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Early selection of diagnostic facial information in the human visual cortex

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Abstract

There is behavioral evidence that different visual categorization tasks on various types of stimuli (e.g., faces) are sensitive to distinct visual characteristics of the same image, for example, spatial frequencies. However, it has been more difficult to address the question of how early in the processing stream this sensitivity to the information relevant to the categorization task emerges. The current study uses scalp event-related potentials recorded in humans to examine how and when information diagnostic to a particular task is processed during that task versus during a task for which it is not diagnostic. Subjects were shown diagnostic and anti-diagnostic face images for both expression and gender decisions (created using Gosselin and Schyns' *Bubbles* technique), and asked to perform both tasks on all stimuli. Behaviorally, there was a larger advantage of diagnostic over anti-diagnostic facial images when images designed to be diagnostic for a particular task were shown when performing that task, as compared to performing the other task. Most importantly, this interaction was seen in the amplitude of the occipito-temporal N170, a visual component reflecting a perceptual stage of processing associated with the categorization of faces. When participants performed the gender categorization task, the N170 amplitude was larger when they were presented with gender diagnostic images than with expression-diagnostic images, relative to their respective non-diagnostic stimuli. However, categorizing faces according to their facial expression was not significantly associated with a larger N170 when subjects categorized expression diagnostic cues relative to gender-diagnostic cues. These results show that the influence of higher-level task-oriented processing may take place at the level of visual categorization stages for faces, at least for processes relying on shared diagnostic features with facial identity judgments, such as gender cues.

Keywords: Face perception; Event-related potentials; N170; Diagnostic information

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1. Introduction

To reliably categorize stimuli such as the face in Fig. 1, observers must attend to the information that is most appropriate—i.e., diagnostic—for the task at hand. For example, if the task were to determine the gender of the face, a typical human observer would only require the diagnostic face information that is represented in Fig. 1C. If the task was instead to judge whether the faces are smiling or not, the same observer would use the diagnostic cues represented in Fig. 1A (Schyns, Bonnar, & Gosselin, 2002). Such selective use of diagnostic information is critical to the understanding of high-level visual recognition processes (Schyns, 1998).

The complement of diagnostic information will be here called "anti-diagnostic" as it captures the information that is less useful for the task at hand. For example, the information shown in Fig. 1D is the least useful to resolve gender, while Fig. 1B represents the anti-diagnostic information to

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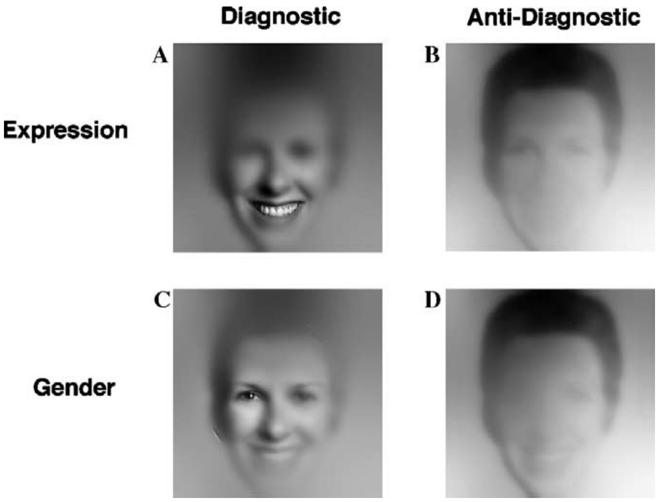

Fig. 1. (A) A face from the 20 greyscale face set from Schyns et al. (2002). (A and B) Pertain to the EXNEX condition: (A) diagnostic, (B) anti-diagnostic. (C and D) Pertain to the GENDER condition: (C) diagnostic, (D) anti-diagnostic.

distinguish between neutral and happy faces. Diagnostic and anti-diagnostic information for these different categorization tasks were disclosed using the *Bubbles* technique (for special issues on this and related techniques, such as reverse correlation, see Gosselin & Schyns, 2004 & Eckstein & Ahumada, 2002). This technique confronts an observer with visual information randomly sampled from stimuli in order to derive the information samples leading to better recognition performance, namely the diagnostic information to perform the task. By applying *Bubbles* to the categorization of faces, one can obtain a view of the facial cues diagnostic for the task at hand (Gosselin & Schyns, 2001; Schyns et al., 2002; for applications of reverse correlation to faces see also Mangini & Biederman, 2004 & Sekuler et al., Sekuler, Gaspar, Gold, & Bennett, 2004).

These experiments, however, do not inform a critical question: How early, in terms of processing stages, is diagnostic information extracted? In a “late” scenario, the visual system extracts identical perceptual representations in different categorization tasks, and diagnostic information is then selected from memory to make categorization decisions. In an “early” scenario, the categorization task determines a selective perceptual representation of the input, in terms of the information required for the task at hand. This debate about whether top-down processes can influence perception can be traced back to the seminal work of Bruner and Postman (1949). In support of this ”early” view, evidence has been collected that experience in extracting diagnostic information for categorization seem to modify how objects are perceptually structured (e.g., Goldstone, 1995, 1994; Goldstone, Lippa, & Shiffrin, 2001; Niedenthal, Halbestadt, Margolin, & Innes-Ker, 2000; Schyns & Rodet, 1997). Yet, proponents of the cognitive impenetrability of vision (e.g., Fodor, 1983; Pylyshyn, 1999, 1980) support a “late” scenario, arguing that these effects take place after perceptual stages, and thus that perception operates prior to and independent of cognitive processes.

Several studies indicate that different categorization tasks on simple stimuli (e.g., gratings) or complex stimuli (faces, objects, letters, and scenes) are sensitive to distinct visual characteristics of the same image, for example particular spatial frequencies (Schyns et al., 2002; Schyns & Oliva, 1999, 1997; Sowden, Özgen, Schyns, & Daoutis, 2003). Since spatial frequency processing is known to occur quite early in the visual system (De Valois & De Valois, 1990), this is taken as evidence that categorization influences early vision. However, this evidence remains indirect, given that the researcher does not have access to perceptual processes as they unfold, but only to the output of categorization tasks. A powerful way to circumvent this problem, as exemplified by studies of visual attention (e.g., Hillyard & Anllo-Vento, 1998), is to rely on event-related potentials (ERPs) to track the temporal course of perceptual processes. Although the recording of scalp ERPs offers a poor spatial resolution, making it difficult to define precisely the neural structures involved in a task, the technique offers a view of the modifications taking place at the whole system level, non-invasively, with a millisecond time resolution (Regan, 1989; Rugg & Coles, 1995).

