Research Article

Receptive Fields for Flexible Face Categorizations

Marie L. Smith,[1] **Frédéric Gosselin,**[2] **and Philippe G. Schyns**[1]

[1]*University of Glasgow, Glasgow, United Kingdom, and* [2]*Université de Montréal, Montreal, Quebec, Canada*

ABSTRACT—*Examining the receptive fields of brain signals can elucidate how information impinging on the former modulates the latter. We applied this time-honored approach in early vision to the higher-level brain processes underlying face categorizations. Electroencephalograms in response to face-information samples were recorded while observers resolved two different categorizations (gender, expressive or not). Using a method with low bias and low variance, we compared, in a common space of information states, the information determining behavior (accuracy and reaction time) with the information that modulates emergent brain signals associated with early face encoding and later category decision. Our results provide a time line for face processing in which selective attention to diagnostic information for categorizing stimuli (the eyes and their second-order relationships in gender categorization; the mouth in expressive-or-not categorization) correlates with late electrophysiological (P300) activity, whereas early face-sensitive occipito-temporal (N170) activity is mainly driven by the contralateral eye, irrespective of the categorization task.*

One of the most pressing issues in relating brain function to perception and cognition concerns the functional interpretation of brain responses to complex visual stimuli. Although it is obvious that visual stimuli elicit brain signals, it is a challenge to narrow down the relevant visual features that modulate the signal, and to relate these to the behavior of the observer. For example, single-cell studies concerned with the mechanisms of visual categorization have established that infero-temporal neurons respond specifically to the sight of complex objects such as faces and hands (Desimone, Albright, Gross, & Bruce, 1984; Gross, Rocha-Miranda, & Bender, 1972; Perrett, Rolls, & Cann, 1982). However, further investigations have revealed that

the effective stimulus is represented in an abstract-feature space (Desimone et al., 1984; K. Tanaka, Saito, Fukada, & Moriya, 1991) or parameter space (Op de Beeck, Wagemans, & Vogels, 2001; Sigala & Logothetis, 2002; see also Pasupathy & Connor, 2002, for V4 neurons) of much lower dimensionality. In a related vein, electroencephalogram (EEG), magnetoencephalogram (MEG), and neuroimaging studies have established sensitivity of brain signals to faces (e.g., the N170 in EEG—Bentin, Allison, Puce, Perez, & McCarthy, 1996; Carmel & Bentin, 2002), and neuroimaging has shown that faces elicit activity in the middle fusiform gyrus (Gauthier, Tarr, et al., 2000; Kanwisher, McDermott, & Chun, 1997), but further studies have revealed that similar brain responses are elicited when people categorize objects in other areas of expertise (Gauthier, Skudlarski, Gore, & Anderson, 2000) and when they categorize novel objects (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999), leaving unresolved the question of the specific features that determine the identified brain activity.

The functional interpretation of a brain signal represents the solution of a multidimensional credit-assignment problem (Barlow, 1959): What stimulus features determine the amplitude of the brain signal? To resolve this question, a suitable method must allow for the flexible testing of many sorts of features (have low bias) while minimizing spurious features (keep low variance), in a reasonable amount of trials (Geman, Bienenstock, & Doursat, 1992; Stone, 1982). Because of this dilemma between bias and variance (Geman et al., 1992), it is questionable whether a faithful mapping between stimulus features and brain signals can be computed in the limited number of trials that is typical of categorization experiments (Edelman & Intrator, 1997).

In the study we report here, we established this mapping between scalp EEG activity and stimulus features in the context of the categorization of realistic faces (gender, expressive or not). Faces are a natural stimulus category with several advantages over others: They have a privileged biological significance to the normal functioning of the human species (Farah, 1996; Nachson, 1995), levels of expertise in processing faces are similar across observers (Gauthier, Skudlarski, et al.,

Address correspondence to Philippe G. Schyns, Department of Psychology, University of Glasgow, Glasgow G12 8QB, United Kingdom; e-mail: philippe@psy.gla.ac.uk.

