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Report

Dynamics of Visual Information Integration in the Brain for Categorizing Facial Expressions

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Summary

A key to understanding visual cognition is to determine when, how, and with what information the human brain distinguishes between visual categories. So far, the dynamics of information processing for categorization of visual stimuli has not been elucidated. By using an ecologically important categorization task (seven expressions of emotion), we demonstrate, in three human observers, that an early brain event (the N170 Event Related Potential, occurring 170 ms after stimulus onset [1–16]) integrates visual information specific to each expression, according to a pattern. Specifically, starting 50 ms prior to the ERP peak, facial information tends to be integrated from the eyes downward in the face. This integration stops, and the ERP peaks, when the information diagnostic for judging a particular expression has been integrated (e.g., the eyes in fear, the corners of the nose in disgust, or the mouth in happiness). Consequently, the duration of information integration from the eyes down determines the latency of the N170 for each expression (e.g., with "fear" being faster than "disgust," itself faster than "happy"). For the first time in visual categorization, we relate the dynamics of an important brain event to the dynamics of a precise information-processing function.

Results and Discussion

We instructed three observers to resolve seven biologically relevant face categorizations ("happy," "fear," "surprise," "disgust," "anger," "sad," and "neutral") of FACS-coded faces [17, 18] (five males and five females) displaying each expression of emotion (for a total of 70 original stimuli). The experiment sought to establish a one-to-one correspondence between random samples of facial information presented on each trial (sampled from the original faces, with Gaussian windows smoothly revealing information from five nonoverlapping spatial frequency—SF–bandwidths; see Figure 1) and behavioral [19–21] and brain responses to this facial information [22–24]. With classification image techniques, we estimated, for each observer, across the 21,000 trials of the experiment (3000 trials per expression) how facial information modulated behavior (categorization accuracy) and brain responses (modulations of EEG voltage over the time course of the N170).

Facial Information Modulates Categorization Accuracy

By using classification image techniques, we first analyzed for each observer, expression, and spatial frequency band the diagnostic facial features associated with categorization accuracy (set to be at 75% for each individual expression, by calibrating online sampling density). We then rendered the facial features diagnostic of each expression with an effective image (see "(1) Computation: Behavioral Classification Image" in Experimental Procedures in the Supplemental Data available online; see "Behavior" in Figure 2 and Figures S2–S4 for the spatial frequency decomposition of each behavioral image). For illustration, the facial features diagnostic of "fear" are primarily the wide-opened eyes, whereas the region around the wrinkled nose is diagnostic of "disgust," and the smiling mouth diagnostic of "happy."

Facial Information Modulates EEG Voltage

Again by using classification image techniques, we analyzed, at a 4 ms resolution, for each observer, expression, and spatial frequency band the facial features associated with modulations of EEG voltages—measured on the right and left occipitotemporal (OTR and OTL) electrodes—with the largest negative deflection within the 140–212 ms time interval of the N170 (see Figure S1 for the observers' ERPs). For each expression and OTR and OTL electrode, Figure 2 represents the EEG classification images at each time step. Together, they form "movies" representing over time the dynamics of the sensitivity of the EEG to facial features (see Figure 2 and "(2) Computation: Sensor-Based EEG Classification Images" in the Supplemental Experimental Procedures). For illustration, the gray-level OTR and OTL movies for "disgust" on Figure 2 reveal that the dynamics of sensitivity of the EEG moves from the location of the eyes progressively toward the lateral sides of the wrinkled nose over the N170 time course.

In the context of the categorization of seven facial expressions of emotion, we report the following three main findings regarding the information processing function of the N170: (1) The N170 integrates facial features over time, starting 50 ms prior to the N170 peak; (2) the integration of facial information tends to proceed from the eyes and moves down the face, irrespective of expression; and critically, (3) the integration of facial information stops, and the N170 peaks, when the information critical for behavior (i.e., a category decision) has been integrated (e.g., the eyes in "fear," the corners of the nose in "disgust" or the mouth in "happy").