In the present study, our goal was to inform the question of the stage at which diagnostic facial information is extracted, by measuring the processing of diagnostic information as perceptual categorizations occur. To this end, we examined how task-dependent diagnostic and anti-diagnostic facial information influenced early perceptual categorization stages using ERPs. High-level visual stimuli such as those displayed in Fig. 1 trigger a sequence of electrophysiological processes that can be recorded as field potentials on the scalp, and are thought to reflect the activation of multiple cortical areas in interlocked time-courses (Regan, 1989). The temporal parameters of these potentials, or of differential electrophysiological responses, provide information about the speed and temporal course of visual processes (e.g., Clark, Fan, & Hillyard, 1995; Di Russo & Spinello, 2002; Jeffreys & Axford, 1972; Thorpe, Fize, & Marlot, 1996).

Here, we focused on a large occipito-temporal negativity, commonly referred as the N170 (Bentin, Allison, Puce, Perez, & McCarthy, 1996). The N170 follows lower level visual components C1 (peaking around 70 ms at occipital sites) and P1 (around 100 ms; see, e.g., Clark et al., 1995; Jeffreys & Axford, 1972), and peaks around 160 ms following the onset of a visual stimulus. The N170, also referred to as occipito-temporal N1, is thought to reflect early visual categorization processes (Kiefer, 2001; Luck, Woodman, & Vogel, 2000; Tanaka, Luu, Weisbrod, & Kiefer, 1999), since it is at the level of this visual component that the earliest reliable differences between object categories are observed (Bötzel, Schulze, & Stodieck, 1995; Curran, Tanaka, & Weiskopf, 2002; Kiefer, 2001; Rossion et al., 2000; Rossion, Joyce, Cottrell, & Tarr, 2003; Schendan, Ganis, & Kutas, 1998; Tanaka et al., 1999).

When evoked by face stimuli, the N170 is greatly enhanced compared to non-face objects (Bentin et al., 1996; Bötzel et al., 1995; Itier & Taylor, 2004b; Rossion et al., 2003, 2000; Rousselet, Macé, & Fabre-Thorpe, 2004) and appears to be the earliest and only consistent processing stage at which faces are discriminated from other object categories. Its onset latency is compatible with the timing of discharge of face selective cells in anterior infero-temporal cortex and superior temporal sulcus of the monkey that are sensitive to facial identity, eye-gaze or expression (e.g., Hasselmo, Rolls, & Baylis, 1989; Perrett, Rolls, & Caan, 1982; Rolls, 1992; Rolls & Tovee, 1995). Accordingly, the N170 in response to faces can be conceived as reflecting the occurrence of multiple face categorization processes, taking place in a network of high-level occipito-temporal visual areas (Henson et al., 2003; Horovitz, Rossion, Skudlarski, & Gore, 2004; Itier & Taylor, 2004a; Rossion, Curran, & Gauthier, 2002). Even though there is evidence that the N170 can be modulated by categorical experience (Curran et al., 2002; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002; Rossion, Kung, & Tarr, 2004; Schendan et al., 1998; Tanaka & Curran, 2001) and attention (Eimer, 2000a), it is thought to reflect a relatively early stage of visual processing, being immune to the long-term familiarity of specific exemplar of faces and objects, and to semantic information (Curran et al., 2002; Eimer, 2000b; Rossion et al., 1999; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002).

On the assumption that the N170 reflects a perceptual stage of processing where diagnostic visual information allowing efficient and fast face categorization is extracted, we targeted this electrophysiological process to test the hypothesis that the difference in N170 amplitude to diagnostic and anti-diagnostic facial information should be larger and/or take place faster when diagnosticity is relevant to the categorization task at hand. This is because the presence of the particular salient information should yield a larger advantage over when that information is absent during the corresponding face classification task. This hypothesis follows our assumption that the *Bubbles* technique captures the perceptual representations used to perform a face categorization task.

The influence of top-down factors on visual processes reflected by the N170 has been tested previously, with moderate success. Previous studies have consistently failed to find any task-related modulation of the face-N170 when evoked by full-face photographs (e.g., Carmel & Bentin, 2002; Eimer, 2000b; Rossion et al., 1999). However, under certain conditions of stimulation, the amplitude of the N170 can be increased by attention (Eimer, 2000a), visual expertise (Busey & Vanderkolk, 2005; Rossion et al., 2004; Tanaka & Curran, 2001) or perceptual priming (Bentin & Golland, 2002; Bentin, Sagiv, Mecklinger, Friederici, & von Cramon, 2002). In addition, a recent ERP study has provided evidence that the task performed may modulate the processing of spatial frequency information on faces at the level of the N170 (Goffaux, Jemel, Jacques, Rossion, & Schyns, 2003), suggesting that this component may be a good candidate to test our hypotheses about the time course of diagnostic information selection.

Practically, we recorded scalp ERPs with a 64-channel system in 16 subjects presented with facial images that revealed only the diagnostic information used by normal subjects in previous behavioral studies to perform either a gender task or an expression judgment task (Schyns et al., 2002). We also presented subjects with anti-diagnostic information images, which contained all the information minus the diagnostic (Fig. 1). Thus, subjects saw two types of images (diagnostic for expression vs. gender) each with two levels of diagnosticity (diagnostic, anti-diagnostic) while they performed two counterbalanced binary tasks: gender categorization (male/female) and expression (happy/neutral). Independently of the task, we expected the N170 to be increased/decreased to the presence/absence of facial diagnostic information, given that internal features are highlighted in these stimuli (see Schyns, Jentzsch, Johnson, Schweinberger, & Gosselin, 2003). Of primary interest was whether or not diagnostic images showed a larger advantage over anti-diagnostic images for their respective task. Thus, to isolate any potential effect of diagnosticity, latency and amplitude differences caused by the tasks themselves had to be factored out. To accomplish this, the differences between diagnostic and anti-diagnostic images (D-AD) for each task were analyzed with the factors *task* (expression vs. gender) and *stimulus* (expression vs. gender). Our hypothesis was that there would be an interaction between these two factors at the level of the N170.

2. Methods

2.1. Subjects

Participants were 16 students (10 males, 6 females; all right handed; 21–39 years of age, mean = 27.5) from the University of California. Subjects were paid for participating in a single, 2 h experimental session. One subject's data were removed for a poor SNR due to movement artefact.

2.2. Stimuli

Our stimulus set is based on the results of Schyns et al. (2002). In the next section, we give an overview of their experiment.

2.2.1. The origin of diagnostic stimuli

A subset of 20 grayscale faces from Schyns and Oliva (1999) (5 males, 5 females each of whom displayed two different expressions, neutral and happy, with normalized hairstyle, global orientation, and lighting) were used. The faces subtended 5.72 × 5.72° of visual angle. To search for diagnostic information, the *Bubbles* technique (Gosselin & Schyns, 2001) was applied to an image generation space composed of three dimensions (the standard *X* and *Y* axes of the image plane, plus a third *Z* axis representing spatial frequencies). To compute each stimulus, an original face was first decomposed into six independent bands of spatial frequencies of one octave each—with cutoffs at 90, 45, 22,5, 11.25, 5.62, and 2.81 cycles per face, from fine to coarse, respectively, using the Matlab Pyramid Toolbox (Simoncelli, 1997). The coarsest band was a constant background. The face represented at each band was then partly revealed by a mid-grey mask covering the face area of the image, and punctured by a number of randomly located Gaussian "bubbles". The number of cycles per face that any bubble could reveal was normalized to 3 (i.e., the standard deviations of bubbles were .13, .27, .54, 1.08, and 2.15 deg of visual angle, from fine to coarse scales). The average total area of the face revealed across scales was also normalized. To generate a sparse face, the partial face information revealed at each scale was added together. To maintain categorization of sparse faces at 75% correct, the number of bubbles was adjusted online.