2000), and they afford multiple categorizations and are fairly homogeneous as a class. We searched the EEG for signals modulated by facial information, using a 4-ms recording window from stimulus onset and focusing on electrode sites that were known from prior studies to be sensitive to the encoding of facial information relatively early (low occipito-temporal P9 and P10; Bentin et al., 1996; Carmel & Bentin, 2002; Rossion & Gauthier, 2002) and to decision making later on (centro-parietal Pz; Donchin & Coles, 1998; Verleger, 1997, 1998), and that displayed the largest amplitude of the components of interest.

EXPERIMENT

In this experiment, 2 observers performed 4,000 trials of each of two categorization tasks (gender, expressiveness). On each trial, observers saw information sampled from a randomly chosen face picture using the Bubbles technique (Gosselin & Schyns, 2001; Schyns, Bonnar, & Gosselin, 2002). Specifically, 14 randomly located two-dimensional Gaussian apertures revealed facial information—the rest was hidden from view. EEG activity of the observers while they performed these tasks was simultaneously recorded with a 32-electrode cap. The data are those gathered for a study reported elsewhere (Schyns, Jentzsch, Johnson, Schweinberger, & Gosselin, 2003); the analysis methods and results are all new.

This application of Bubbles keeps bias low because facial information is sampled with 14 (randomly distributed) circularly symmetric Gaussian apertures, approximating a uniform sampling of all face regions. We also kept variance low because we correlated the set of 4,000 information samples with their corresponding EEG amplitudes independently for each time of measurement. Hence, whenever facial information modulated EEG amplitude, an association between a brain signal and its determinant features emerged (see Fig. 1). Consequently, our approach is a low-bias and low-variance method for determining what constitutes a relevant brain signal in the context of our categorization tasks: a modulation of brain activity that is determined by facial information.

METHOD

Participants
Participants were 2 paid naive observers (B.B. and M.L.) from Glasgow University, United Kingdom.

Stimuli
Face stimuli were computed from 256 gray-scale pictures of 10 actors (5 males, 5 females), each displaying two expressions (neutral, happy). All photographs were taken under standardized conditions of illumination. Hairstyle was normalized across faces to eliminate information from this feature. Stimuli were presented on a light gray background at the center of a computer

monitor. A fixed chin rest maintained a constant 1-m viewing distance (visual angle of $4.6° \times 4.6°$).

Procedure
The experiment was programmed with the Psychophysics Toolbox for Matlab (Brainard, 1997; Pelli, 1997). Each trial started with one 500-ms fixation cross ($0.4°$ of visual angle), immediately followed by a randomly selected face picture whose information was revealed through 14 two-dimensional Gaussian apertures ($\sigma = 0.22°$ of visual angle) randomly allocated with the constraint that each aperture remained within the area of the face. Previous experiments (Gosselin & Schyns, 2001) revealed that 14 apertures are required to reach a minimum of 75% correct in gender and expressive-or-not categorizations.[1] The sparse face remained on the screen for 1,500 ms, and observers were instructed to respond as quickly as possible without making mistakes. Short breaks were allowed every 100 trials.

In one session of 4,000 trials (gender task), the observers indicated the gender of each sparse face by pressing the appropriate key of a two-key response box. In another 4,000-trial session (expressiveness task), they indicated whether each stimulus was smiling or not. Order of task was counterbalanced across observers (B.B. vs. M.L.). After rejection of trials with artifacts, the following numbers of trials remained: for B.B., 3,624 expressiveness trials and 3,577 gender trials; for M.L., 3,913 expressiveness trials and 3,798 gender trials.

EEG activity was continuously recorded with sintered Ag/AgCl electrodes mounted in an electrode cap (Easy-Cap™) at the scalp positions Fz, Cz, Pz, Iz, FP1, FP2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, F9, F10, FT9, FT10, P9, P10, PO9, PO10, F9′, F10′, and TP9 (Pivik et al., 1993). The right mastoid (TP10) served as initial common reference, and the AFz electrode as ground. The F9′ and F10′ electrodes were positioned 2 cm anterior to F9 and F10 at the outer canthi of the left and right eyes. Vertical electro-oculogram (vEOG) was bipolarly registered above and below the right eye. EEG and EOG recordings were sampled at 250 Hz. Electrode impedance was kept below 10 kΩ. All signals were recorded with a band-pass filter (0.05–40 Hz, −6-dB attenuation, 12 dB/octave). Analysis epochs were generated off-line, starting 200 ms prior to stimulus onset and lasting for a total duration of 800 ms. Epochs were aligned to a 200-ms prestimulus baseline. To sort trials, we ran artifact-detection software and visually inspected each trial for ocular and nonocular artifacts. Artifact-free event-related