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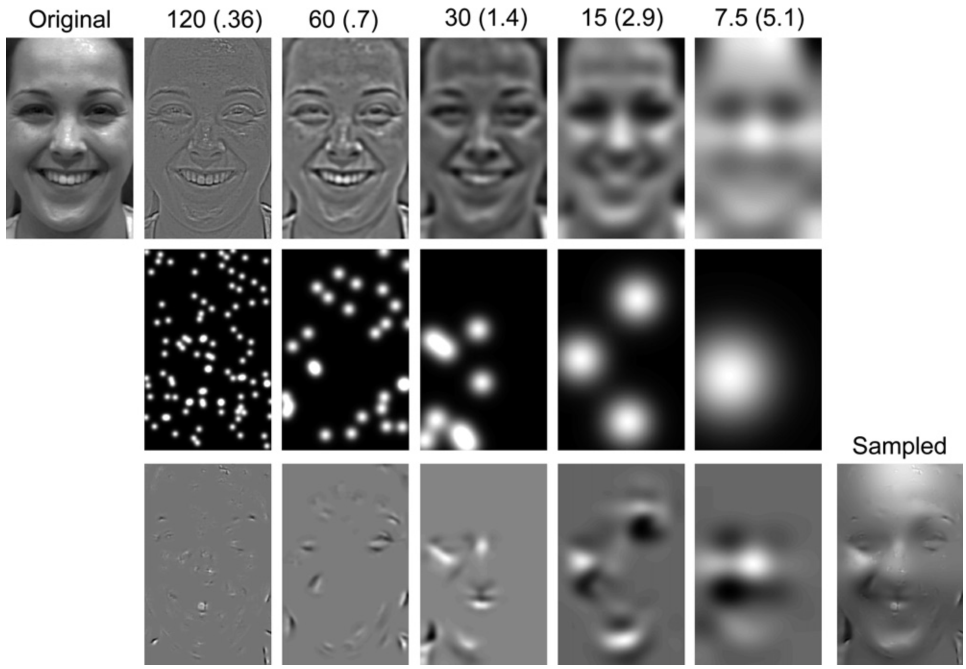

Figure 1. Stimulus Generation Process

Shown in the first row: On each trial a randomly chosen original stimulus is decomposed into five nonoverlapping spatial frequency (SF) bands of one octave each (120–60, 60–30, 30–15, 15–7.5, and 7.5–3.8 cycles/face). Shown in the second row: Gaussian apertures each revealing six cycles per face, irrespective of SF band, are randomly positioned (standard deviations of the bubbles were 0.36, 0.7, 1.4, 2.9, and 5.1 cycles/degree of visual angle from the fine to the coarse SF band). Shown in the third row: The SF-band facial information from the first row is sampled with the Gaussian apertures of the second row. The addition of the randomly sampled face information from each SF band produces one stimulus image.

(1) The N170 Integrates Facial Features over Time

To frame the function of the N170, every 4 ms we computed on OTR and OTL electrodes the overall quantity of SF information to which the EEG was sensitive (see "(3) SF Information Measurement over the Time Course of the ERP and Its Integration" over the N170 in the Supplemental Experimental Procedures). The red curves in Figure 2 (dashed for OTL) report this measure. It is immediately apparent that an almost monotonic increase in SF information sensitivity is followed by an almost monotonic decrease, itself followed by the ERP peak (indicated with a blue box in Figure 2). This shape of the information sensitivity curve characterized all seven expressions and three observers, both on OTL and OTR ($n = 42$, see Figures S5 and S6 for further illustrations).

The red curves reflect a dynamic of information sensitivity characteristic of the derivative of an integrated function: The instantaneous slope of the ERP would closely reflect the slope of an information accumulation function. To test this hypothesis, we integrated the red curves over time to produce the black curves (see Figure 2, OTL dashed) and correlated, independently for each observer and electrode, the resulting integrated function with the ERP curve of each expression (represented in blue in Figure 2, OTL dashed). We computed confidence intervals by using a bootstrap with replacement, 999 resampling trials, at $p < .05$ [25]. Table 1 presents the correlations averaged across expressions, for each observer and OTL and OTR electrodes. The high correlations suggest that the unfolding of the N170 on both electrodes closely reflects processes of integration of SF information starting from approximately 50 ms before the N170 peaks.