Prior to experimentation, to normalize exposure to stimuli, all participants learned to criterion (perfect identification of all faces twice in a row) the gender, expression and the name attached to each face from printed pictures with corresponding name at the bottom. The experiment comprised two sessions of 500 trials (25 presentations of the 20 faces), but we only used the data of the last 500 trials, when subjects were really familiar with the faces and experimental procedure. In a trial, one sparse face computed as described earlier appeared on the screen. Participants in the GENDER group were instructed to decide whether the stimulus was male or female; those in the EXPRESSIVE OR NOT (EXNEX for short) group whether the sparse face was expressing happiness or neutrality; and those in the IDENTITY group the name of the individual sparsely revealed. The identity task is not relevant to the design of our stimulus set in the present ERP study.

Schyns, Bonnar, and Gosselin created one CorrectPlane per group and per scale (henceforth, CorrectPlane$_{GENDER}$(scale) and CorrectPlane$_{EXNEX}$(scale), for scale $= 1$–5, from fine to coarse) in which they added the masks of bubbles leading to correct categorizations. Similarly, they created two TotalPlanes, TotalPlane$_{GENDER}$(scale), and TotalPlane$_{EXNEX}$(scale), the sum of all bubble masks in each group. They then derived two ProportionPlanes: ProportionPlanes$_X$(scale) = CorrectPlane$_X$(scale)/TotalPlane$_X$(scale), with X standing either for GENDER or for EXNEX. These ProportionPlanes give the ratio of the number of times a specific region of the input space has led to a successful categorization over the number of times this region has been presented. If all regions had equal diagnosticity, ProportionPlanes would be uniform. That is, the probability that any randomly chosen bubble of information led to a correct categorization of the input would be equal to the performance criterion—here, .75. To compute the DiagnosticPlanes, a confidence interval was built around the mean of the ProportionPlanes, for each proportion ($p < 0.01$). The GENDER and EXNEX diagnostic stimuli used in this article were obtained by multiplying the face information of the 20 faces used by Schyns, Bonnar, and Gosselin at each scale with the corresponding DiagnosticPlane$_X$(scale). Figs. 1A and C show the diagnostic information for the EXNEX and GENDER task, respectively. Here, we used 32 (16 original faces [(4 females + 4 males) * 2 expressions] * 2 DiagnosticPlanes, i.e., GENDER and EXNEX) of these 40 diagnostic faces.

2.2.2. *The making of anti-diagnostic stimuli*

To contrast the performance of subjects on a GENDER or an EXNEX recognition task with faces filtered with the DiagnosticPlanes, we created *anti-diagnostic* faces as well (Gosselin & Schyns, 2001), for a total of 64 face stimuli (16 original faces * 2 DiagnosticPlanes * 2 filtering conditions, i.e., diagnostic and anti-diagnostic).

The anti-diagnostic faces were obtained by multiplying the face information at each scale by the complement of (one minus) the DiagnosticPlane$_X$(scale) within the face mask area depicted in Fig. 1B (i.e., AntiDiagnosticPlane$_X$(scale)) and by $\sqrt{}$[energy $_X$(scale)/energy$_{ANTI\text{-}X}$(scale)], where energy$_X$(scale) is the energy[1] of the DiagnosticPlane$_X$(scale) and energy$_{ANTI\text{-}X}$(scale) is the energy of the AntiDiagnosticPlane$_X$(scale). The last factor equates the energy of the diagnostic and anti-diagnostic filters at each scale. Fig. 1b and d show the anti-diagnostic information for the EXNEX and for the GENDER task, respectively.

It should be noted that this manipulation does not necessarily lead to stimuli with normalized power spectra. First, individual faces have slightly different power spectra. This realistic source of variability is preserved here. Second, given that spectral energy is not distributed homogeneously over face photographs, they could have different power spectra in the DIAGNOSTIC and the ANTI-DIAGNOSTIC conditions. Suppose, for example, that the eyes of a particular face, i.e., the most diagnostic location for the GENDER task (Schyns et al., 2002; see Fig. 1), contained all the spectral energy of that face in the spatial frequencies between 5.62 and 22.5 cycles per face, i.e., the most diagnostic bandwidth for the GENDER task (Schyns et al., 2002). If this was the case, the DIAGNOSTIC GENDER version of this face would have a lot of energy in the critical bandwidth and the ANTI-DIAGNOSTIC GENDER version of this face would not. We verified whether this was, in fact, the case by comparing the average power spectra collapsed across orientations for the DIAGNOSTIC (16 original faces * 2 expressions = 32 stimuli) and ANTI-DIAGNOSTIC stimuli. The energy content in the two conditions does differ significantly ($p \leqslant 0.05$) for spatial frequencies lower than about 2.5 cycles per face (DIAGNOSTIC < ANTI-DIAGNOSTIC) and for spatial frequencies higher than about 55 cycles per face (DIAGNOSTIC > ANTI-DIAGNOSTIC). Importantly, for the bandwidths identified as criti-

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[1] Values in the DiagnosticPlanes and face mask vary between 0 and 1, and can be interpreted as contrasts. Energy was defined as the sum of all squared contrasts.

cal for the GENDER (5.62–22.5 cycles per face) and EXNEX (5.62–11.25 cycles per face) tasks the power spectra were not significantly different. Stimuli as used during the ERP recordings were grayscale, full frontal images of 8 different Caucasian individuals, 4 males (2 smiling, 2 with a neutral expression), and 4 females (2 smiling, 2 with a neutral expression) (see Fig. 1). From these original images, 4 different images of each individual were used: one with the gender-diagnostic mask, one with the gender-anti-diagnostic mask, one with the expression-diagnostic mask, one with the expression-anti-diagnostic mask (see Fig. 1). A normalized condition was also presented to subjects in which the face information at each scale was multiplied by $\sqrt{}[\text{energy}_X(\text{scale})/\text{energy}_{\text{FaceMask}}]$, where $\text{energy}_{\text{FaceMask}}$ is the energy of the anti-diagnostic face mask. However, because there were no behavioural differences between diagnostic and normalized stimuli for this presentation duration (see Gosselin & Schyns, 2001), the latter were not included in the analyses. At a 100 cm distance from the monitor, face images (8.8 × 8.8 cm) subtended ~5.04 × 5.04° of visual angle.