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[1]Our method has low bias because it approximates a uniform sampling of the face using several circularly symmetric (i.e., not orientation biased) Gaussian apertures that reveal information at full contrast energy (as opposed to low-contrast additive Gaussian noise). The method does not prejudge where the information is in the face, nor whether or not the responsive neuron assemblies are linear in their response. However, the relationship between the sigma of the bubble, the number of bubbles, and the scale of the features must be carefully considered. In this study, the bubble number and sigma size of Gosselin and Schyns (2001) ensured sufficient sampling density to reveal the relevant facial information.

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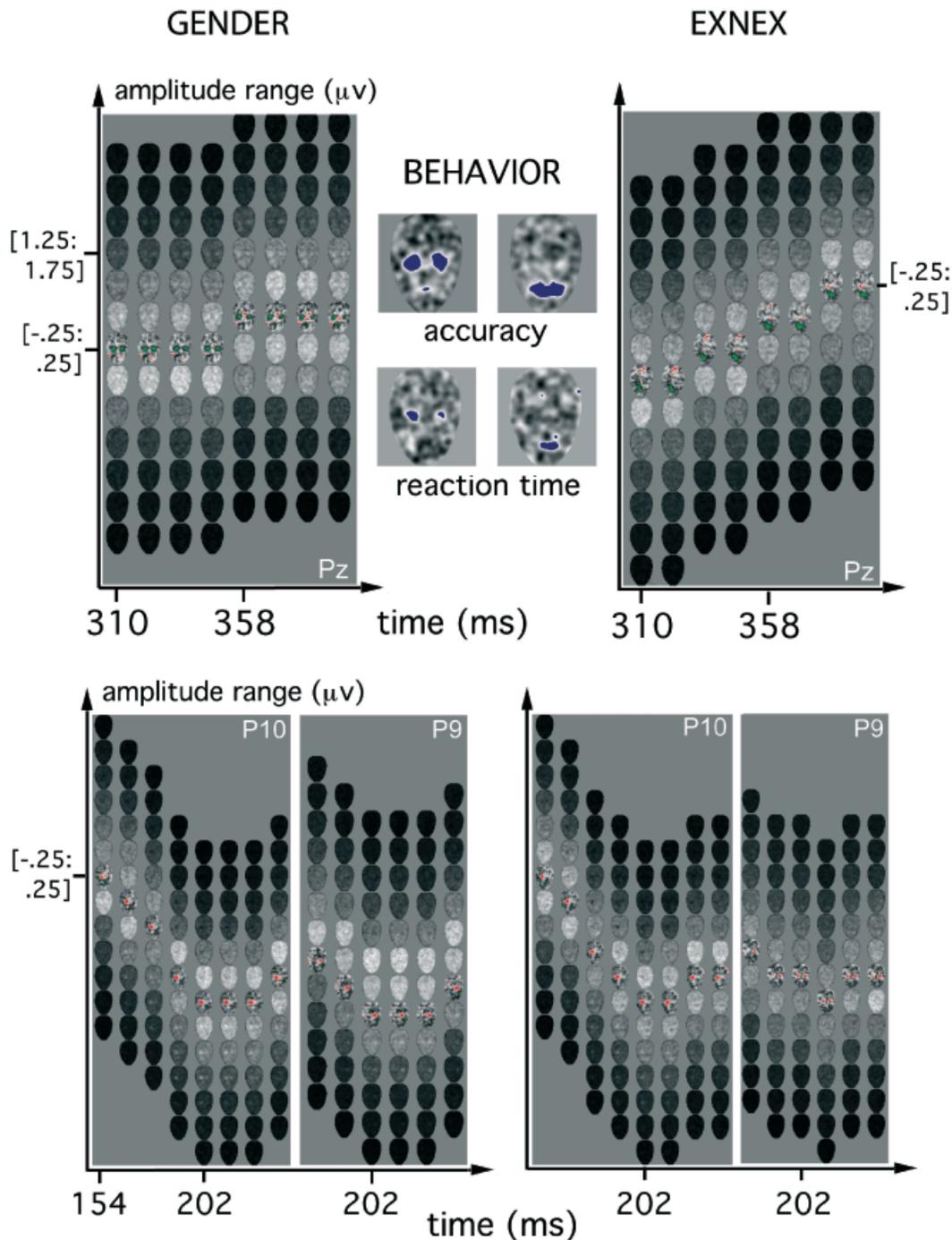
Fig. 1. Illustration of the method used in this study. Results are shown for electrode Pz between 310 and 394 ms following stimulus onset and for electrodes P10 and P9 between 154 and 238 ms following stimulus onset. (We analyzed recordings from 0 through 400 ms following stimulus onset, but present here a partial analysis covering the most relevant portion of this time window.) Every 12 ms, the recorded distribution of brain signals was split into bins of amplitude intervals (of 0.5 σ each, with the interval from −0.25 σ to 0.25 σ at the center of the distribution). The samples of face information were assigned to these bins according to the amplitude they elicited. In each central bin is the Z-scored discrimination image that represents the subtraction of the information bins above and below the mean; significant ($p < .05$, two-tailed) differences are indicated in green (positive) and red (negative). Results for the gender (GENDER) task are in the left half of the figure, and results for the expressiveness (EXNEX) task are in the right half of the figure. The upper panels reveal the emergence of the P300 brain signal, together with the features associated with it. For comparison, the blue areas in the illustrations labeled ''behavior'' show the features that determined categorization accuracy and reaction time (gender task on the left, expressiveness task on the right). The lower panels reveal the emergence of the N170 brain signal, together with the features associated with it.

