly longer latencies, around 170 ms (Bentin et al., 2002). We add to this previous literature an earlier effect of experience, located on the lateral convexity. This latter region is known to be sensitive not only to faces (Allison et al., 1999) but also more specifically to eyes (Puce et al., 1998), and it seems to be particularly sensitive to new faces as early as 75 ms (Pourtois et al., 2005; Seeck et al., 1997).

The very first steps of neural categorization also involved an anterior route with a differential activation of the orbitofrontal cortex and of the temporal pole around 70 ms. These two structures are known to be tightly coupled both anatomically (Barbas, 2007; Carmichael and Price, 1995b; Markowitsch et al., 1985; Pandya and Seltzer, 1982) and functionally (Olson et al., 2007; Simmons et al., 2010), and they both belong to the social brain (Olson et al., 2007; Rolls, 2007). The temporal pole region has been consistently found to respond at surprisingly early latencies, including responses in the 60–90 ms range (Chaumon et al., 2009; Eifuku et al., 2004; Kiani et al., 2005; Wilson et al., 1983; Xiang and Brown, 1998). With regard to the orbitofrontal region, Bar et al. (2006a) reported an activation in the 100–150 ms time range, whereas Chaumon et al. (2009) and Rudrauf et al. (2008) reported orbitofrontal and temporopolar activities around 100 ms and Bayle and Taylor (2010) found medial orbital frontal sources of MEG signals around 90 ms. The orbitofrontal involvement in the present study was even earlier, beginning in the 60–85 ms time window. The source of this discrepancy is somewhat unclear as the material and paradigm were very different across studies. Chaumon et al. (2009) studied implicit visual memory associated with visual scenes composed of T and L, Bar et al. (2006a) focused on visual (non face) object recognition, whereas Rudrauf et al. (2008) and Bayle and Taylor (2010) studied emotion perception from scenes and faces respectively (see also Kawasaki et al., 2001). It is possible that the nature of both tasks and stimuli as well as the type of top-down influence manipulated may influence the latency of the effects found. In our case, the conjunction of the use of highly relevant stimuli (i.e. faces) in a categorical person perception task (to which humans appear to be naturally inclined (Macrae and Bodenhausen, 2000)) might have fostered the observation of particularly early effects involving the temporopolar and orbitofrontal regions.

There are a number of potential connectivity patterns which may subtend these fast responses. Inputs going through the geniculo-striate pathway could reach the temporal pole directly from area V4 through the inferior longitudinal fasciculus (Catani et al., 2003), or the orbitofrontal cortex through a dorsal relay (Carmichael and Price, 1995a; Cavada and Goldman-Rakic, 1989). Two subcortical pathways could also be involved. The first one is the hypothetical direct route toward the amygdala (LeDoux, 1996; Liddell et al., 2005). This region can be activated as soon as 20–30 ms (Luo et al., 2007) and is closely connected with orbitofrontal and temporopolar areas (Amaral and Price, 1984; Cavada et al., 2000; Ghashghaei and Barbas, 2002; Markowitsch et al., 1985; Rolls, 1999). The other potential subcortical pathway implies the pulvinar, since this structure is connected to both the orbitofrontal and temporopolar cortices (Bos and Benevento, 1975; Romanski et al., 1997; Webster et al., 1993) and can be strongly activated as early as 80 ms (Ouellette and Casanova, 2006).

In our experiment, the orbitofrontal and temporopolar regions were differentially activated in the same latency range and influenced the ventral stream in a quite similar manner. The temporal pole is known to link person-specific memories to perceptual representations of faces (Olson et al., 2007; Simmons et al., 2010; Tsukiura et al., 2003). However the information learnt in the present experiment was not specific to a given face; rather, it reflected a social rule linking a physical feature to a personality trait. In that sense, our results are in line with the proposal that the temporal pole could support conceptual knowledge of social behaviors (Zahn et al., 2007). The orbitofrontal region is also well known as an emotional and social region (Barbas, 2007; Rolls, 2007). Furthermore, it is more generally involved in reinforcement-guided behavior (Rushworth et al., 2007). Taken together, this suggests a role for the orbito-temporopolar complex in establishing socially relevant association rules (Rushworth et al., 2007).

Our results highlight two parallel processing routes that were activated rapidly and initially independently. These two routes influenced each other after about 150 ms of neural processing. This is in the line with recent models that suggest an activation of anterior regions in parallel with the well-established visual stream. One of these models is the two-pathway model of emotional processing (LeDoux, 1996; Rudrauf et al., 2008; Vlamings et al., 2009; Vuilleumier, 2005) which assumes that visual ventral stream activation occurs in parallel with a short-cut pathway through anterior regions such as the orbitofrontal area and temporal poles. This anterior route would enhance the saliency of emotional stimuli by modulating responses in the ventral visual pathway (Morris et al., 1998). A related view posits that the orbitofrontal region integrates somatic markers with incoming events to help subjects to navigate themselves through emotionally laden situations (Dalgleish, 2004). The other model deals more generally with visual perception (Bar, 2003; Kveraga et al., 2007b) and holds that a coarse representation, based on magno-cellular inputs (Kveraga et al., 2007a), would be quickly activated in the orbitofrontal region as an initial guess about the nature of the object presented (Bar et al., 2006a). This representation would then be refined by interactions with the ventral pathway. In the present experiment, we find a modulation of early brain responses involving both anterior and ventral visual pathways, which were activated initially independently and influenced each other reciprocally around 150 ms. This modulation was induced by a recent exposure to a reinforcement schema and was specific of the reinforced feature. We propose that the two types of dual route models dealing with either emotion or visual perception could be integrated into a more comprehensive view. In this view, the role of the anterior route would be to link relevant prior experience to current sensory inputs. The nature of the experience could in principle vary a lot, including emotional context, motivational factors, guesses about the most likely object identity, or relevance of specific features as in the present case, but the anatomical substrate could remain the same and constitute the basis for a generic proactive neural mechanism (Bar, 2009; Bechara et al., 2000).

Conclusion

To conclude, our results underline the ability of the visual system to modulate even its earliest responses to incoming sensory inputs as a function of recent and unconscious experience. Our results further confirm the idea of an anterior route involving the temporal poles and orbitofrontal cortex, activated at very early latencies, and whose role would be to link prior experience with the current sensory inputs encoded in parallel in the ventral visual pathway. In the particular case of person perception, the ability of the anterior and ventral routes to signal the existence of an association between a facial feature and a personality label may be one of the basic components of the neural machinery subtending the automatic and pervasive process of personality inference from facial appearance.

Acknowledgments

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