2.3. Procedure

Following electrode application, participants were seated in a sound-attenuating, electrically shielded chamber facing a computer monitor. They were told to fixate the centre of the screen during the presentation of 8 consecutive blocks (~1 min pause in between) of 96 trials each: 4 blocks during the gender decision task, and 4 blocks during the expression decision task. The order of task presentation was counterbalanced across subjects, and within a task, the order of the stimulus presentation was randomized. During a single trial, subjects were presented with a face picture for 200 ms (ISI randomized between 1050 and 1550 ms). During the gender judgment task, subjects were asked to press a button with the index finger on their dominant hand if the face was male, and another button with the middle finger of their dominant hand if the face was a female. During the expression judgment, subjects were asked to press one button with the index finger of their dominant hand if the face was expressive, and another button with the middle finger of their dominant hand if the expression was neutral.

2.4. EEG recording

Subjects were instructed to refrain from blinking and moving their eyes and bodies, as corresponding artefacts interfere with the recording of the electroencephalogram (EEG). Scalp recordings were made via 53 tin electrodes (10–20 system + additional sites) embedded in an elastic cap. Four additional electrodes were used to monitor eye movement and blinks: one placed under each eye and one placed on the outer canthus of each eye. The online reference was an electrode placed on the left mastoid. Electrical activity was amplified with a bandpass filter of 0.01–100 Hz and digitized at a rate of 500 Hz.

2.5. EEG/ERP analyses

EEG data were analyzed using Eeprobe (ANT, Inc.) running on Red Hat Linux 7.0. The EEG was filtered with a 201-point digital 30 Hz Hamming low-pass filter, with cut-off frequencies of 29 (−3 dB point), and a stop-band attenuation of −63.3 dB (50 Hz and above). Then EEG and EOG artefacts were removed using a [−40; +40 μV] deviation over 200 ms intervals on frontal electrodes and using a [−35; +35 μV] deviation over 200 ms intervals on all other electrodes. In case of too many blink artefacts, they were corrected by a subtraction of VEOG propagation factors, based on PCA-transformed EOG components (Nowagk & Pfeifer, 1996). After VEOG correction and rejection of artefact-contaminated ERPs, the number of sweeps was equalized across conditions for each subject. Averaged ERPs were re-referenced using a common average reference.

2.6. Statistical analysis

After examination of the grand average topographies, peak latency, and amplitude values of the N170 were extracted automatically at the maximum (negative) amplitude value between 140 and 190 ms at a single occipito-temporal electrode site (LLOC/RLOC), 2 cm below T5 and T6 in the 10/20 system. It is also at this occipito-temporal electrode site that the N170 was found to be maximal to pictures of normal faces in the same group of subjects in an independent experiment (Rossion et al., 2003). At these sites, the peak amplitude and latency values of the preceding positivity (P1) were also extracted (80–140 ms). The choice of using a single site—where the N170 was maximum—for latency analysis was made because it was only at that electrode site that the components peaks could be reliably identified in all conditions for all subjects and thus that peak latency values could be extracted without errors (Picton et al., 2000). In addition, we performed an analysis on the average amplitudes computed between 140 and 190 ms at four occipito-temporal sites where the N170 was prominent. To test our hypotheses, repeated-measure ANOVAs were computed on differential (diagnostic–anti-diagnostic) peak amplitude of the N170 as measured at these sites. For the electrophysiological analyses on these differential values, the factors were *Task* (Expression/Gender), *Stimulus* (Expression/Gender), and *Laterality* (Left/Right hemisphere). Post hocs t tests were used when necessary to characterize the effects.

3. Results

3.1. Behavioral data

Accuracy rates and mean correct response times are reported in Table 1.

Table 1
Accuracy means (% correct, ±SE)

Accuracy (% correct)	Stimuli: Expression		Stimuli: Gender	
	Diagnostic	Anti-diagnostic	Diagnostic	Anti-diagnostic
Task				
Expression	89 ± 1.1	79 ± 1.3	90 ± 1.4	90 ± 1.3
Gender	78 ± 1.1	83 ± 1.1	93 ± 0.9	82 ± 1.2

Table 2
Response time means (ms, ± SE)

Correct RTs	Stimuli: Expression		Stimuli: Gender	
	Diagnostic	Anti-diagnostic	Diagnostic	Anti-diagnostic
Task				
Expression	604 ± 20	699 ± 22	599 ± 19	638 ± 23
Gender	670 ± 20	656 ± 17	628 ± 16	664 ± 17

3.1.1. Accuracy

There was a significant *task* × *stimulus* interaction [$F(1,60) = 22.24$, $p < 0.0001$], such that there was a larger D-AD difference for gender images during the gender task, than for those same images during the expression task ($p < 0.05$); while there was a larger D-AD difference for expression images during the expression task than for those same images during the gender task ($p < 0.005$; see Fig. 3; Table 1).

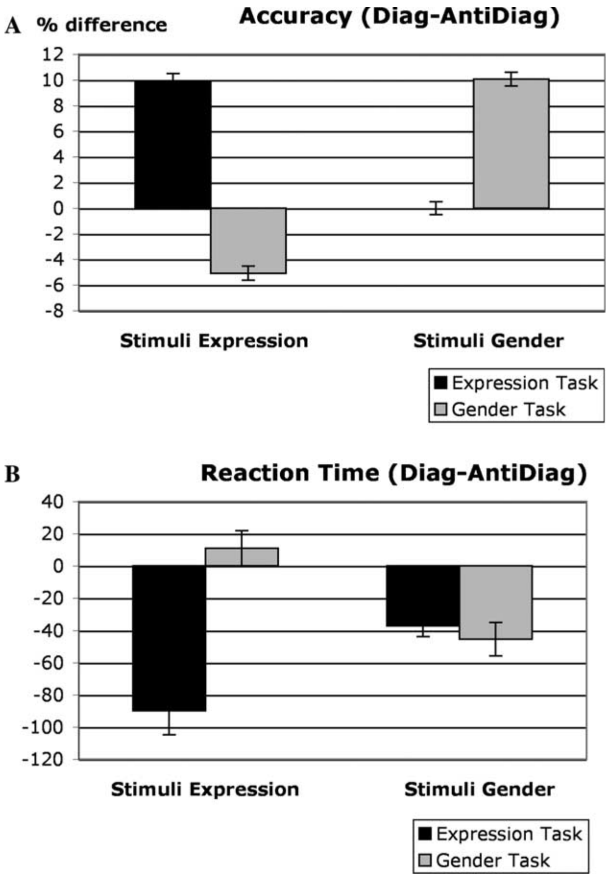

Fig. 2. Behavioral results in graphs: (A) accuracy (%), (B) response time (RTs).