potentials were low-pass filtered at 10 Hz (zero phase shift) and rereferenced to average reference, excluding the vEOG channel.

RESULTS AND DISCUSSION

Response Analysis

To determine the information responsible for categorization behavior, we used Bubbles. First, we analyzed the facial information associated with accuracy (gender task: 88% correct for M.L. and 81% correct for B.B.; expressiveness task: 87% correct for M.L. and 80% correct for B.B.). On each trial, the 14 randomly located Gaussian apertures made up a two-dimensional mask that revealed a sparse face. Observers would tend to be correct if the sampled information revealed the features that were diagnostic for the categorization task to be performed. Across trials, we computed the probability that each aperture led to a correct response, by subtracting the frequency of incorrect responses when that aperture appeared from the frequency of correct responses when that aperture appeared. We transformed the probabilities into Z scores. These analyses of accuracy revealed that both observers used the eyes diagnostically in the gender task but used the mouth diagnostically in the expressiveness task. The accuracy results in the top panel of Figure 1 show the diagnostic areas ($p < .025$, one-tailed) for B.B.; M.L.'s results were qualitatively similar and are therefore not illustrated.

Reaction Time Analysis

To determine the features discriminating between fast and slow reaction times, we fitted a Gaussian curve to the distribution of reaction times for each task. We segmented this distribution into 13 amplitude bins (organized symmetrically around the mean in increments of 0.5 σ) and for each of the 4,000 trials positioned the bubble mask in the appropriate reaction time bin. We derived a discrimination image by summing the masks leading to reaction times greater than the mean, summing the masks leading to reaction times lower than the mean (with the masks of each bin weighted by its sigma; bins more than 2.75 SD from the mean were treated as outliers and removed from the analysis), and computing the difference. The resulting probabilities were transformed into Z scores. The statistically significant ($p < .025$, one-tailed) regions (for B.B.) are marked in blue in the top panel of Figure 1. Reaction time analyses of trials with correct responses confirmed that the eyes and the mouth discriminated between fast and slow responses in the gender task (overall performance—M.L.: $\mu = 790$ ms, $\sigma = 210$ ms; B.B.: $\mu = 846$ ms, $\sigma = 168$ ms) and the expressiveness task (overall performance—M.L.: $\mu = 730$ ms, $\sigma = 185$ ms; B.B.: $\mu = 760$ ms, $\sigma = 152$ ms), respectively.

From the behavioral analyses (accuracy and reaction time), we conclude that selective attention to the eyes and to the mouth modulates the accuracy and speed of categorization decisions in the gender and expressiveness tasks, respectively.