(2) The Integration of Facial Information Tends to Proceed from the Eyes and Moves down the Face

Information integration across expressions was similar on both electrodes, for all observers. For illustration, consider Figure 3 in which three plots represent a different observer (see "(4) Further Characterization of Facial Information Integration" in the Supplemental Experimental Procedures). The x coordinate of each plot indicates the time interval of the ERP on both electrodes; the y coordinate represents the y face coordinate of the maximum of SF information present in the EEG classification images and summed across all expressions. At each time step, two points (one for OTL, one for OTR; see blue circles) illustrate the relationship between the dynamics of the N170 and the information that is being integrated—the background face should only be used to facilitate the y coordinate localization of the facial features corresponding with the SF information maxima. Linear regressions (performed collapsing OTL and OTR coordinates) indicate linear relationships between the two factors ($p < .05$, confidence interval indicated in green). Thus, OTL and OTR N170s tend to integrate facial features from the top of the face (i.e., the eyes) and progress downward on a vertical axis to the bottom of the face (see also Figure S7 for illustrations of individual examples of scanpaths per observer, expression, and electrode).

(3) The Integration of Facial Information Stops, and the N170 Peaks, when Diagnostic Information Is Reached

The integration scanpath on the face suggests that the latency of each ERP could depend on the vertical distance of the expression-specific diagnostic information