3.1.2. RTs

Mean response times are given in Table 2 for all conditions. There was a main effect of *task* [$F(1,60) = 18.24$, $p = 0.0001$], due to smaller overall D-AD differences for the gender task than for the expression task. Most importantly, as with accuracy, there was a significant *task* × *stimulus* interaction [$F(1,60) = 25.33$, $p < 0.0001$] such that D-AD differences were larger when the task matched the stimulus (Fig. 2). Post hoc *t* tests showed that the speeding up for diagnostic information was larger for expression stimuli during the expression task than for the same stimuli during the gender task ($p < 0.0001$), but the D-AD difference for gender stimuli during the gender task was not larger for the same stimuli than during the expression task ($p > 0.9$, see Fig. 2).

3.2. ERP data

Following the occipital P1 (80–120 ms), the occipito-temporal N170 (coupled with the centro-frontal VPP; see Jeffreys, 1996; Joyce & Rossion, in press; Rossion et al., 2003) was best observed between 140 and 180 ms for all categories of stimuli. The amplitude and latency values of the grand-average N170 are reported in Tables 3 and 4. The N170 was maximal at the same electrodes (LLOC/RLOC) for all conditions and the component was prominent in four occipito-temporal channels. The clearest observation in the grand-average waves is a substantial increase of the N170 amplitude for diagnostic images compared to anti-diagnostic images, at both hemisphere sites (Figs. 3 and 4). The amplitude difference between diagnostic and anti-diagnostic stimuli data collapsed across hemisphere, stimulus and task was highly significant ($t_{14} = 4.8$; $p < 0.001$), and diagnostic stimuli also led to a N170 peaking earlier on average than anti-diagnostic stimuli (173 vs. 167 ms on average; $t_{14} = 4.35$ $p < 0.005$). This difference was not present on the preceding P1 peak (Fig. 5; amplitude: $t_{14} = 1.03$; $p = 0.32$; Latencies: $t_{14} = 0.35$; $p = 0.72$). Most importantly for our hypotheses, there appears to be an interaction between diagnostic features and

Table 3
Grand-average Latency values (ms, ± SE) of the N170

N170 latency (ms)	Stimuli: Expression		Stimuli: Gender	
	Diagnostic	Anti-diagnostic	Diagnostic	Anti-diagnostic
Task				
Expression				
Left	166 ± 4.3	166 ± 6.0	164 ± 5.7	166 ± 5.5
Right	164 ± 4.1	166 ± 5.2	156 ± 5.1	166 ± 4.7
Gender				
Left	164 ± 4.0	168 ± 5.8	164 ± 5.6	168 ± 5.5
Right	164 ± 4.3	166 ± 5.3	158 ± 4.3	164 ± 5.4

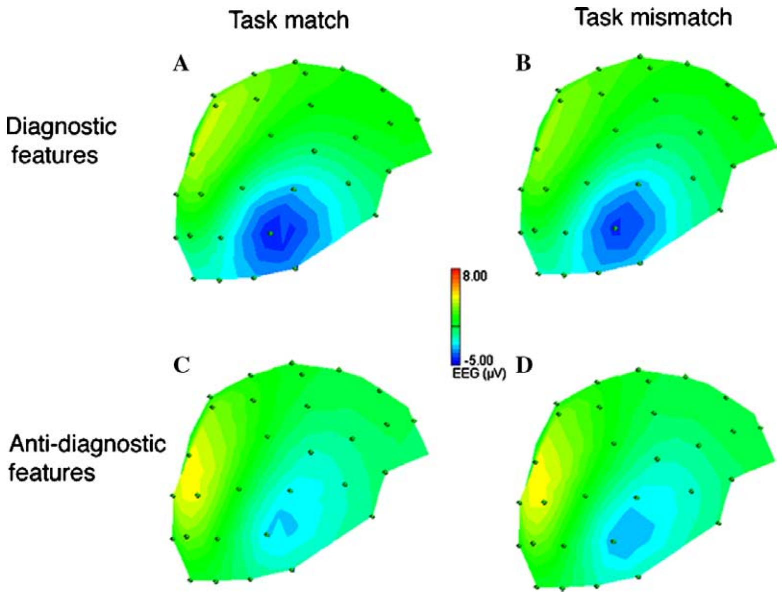

Fig. 3. Topographical maps showing the right hemisphere N170 in response to the pictures presented in Fig. 1 when they match the task at hand (A and C) or not (B and D). Expression and Gender are averaged together. The topography is taken at peak values (Table 3) for each of the conditions.

task performed. That is, the difference between the N170 elicited by diagnostic and anti-diagnostic face features when they match the task (Figs. 3A–C) appears larger than when they do not match the task (Figs. 3–5B–D), an interaction confirmed by the statistical analysis presented below.

1. *Peak latency difference analysis*: Peak values on right and left LOC electrodes for anti-diagnostic images were subtracted from those for diagnostic images within each category and repeated measures ANOVAS (factors: task, stimulus, and hemisphere) were performed on the resulting differential latency values. Although there was a trend for a larger D-AD difference when the task matched the stimulus (interaction task × stimuli: $F(1,14) = 3.56$, $p < 0.08$), the slight latency delay of the N170 observed for anti-diagnostic stimuli did not differ across task, stimuli (expression of gender) or hemisphere (all p values > 0.2). An analysis conducted on the preceding peak (P1) also failed to disclose any effect of *task*, *stimulus*, *hemisphere* or any significant interactions between these factors (all p values > 0.2).
2. *N170 amplitude difference analysis*: Following the approach taken in the behavioral analysis, peak values for anti-diagnostic images were subtracted from those for diagnostic images within each category and analyses were performed on the resulting values (using the four occipito-temporal channels where N170 was prominent, see methods) Critically, there was a significant interaction of *task* with *stimulus* [$F(1,416) = 11.83$, $p = 0.0006$], reflecting the larger D-AD N170 amplitude difference when the task matched the stimulus (Figs. 3–5). Post hoc t tests showed that the D-AD N170 amplitude was larger for gender stimuli during the gender task than for those same stimuli during the expression task ($p < 0.01$). N170 amplitude for expression stimuli during the expression task, however, was not significantly larger than expression stimuli during the gender task ($p > 0.3$) or than gender stimuli during the expression task ($p > 0.2$, See Figs. 4 and 5). There was no main effect of hemisphere ($p > 0.8$) or any interaction of hemisphere with the differences of interest (all p's > 0.17).
3. *P1 amplitude difference analysis*: In the time window of the P1, the only comparison to reach significance was a main effect of *stimulus* [$F(1,416) = 5.39$, $p = 0.02$]: D-AD differences for gender stimuli were larger overall than D-AD differences for expression stimuli. However, there