EEG Analysis

To determine the information driving the EEG signals, we extended Bubbles to single-trial raw electrode amplitudes. On each trial, we measured independently for each electrode how the brain responded to the 14 randomly located samples of facial information (the bubble mask), sampling the EEG signal from 200 ms before stimulus onset until 600 ms after stimulus onset, using an averaged 12-ms time window. In each window, we modeled how the 4,000 trials of sampled face information modulated the recorded EEG amplitudes. To this end, for correct trials, we first fitted a Gaussian curve to the recorded distribution of amplitudes, segmented the modeled distribution into 13 amplitude bins (organized symmetrically by increments of 0.5 σ around a center bin ranging from -0.25 to 0.25 σ), and assigned the bubble mask for each of the 4,000 trials to its appropriate amplitude bin. This model depicts the mapping between samples of facial information and EEG amplitude responses, at a given time of measurement (see Fig. 1).

A simple computation isolated the face regions that drove low versus high EEG amplitudes: We subtracted the sum of the information in the bins below the central one from the sum of the information in the bins above the central one. The resulting discrimination image was Z-transformed. Figure 1 shows regions with significant ($p < .05$, two-tailed) negative (red) and positive (green) amplitude differences. The operations of modeling the amplitude distribution, assigning the bubble masks to amplitude bins, and determining the facial information eliciting negative and positive amplitudes were repeated for each measurement time and each electrode, resulting in a dynamic mapping of the use of facial information in the brain (see Fig. 1).

P300

Analyses of EEG activity over the Pz electrode, known to be sensitive to category decisions, revealed the emergence of a brain signal referred to as the P300 (Donchin & Coles, 1998; Verleger, 1997, 1998). Figure 1 represents this response with an increase in mean EEG amplitude over the 310- to 394-ms time window. The emergence of the signal is associated with the features modulating its amplitude (Fig. 1 represents these features in green). Significant positive differences between the EEG amplitudes above and below the mean were associated with eye information in the gender task and mouth information in the expressiveness task. Even casual inspection of Figure 1 reveals that for B.B., the features associated with the P300 were strongly correlated (Pearson) with the features diagnostic for categorization accuracy and reaction time (.57 and .52 in the gender task, .64 and .58 in the expressiveness task). Similar results were obtained for the Cz and Fz electrodes, and for M.L.

Functional interpretation of the P300 remains controversial (Donchin & Coles, 1998; Verleger, 1998), but it has been proposed that the superior regions determining P300 activity are involved in "what" categorization decisions (Goodale & Milner, 1992; Verleger, 1998). The current study shows that selective attention to diagnostic features (Schyns, 1998) does indeed modulate this brain signal. These modulations reflect a process that is active, top-down, strategic, and task-dependent, because the stimuli were identical in the two tasks, normalizing bottom-up, stimulus-driven effects.

N170

Analyses of EEG activity over the right-hemisphere occipito-temporal site (P10) known to be sensitive to stimulus encoding revealed the emergence of a signal referred to as the N170 (Bentin et al., 1996). Figure 1 represents this response with an increase in mean EEG amplitude (negative polarity) over the 154- to 202-ms time interval following stimulus onset. The facial features modulating this signal are marked in red in the discrimination images. Significant negative differences between the EEG amplitudes above and below the mean were associated with eye information in both the gender task and the expressiveness task. The fact that the left eye modulated the N170 at this electrode is clearly visible in Figure 1: From 154 ms onward, the amplitude bins lower than the mean EEG reveal the presence of the eye, and the corresponding amplitude bins above the mean reveal the absence of the eye. A symmetric response to the right eye was observed at the left-hemisphere P9 electrode (see Fig. 1). Note that the facial features associated with the N170 were clearly correlated with the features associated with categorization accuracy (.6), speed (.45), and the P300 (.44) in the gender task only. The correlations with the features identified in the expressiveness task were, respectively, −.06, −.04, and −.05. These results were replicated over the P7, P8, PO9, and PO10 electrodes, and the inverse polarity was seen at Cz.