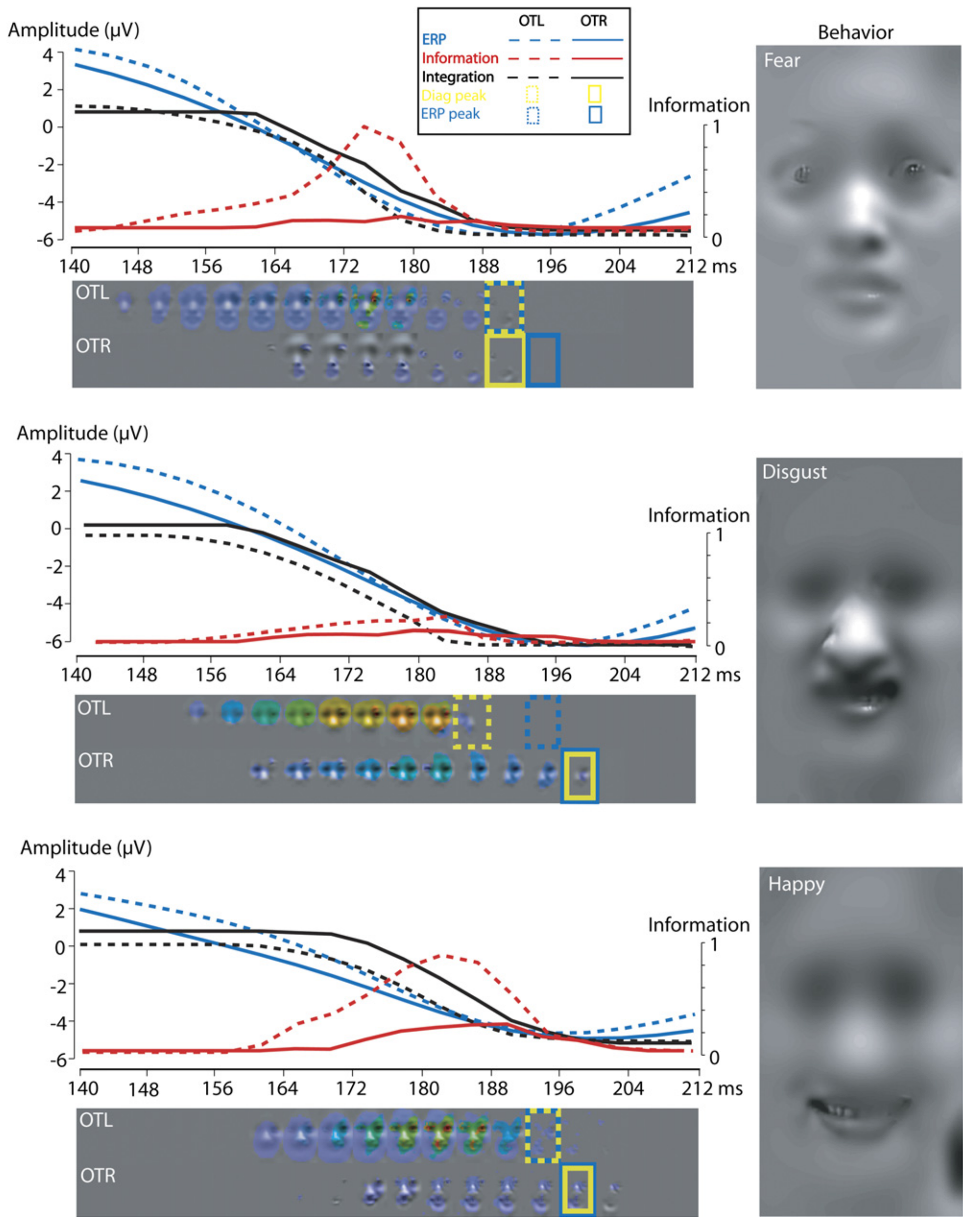

Figure 2. The N170 Integrates SF Facial Information

Illustration for UM and expressions "fear," "disgust," "happy." Shown under "Behavior": Representation of the facial SF features required for correct behavior. Shown in the left panel: For left and right occipitotemporal electrodes (OTL and OTR, OTL dashed lines), the blue curves indicate the typical N170 negative deflection. With *Bubbles*, we derive, in a movie of classification images, the dynamics of the sensitivity of the N170 to any facial information (see the OTL and OTR classification images; time resolution is 4 ms). Note that this analysis concerns strictly the EEG: It is not related to behavior at this stage. The red curves quantify this sensitivity to facial information, which peaks for each expression and electrode before the ERP peak (indicated with blue boxes). The color coding of the classification images localizes this SF information in the face, with red indicating higher information values and blue indicating lower information values. The black curves integrate the red curve over time—they are negated and rescaled to the ERP peak for comparison purposes—demonstrating that the N170 reflects a process that integrates facial features over time. The dashed yellow boxes indicate the maximum of the integration of the information required for categorization behavior (the diagnostic information). (See "(3) SF Information Measurement over the Time Course of the ERP and its Integration" in the Supplemental Experimental Procedures for details).

from the two eyes. In this case, the eyes in "fear" would lead to an early ERP, and the mouth in "happy" would lead to a later ERP; see "Behavior" in Figure 2 (see also Figure S1 for the ERPs). We tested this hypothesis for each observer, electrode, and expression (n = 42) by extracting the SF information common to the behavioral and to the EEG classification images—i.e., by computing an intersection between the thresholded behavioral and EEG classification images (see "Time Course of the N170 and Diagnostic Information" in the Supplemental Experimental Procedures). The resulting function reflects only the integration of diagnostic, behavior-relevant information in the EGG classification images over time. We computed the maxima of this integration over

Table 1. Observer, UM, LP, and LF, Mean Correlations, n = 7 Expressions, and SDs between the ERP Curves and the Function of Integration of SF Facial Information, on Electrodes OTL and OTR

	OTL		OTR	
	M	STD	M	STD
UM	0.98	0.02	0.97	0.03
LP	0.93	0.06	0.97	0.02
LF	0.93	0.04	0.98	0.01

the time course of each ERP (maxima are rendered with yellow boxes in Figure 2) and regressed them with the ERP latencies. In Figure 4, the resulting regressions present a linear relationship between the timing of the maximum integration of diagnostic information and the latency of the ERP. Thus, the N170 latency marks then the end of a process, starting at the location of the eyes and ending at the location of the expression-specific diagnostic information, that integrates SF facial features. This explains why "fear" (involving mostly the eyes) peaks earlier than "disgust" (involving the corners of the nose) and "happy" (involving the mouth). It also implies that the information processed over the N170 conveys sufficient information for predicting categorization behavior.

We have shown in three observers that the dynamics of the N170 wave, on the left and right occipitotemporal regions, closely correlate with a function integrating facial features over time. This integration proceeds over a 50 ms time window prior to the N170 peak, in a scanpath starting from the location of the eyes downward in the face. We have shown that the vertical distance between the two eyes and the facial location of the expression-specific diagnostic information (e.g., the mouth in "happy") determines the latency of the N170 for this expression. Note that we have confined the analysis to the relationship between N170 latencies and the underlying information processing function (see Garrod, Schyns and Smith, Neuroimage, 36, Supp 1, S42 (2007) for a discussion of how the information processing function of amplitude could be isolated).

The N170 ERP Reflects a Cognitive Process

There has been considerable debate regarding the nature of category effects on the N170 [1–16]. The evidence reported here demonstrates that the N170 reflects a process under cognitive control, not a low-level effect. In recapitulation, the N170 curve (on OTL and OTR) integrates SF information over time with evidence for a mixture of automatic and goal-directed control. It is automatic because it tends to start with the eyes and then integrates information downward on the y axis of the face plane. It is goal directed because the downward integration stops when the diagnostic features have been integrated. Thus, claims to the effect that low-level properties might explain modulations of the N170 will need to be revised [26]. Specifically, if a process integrates information, including diagnostic information, variations in the location of this information in the stimulus will have an impact on the shape of the N170—as demonstrated here between the early ERP to the eye information in "fear" and the late ERP to the mouth information in "happy." However, as we have shown, it is the knowledge of the location of the information used in the image, together with an understanding of the dynamics of the overall processing of this information (here from the eyes to the mouth), that enables specific predictions about the shape of the N170 ERP.