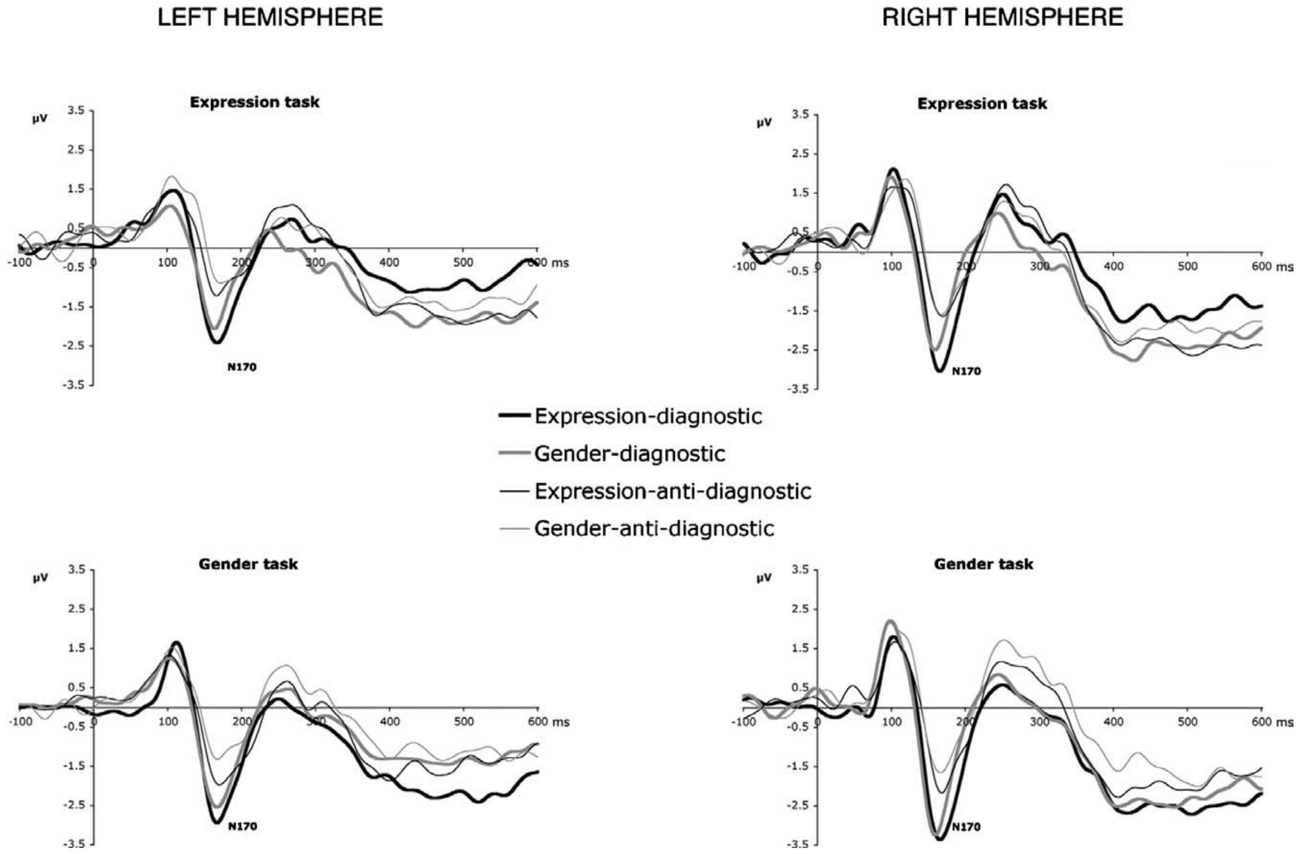

Fig. 4. Main diagnosticity effects at left (LLOC) and right (RLOC) occipito-temporal sites, separately by task.

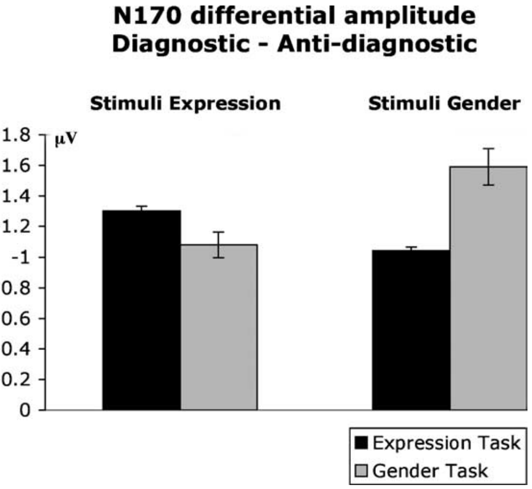

Fig. 5. Graphical representation of the D-AD N170 amplitude differences (collapsed across hemisphere) in each condition. Values are difference in μVs.

was no interaction of *stimulus* with *task* ($p > 0.7$, all post hoc p's > 0.2). There was no main effect of *hemisphere* ($p > 0.08$) or any interactions of *hemisphere* with any other variables (all p's > 0.07).

4. *(N170 - P1) amplitude difference analysis*: To ensure that the D-AD interaction with task at the level of the N170 is not a carryover effect from task differences observed at the earlier P1, an additional analysis was carried out on the same factors using the peak amplitude difference between the P1 and N170. When the peak amplitude of the D-AD difference for the P1 is subtracted from that of the N170, there is also a significant interaction of *task* with *stimulus* [$F(1,416) = 7.7, p = 0.0058$], again reflecting the larger D-AD N170 amplitude difference when the task matched the stimulus (Figs. 3–5). Post hoc t tests showed that the D-AD N170-P1 peak differences were larger for gender stimuli during the gender task than for those same stimuli during the expression task ($p < 0.025$), but non-significantly larger for expression stimuli during the expression task than those same stimuli during the gender task ($p > 0.6$). There was no main effect of *hemisphere* ($p > 0.15$) or any interaction of hemisphere with the differences of interest (all p's > 0.3).

4. Discussion

Our behavioral data (Tables 1 and 2) show clearly that providing human subjects with diagnostic facial information as extracted previously using *Bubbles* provides an advantage for categorizing faces, both in terms of performance and speed. This result confirms that the pre-selected information is important for task performance. When this diagnostic information is selectively removed from the face pictures, performance drops significantly and the subjects are slower to perform the categorization tasks. We believe that the behavioral differences observed between the GENDER and EXNEX is due to the difficulty of the tasks and

Table 4
Grand-average Amplitude values (μV, ± SE) of the N170

N170 mean amplitude on grand averages (μV)	Stimuli: Expression			Stimuli: Gender		
	Diagnostic	Anti-diagnostic	Difference	Diagnostic	Anti-diagnostic	Difference
Task						
Expression						
Left	−2.43 ± 0.7	−1.23 ± 0.8	**−1.20**	−2.07 ± 0.7	0.90 ± 0.6	1.17
Right	−3.05 ± 1.1	−1.65 ± 0.8	**−1.40**	−2.51 ± 0.9	−1.60 ± 0.9	−0.91
Gender						
Left	−2.95 ± 0.9	−1.98 ± 0.7	−0.97	−2.56 ± 0.7	−1.33 ± 0.7	**−1.23**
Right	−3.37 ± 1.0	−2.18 ± 1.0	−1.19	−3.25 ± 1.1	−1.68 ± 1.0	**−1.96**

The values in bold refer to the diagnostic–anti-diagnostic difference for the corresponding task, i.e., where the largest difference is expected to be.

to the area of the diagnostic masks. In Schyns et al. (2002), performance was maintained constant at 75% correct by adjusting the number of bubbles. An average of 15 bubbles were required in the EXNEX condition and 20 in the GENDER condition, for a ratio of revealed area equal to 15/20 = 0.75. In the experiment reported here, however, the ratio of revealed area in the diagnostic masks was greater (0.93), which might have led to a better performance in the EXNEX task with the DIAGNOSTIC and thus to a greater D-AD.