Extrastriate occipito-temporal cortex regions in inferior occipito-temporal gyrus, the adjacent temporal sulcus, or both probably generate the N170 (Bentin et al., 1996; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002). The functional interpretations of this brain signal have included face detection (Bentin et al., 1996), emotion categorization (De Hann, Nelson, Gunnar, & Tout, 1998; Eimer & Holmes, 2002), eye detection (Bentin et al., 1996; but see Cauquil, Edmonds, & Taylor, 2000, and Eimer, 1998, for opposite results), encoding of facial structure (De Hann et al., 1998; Rossion et al., 1999; Sagiv & Bentin, 2001), and more generally the diagnostic encoding of features associated with expertise for faces (Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002; Rossion et al., 2000) and other categories (J.W. Tanaka & Curran, 2001). Here we have shown that the contralateral eye, not the information diagnostic in the task, modulated the N170 in both the gender and the expressiveness tasks. In contrast to the P300, the N170

does not appear to reflect a strategic task-dependent selective attention process; rather, it is an automatic, task-independent response to the eyes of a face (see also Schyns et al., 2003). The response to the contralateral eye also suggests that the neurons contributing to the N170 might not yet have contralateral input. Future experiments that manipulate information across the visual hemifields will further probe the implications of this result for theories of recognition.

Models of EEG Modulations Associated With Single Features and Configurations of Features (Second-Order Relationships)

The forward analysis we have discussed thus far modeled the response of each electrode to facial features. To derive a more precise account of EEG, we reversed the analysis and used the features as an orthogonal basis for decomposing the global activity into its feature-specific EEG components. Small (but significant) amplitude modulations (e.g., those corresponding to the facial information associated with the most extreme amplitude bins) could have been lost in the averaging of the forward analysis. The reverse analysis, by isolating the modulations associated with specific features, might be more sensitive to the finer EEG modulations. The forward, low-bias and the reverse, feature-specific analyses are complementary passes on the EEG data to extract informational determinants of the brain signals.

We were particularly interested in using the reverse analyses to ascertain the relative contributions of features in isolation (e.g., left eye, right eye, mouth) and features in conjunction (left eye with right eye, etc.). That is, we wanted to determine the relative contributions of first-order (i.e., single feature) and second-order (i.e., configurations of features) effects on the emergent brain signals.

Our feature masks for decomposing the EEG signal were the left eye, the right eye, and the mouth. The remainder of the face area was covered with an additional seven masks. On each of the 4,000 trials of sampled face information for each task, we computed the proportion of the area of each mask sampled by the bubbles. A proportion greater than .15 indicated that the mask region under consideration was sampled on that trial, and we added the corresponding EEG signal into the bin associated with that mask. After completing this analysis for all 4,000 trials, we averaged the content of each feature-specific bin to derive the average EEG signal (see Fig. 2). An average EEG signal for the remainder of the face area was computed from the average signals of the remaining masks (see Fig. 2).