Irrespective of the task, the peak latency of the N170 was slightly delayed for anti-diagnostic stimuli compared to diagnostic pictures (see Table 3, Figs. 4 and 5). These effects at both the electrophysiological and behavioral level suggest a slowing down taking place at face processing stages when the diagnostic facial information is removed. Note that a simpler account, albeit not contradictory to our point, would be that removing internal face features delays the N170 component, given that most diagnostic information is present in internal features. Previous studies have indeed shown that removing or masking the eyes for instance, delays the N170 by about 10 ms (Eimer, 1998; Jemel, George, Chaby, Fiori, & Renault, 1999).

We also observed a clear overall increase in N170 amplitude for diagnostic over anti-diagnostic facial features. This result suggests that there is a large part of early visual face-related processes that are tuned to specific feature information, regardless of the task at hand (see also Schyns et al., 2003; Smith et al., 2004). Indeed, diagnostic images showed an enhanced N170 as compared to anti-diagnostic, regardless of whether the image was specifically diagnostic to the current task. This may be indicative of the somewhat automated nature of face processing (Bruce & Young, 1998; Langton & Bruce, 1999), given that certain features of the face may be relevant to many decisions that are regularly made about faces. According to this view, extended experience with faces and judgments about them has led to the automatic processing of certain facial features, irrespective of the task at hand. For instance, diagnostic images show a much stronger contrast in the region of the eyes compared to anti-diagnostic face (Fig. 1). There is considerable evidence supporting the view that the eyes are dominant in the recognition of facial identity. Human adults can recognize and remember faces from the eyes only (McKelvie, 1976) and experiments designed to measure the relative importance of different facial features for individual face recognition have consistently shown the dominance of the eye/eyebrow combination, followed by the mouth and then the nose (e.g., Davies, Ellis, & Shepherd, 1977; Haig, 1985; Sadr, Jarudi, & Sinha, 2003; Sergent, 1984; Tanaka & Farah, 1993). Moreover, it has been shown that isolated human eyes evoke particularly large and early visual responses compared to whole face stimuli or other isolated facial features (e.g., Bentin et al., 1996; Taylor, Edmonds, McCarthy, & Allison, 2001) and that the N170 evoked by isolated eyes is present earlier in development than the same component elicited by whole face stimuli, suggesting a faster maturation of the eye processing system compared to general face processes (Taylor et al., 2001). Finally, recent evidence using response classification methods in adults suggest that the eyes of a face evoke the earliest and largest face-sensitive ERP responses (Schyns et al., 2003; but see Eimer, 1998).

One may also suggest that the overall advantage of diagnostic images is related to the differential spatial frequency content of the images. The *Bubbles* technique extracted the spatial frequencies that were the most diagnostic for the face categorization tasks. Thus, by virtue of the methodology used, these stimuli were not equalized for spatial frequency power in all bands. As indicated in the methods section, diagnostic images contain less power in the low frequency range (i.e., less than about 2.5 cycles per face) than anti-diagnostic images. Given that N170 to faces is particularly sensitive to low spatial frequencies (<8 cycles/image in Goffaux, Gauthier, & Rossion, 2003), which are more important for processing faces than objects (Dailey & Cottrell, 1999), these overall differences in spatial frequencies between our stimuli are unlikely to contribute to the larger N170 observed for diagnostic images. In addition, in the present study, the overall energy and the frequency distributions between conditions were the same within the most diagnostic bandwidth (i.e., 5.62–22.5 cycles per face). Furthermore, all stimuli exhibited the usual $1/f^2$ power spectrum profiles. It follows that that the increase of the N170 to diagnostic images is related to either the diagnostic face cues independently of their spatial frequency content, or possibly a combination of both. In any case, recent ERP investigations suggest that the relationship between the N170 amplitude and the spatial frequency content of the stimulus is not straightforward: there appears to be a general advantage of low spatial frequencies but this effect is not uniform across object categories (Goffaux, Gauthier et al., 2003), and is modulated by the task at hand (Goffaux, Jemel et al., 2003).

Finally, while the behavioral data indicate that task difficulty differed between conditions, the diagnostic image advantage observed here cannot be simply related to changes in sustained attention. First, the experimental design was completely randomized within task so that subjects would be unable to predict what type of mask/stimulus was coming next. Second, sustained attentional processes would have most likely affected the preceding positivity, the P1 (see Luck et al., 2000 for a review) whereas our effects were observed both on the raw N170 amplitude data and on peak-to-peak analyses, the latter taking into account the preceding P1 amplitude values.

4.1. Task-related modulations of the N170

Viewing diagnostic facial features for a given task causes better performance and speeded response times for both gender and expression judgments, but is perception of the stimuli influenced by these categorization tasks? Our main hypothesis was that the N170 should be (reduced)/enhanced particularly when the (anti-)diagnostic facial information matches the task at hand. The electrophysiological results support this hypothesis in part. There was a significant interaction between task and diagnosticity of the images, as we hypothesized. The amplitude modulation is relatively small (less than a microvolt) but the double dissociation between task and stimuli gives rise to a highly significant interaction (Figs. 3–5). Furthermore, the difference between diagnostic and anti-diagnostic gender facial features was larger during the gender task than during the expression task. However, we did not observe a significant increase of the difference between diagnostic and anti-diagnostic expression images during the expression task as compared to the gender task.

Given the general absence of previous evidence for task modulations before 200 ms following the presentation of a face stimulus (e.g., Carmel & Bentin, 2002; Eimer, 2000b; Rossion et al., 1999), our hypothesis of task-diagnostic interactions at this latency was particularly strong. Yet, recent ERP studies have suggested that subject knowledge may indeed influence the N170 response (Bentin & Golland, 2002; Bentin et al., 2002; Goffaux, Jemel et al., 2003; Jemel, Pisani, Calabria, Crommelinck, & Bruyer, 2003). For instance, Bentin and colleagues (Bentin et al., 2002; Bentin & Golland, 2002) showed that the very same stimuli, either small round shapes (Bentin et al., 2002) or line drawings of scrambled faces (Bentin & Golland, 2002) evoked a conspicuous N170 only after the subject was provided hints that these stimuli were related to eyes and face pictures. More closely related to the present study, Goffaux, Jemel et al. (2003) showed a modulation of N170 amplitude to high and low spatial frequencies dependent on the task being performed. Precisely, there was a larger N170 to low spatial frequencies compared to high-spatial frequencies, but only when subjects had to categorize the gender of the faces, not for face familiarity decisions.