To test for possible effects of configurations of features, we used the masks to single out trials in which information was simultaneously presented over a conjunction of features (e.g., a bubble in the left eye and another bubble in the right eye) and derived the average EEG signature for this conjunction. We tested the conjunctions of left eye and right eye, left eye and mouth, right eye and mouth, left eye and nose, and right eye and nose, whose masks corresponded to approximately equal face
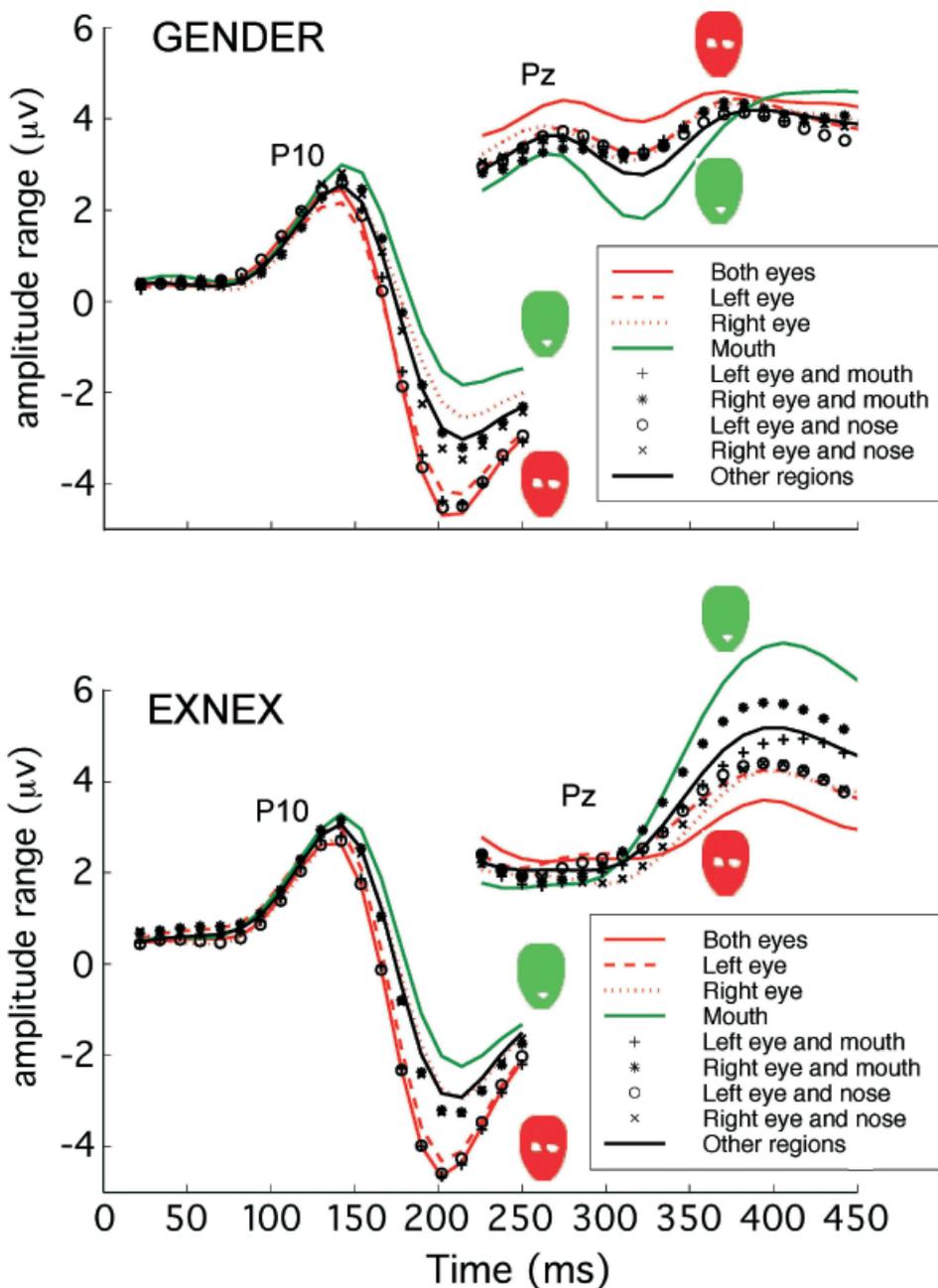
Fig. 2. Decomposition of the global electroencephalographic (EEG) activity into feature-specific EEG components. The feature masks (left eye, right eye, and mouth) generated from the classification images of the initial analysis were used as a basis for this reverse analysis. For each feature mask, we computed the proportion of its area that was sampled on each of the 4,000 trials for each task; we then averaged the signals for trials on which more than .15 of the area was sampled. Average EEG amplitude over time for the sampling of features independently, for configurations of features, and for the remaining areas (''other'') is indicated for the P10 and Pz electrodes in the gender (GENDER) task (top panel) and the expressiveness (EXNEX) task (bottom panel). Feature masks corresponding to the eyes (red) and the mouth (green) are displayed close to the relevant curves.

areas. It is important to emphasize that the conjunctive analysis explicitly excluded the trials on which only one of the features was presented (e.g., a bubble on the left eye, but none in the right eye). Hence, there was no overlap in the EEG trials making

up the response curves for individual features and conjunctions of features.

In the gender task, parietal P300 activity revealed a marked amplitude advantage for eye information, and in particular, the

conjunction of both eyes, over the mouth and other features. In the expressiveness task, this trend was reversed, with the mouth leading to higher activation than the eyes (see Fig. 2). If temporal P300 amplitudes can be used as an index of mental chronometry (Verleger, 1997), one would expect that higher amplitudes in response to the eyes than to the mouth in the gender task would elicit faster categorization responses to the mouth than to the eyes (and similarly, that higher amplitudes in response to the mouth than to the eyes in the expressiveness task would elicit faster categorization responses to the eyes than to the mouth). We found faster behavioral reaction times to the eyes than to the mouth in the gender task and faster reaction times to the mouth than to the eyes in the expressiveness task— $t(2919) = 2.91$, $p < .005$, $d = 0.12$, vs. $t(2742) = 4.55$, $p < .001$, $d = 0.18$—confirming the correlation between higher temporal amplitudes to diagnostic features and categorization speed.