Compared to these recent studies, the present findings go several steps further in terms of reliability and theoretical significance. First, compared to the studies reported by Bentin and colleagues (Bentin et al., 2002; Bentin & Golland, 2002), we observed a task-related effect: the modulations of the visual responses are observed Online, depending on the subject's task, rather than his previous experience or knowledge. Second, contrary to these previous studies, including Goffaux, Jemel et al. (2003), our design was completely randomized across the types of stimuli presented. This additional methodological care prevents the effects from being attributed to any sustained attentional processes. Finally, the present findings suggest a task-related modulation of early visual processes by subtle variations in spatial frequencies and contrast at different locations of the facial image rather than to overall different spatial frequency contents for the face stimulus (Goffaux, Jemel et al., 2003).

An important theoretical consequence of this work is thus that perceptual processing of faces appears to be cognitively penetrable, at least by certain categorization tasks. How early these influences take place in terms of face processing stages and their neural correlates? As discussed in the introduction, functionally, the N170 reflects the earliest stage at which object categories appear to be distinguished. When evoked by faces, it has been related to an early encoding stage of face processing during which an individual face representation is extracted from the visual stimulus, independently of any previous experience with this particular face (Jacques & Rossion, in press). In response to foveally presented stimuli, the N170 is a lateral ERP response that usually follows the large posterior visual component P1 (Jeffreys & Axford, 1972) and starts at around 130 ms. Given that visual information reaches the human primary visual cortex (V1) at around 60–80 ms (Bullier, 2001; Jeffreys & Axford, 1972), both the P1 and the N170, taking place later, are assumed to be generated by multiple sources interlocked in time, in the visual extrastriate cortex (Regan, 1989). More specifically, evidence from electrophysiological studies and source localization of the scalp N170 (e.g., Itier & Taylor, 2004a; Rossion et al., 2003), intracranial recordings of field potentials (e.g., Allison, Puce, Spencer, & McCarthy, 1999), and combination of EEG and fMRI data (Henson et al., 2003; Horovitz et al., 2004) suggest that the N170 originates from a network of occipital and temporal regions including the middle fusiform gyrus, the inferior occipital cortex, and the inferior, middle, and superior temporal gyri. These localizations largely overlap with regions where face-sensitive responses have been described in functional neuroimaging studies (see Haxby, Hoffman, & Gobbini, 2000 for a review) or in single-cell recordings in non-human primates (e.g., Perrett, Hietanen, Oram, & Benson, 1992; Perrett et al., 1982; Rolls, 1992; Tanaka, 1996). Together with its functional response properties (see Joyce & Rossion, in press), these observations suggest that the N170 represents an early stage of visual processing of face that can be modulated by an interaction between the task and the diagnosticity of the stimulus for the task.

We note, however, that this interaction between the task and the diagnosticity of the stimulus for the task at the level of the face-sensitive N170 was found only for gender, not for expression. Although we hypothesized to observe also an effect of diagnosticity for expression at this time latency in the present study, there are several possible explanations for this dissociation. First, it should be noted that the only evidence of a task × diagnosticity interaction taking place at the N170 was for a face gender categorization task also (Goffaux, Gauthier et al., 2003). Second, the N170 is thought to reflect the entry-level of face categorization, at which faces are discriminated from other object categories (e.g., Bentin et al., 1996; Rossion et al., 2000), but also at which distinct facial identities are coded (Jacques & Rossion, 2004; Joyce & Rossion, in press). In contrast, several studies have failed to observe any modulation of the N170 in response to various facial expressions, concluding that emotional expression analysis is not coded at this level (Eimer & Holmes, 2002). Other sources of evidence, coming from the neuroimaging and behavioral literature, suggest that whereas gender and identity would be processed using overlapping cues in the same spatio-temporal pathway (Calder, Burton, Miller, Young, & Akamatsu, 2001; Haxby et al., 2000; Schyns et al., 2002), expression and identity rely on partially distinct cues and neural systems (for dissociations, see Calder et al., 2001; Schyns et al., 2002; Winston et al., 2004; partial commonality between identity and expression: see Cottrell et al., 2002; Ganel, Valyear, Goshen-Gottstein, & Goodale, 2005; Schweinberger & Soukup, 1998; Schweinberger, Burton, & Kelly, 1999). First, in a PCA analysis based on the pixel intensities of faces, Calder and colleagues (2001) have shown that face identity and sex were coded by similar components to one another, but by different components than facial expression. The components explaining most of the variance for both identity and sex show structural changes in rigid elements of the face that change slowly across a number of years, such as head size and nose shape. This is in agreement with the proposal of Haxby et al. (2000) that the invariant properties of the face such as facial identity and gender are processed in the occipito-temporal ventral pathway, including the middle fusiform gyrus, whereas the coding of changeable aspects of the face, such as facial expressions or eye-gaze direction, would rely on the superior temporal sulcus (STS). Perhaps most importantly, previous studies using *Bubbles* during different face categorisation tasks, gender categorisation, facial identification (among 10 possibilities), and expression decision have shown that most if not all of the information used for the gender categorisation task (the shape of the upper part of the head and the eyes region with the eyebrows, see Fig. 1) is contained in the diagnostic information also used for facial identity judgments (see Schyns et al., 2002, Fig. 2). In other words, a gender categorisation task on faces relies on extracting information that is also particularly salient for individual facial discrimination, whereas facial expression judgments, at least for happy vs. neutral discriminations (see Smith, Cottrell, Gosselin, & Schyns, 2005) appear to rely more on the lower part of the face and the mouth region (Fig. 1).

This dissociation between the processing may explain why we found that, in contrast to gender, diagnostic cues for facial expression appears to be processed largely automatically, independent of whether the subject is actually categorizing the face according to facial expression. Even though neuroimaging studies using a strong competing task with a high attentional load may cause modulations of the processing of emotional stimuli (Pessoa, McKenna, Gutierrez, & Ungerleider, 2002), our observations support the view that facial expression is extracted automatically (Ohman, Esteves, & Soares, 1995; Vuilleumier, Armony, Driver, & Dolan, 2001), and will be largely immune to differential task instructions as used in the present study, at least at the latency of the N170.

5. Conclusions

In the current work we show that visual processes for faces below 200 ms are sensitive to the interaction between stimulus information and task requirements. Specifically, it appears that the task at hand primes the system to require certain types of stimulus information that, when provided, enhances N170 amplitude. We believe that the combination of this information with that of previous work showing N170 modulation to certain stimulus features (e.g., spatial frequency), and experience (e.g., expertise training) may lead us to a more comprehensive view of how information in the brain is organized. In particular, it may give us insight as to how high-level object categorization interacts with lower level visual properties. Further, the *Bubbles* technique, in combination with electrophysiological recordings, is a useful tool in that investigation, providing ways to investigate how and when the level of experience with a particular category of stimulus affects the interaction of task demands with stimulus information.

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