Turning to the occipito-temporal N170 activation, we found that the conjunction of the two eyes elicited a signal as strong as the one elicited by the left eye in isolation (on the P10 right-hemisphere electrode; on the P9 left-hemisphere electrode, the conjunction of the two eyes elicited a signal as strong as the one elicited by the right eye in isolation), and both signals were much stronger than that associated with any other facial feature. However, the average N170 amplitude responses arising from other conjunctions of features including either eye were similar in magnitude to responses to both eyes and the eye in isolation. Hence, this detailed analysis revealed a sensitivity of the N170 to the contralateral isolated eye, but no evidence that configurations of facial features modulate N170 amplitude.

Time Course of Face Processing

Our analysis of face processing provides a time line of the information that modulates behavior (accuracy and reaction time) in comparison with the information that modulates brain events (the N170 and the P300), offering a fine time scale to analyze face recognition processes. Specifically, the first EEG event sensitive to facial information, the N170, present after about 200 ms of processing, was not sensitive to task in this experiment, but was unilaterally sensitive to the eyes. Its timing was close to that of the first saccade, which in a face lands on the eyes (Pearson, Henderson, Schyns, & Gosselin, 2003). The P300, present after about 300 ms of processing, was sensitive to task-relevant information (the eyes in the gender task, the mouth in the expressiveness task).

The comparison of brain and behavioral information states suggests task-dependent dynamics for the unfolding of attention in face processing. In the gender task, selective attention to the eyes persists from stimulus onset until behavioral response, a temporal dynamic supported at the finer time scale of brain events. In the expressiveness task, attention appears to be initially hemisphere-specific, rapidly shifting from the contralateral eye to the mouth. In this context, it is interesting to note that the P300 onset occurred about 30 ms earlier in the gender task

(around 286 ms) than in the expressiveness task (around 322 ms, using the appearance of the relevant feature in the classification image as a reference). In addition, note the negative difference (in red) over the eyes for the expressiveness task in Figure 1; this negative difference (which contrasts with the positive difference in the gender task) corresponds to the lowest P300 amplitudes and suggests that for this observer attention had to disengage from the eyes, which were irrelevant for correct expressiveness categorization judgments. Responses occurred about 800 ms following stimulus onset, but the earlier analysis of the time course of brain events has already added a supplementary dimension of analysis, at a finer time scale.

CONCLUDING REMARKS

To conclude, we applied a low-bias, low-variance approach to reveal the low-dimension information subspaces that structure the receptive fields of emergent brain signals and correlated these with the information observers use to categorize multidimensional face stimuli. We found high correlations between the low-dimensional features that modulate speed and accuracy of categorization behavior and the features, including second-order relationships between them, that modulate the amplitude of the P300 brain signal associated with ventral "what" decision mechanisms. These active and task-dependent processes contrast with the N170, which responds automatically to the contralateral eye, without apparent second-order relationships between features, irrespective of the information requirements of the categorization task at hand. The fine time resolution of brain events, together with the coarse scale of behavioral events, enabled us to track the selective attention to facial features across tasks.

Even though there is little doubt that the N170 indicates a response to the eyes in faces, it is worth pointing out that the categorization context in this study was restricted—observers knew that a face would appear on each trial. Hence, the response to the eyes appears to be automatic, but this conclusion is valid specifically for the context of face stimuli. Broader contexts (e.g., in which faces appear together with other kinds of objects) could help to further determine the functionality of the N170: Does the apparently automatic response to the eyes reflect a diagnostic process of face detection? a response to bilaterally symmetric objects? a response to features with high spatial frequency? or something else?

We are aware that the low-bias, low-variance approach developed here could easily generalize to studies of other brain signals, including the firing rates of single cells or cell assemblies, functional magnetic resonance imaging (fMRI) amplitude responses, and other measurable physiological responses. Such studies could offer considerable insights into the response properties of brain signals as a function of stimulus features, attention, and the demands of categorization tasks.

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