Automatic and Goal-Directed Control of Information Integration

An important question for future research concerns the precise nature of the "automatic" versus "goal-directed" aspect of the SF integration process. Crucial to this is the suggestion that prefrontal cortex (PFC) is involved in task-dependent, adaptive coding in working memory, attention, and control [27]. The difficult question is how these different regions interact to process the visual and semantic information leading to different categorizations of a given stimulus. Recent thinking [27, 28] suggests that top-down expectations from PFC become coupled with the visual occipital cortex and the fusiform gyrus so that task-dependent representations for recognition could be progressively constructed.

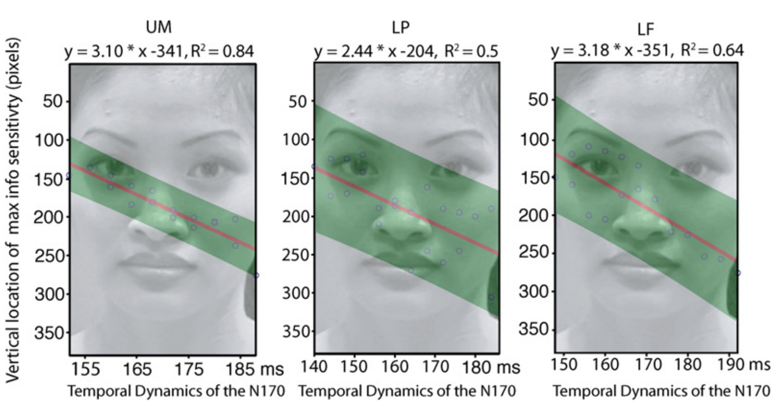

Figure 3. The Integration of Facial Information Tends to Proceed from the Eyes down to the Bottom of the Face

For each observer (UM, LP, and LF), least-mean square linear regression of the location of the maximum of SF information (summed by time window over all seven expressions) within the image space in the vertical dimension (y axis of each image) with the temporal dynamics of the N170 signal (x axis of each image). For each observer, we pooled data over electrodes OTR and OTL, for a total of two data points per time point. Blue circles indicate individual data points (N170 latency, y coordinate of maximum SF information). The red line indicates the linear regression of the data points, and the flanking green boxes the confidence intervals ($p < .05$). Note that the scanpaths are undefined outside the time points indicated on the x axis of the image. (See "(4) Further Characterization of Facial Information Integration" in the Supplemental Experimental Procedures for details).

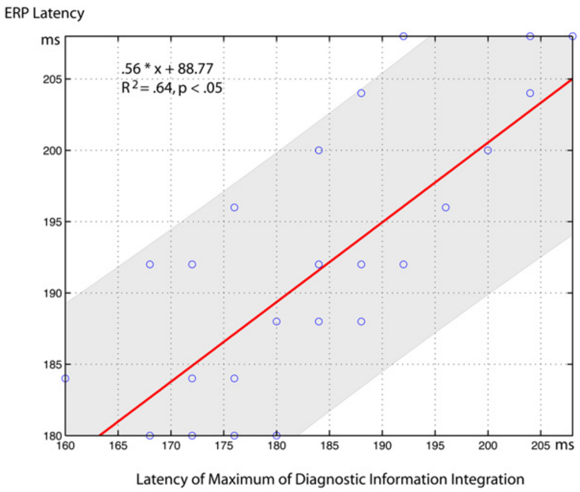

Figure 4. The Integration of Facial Information Stops, and the N170 Peaks, when Diagnostic Information Has Been Integrated

Least-mean square linear regression of the ERP latencies (x axis) with latency of maximum of diagnostic SF integration (y axis). Blue circles indicate individual data points (N170 latency, latency of maximum of diagnostic SF integration). The red line indicates the linear regression of the data points, and the flanking gray boxes the confidence intervals ($p < .05$). Data were pooled across three observers, two electrodes, and seven expressions, for a total of 42 (maximum of diagnostic information, ERP latency) coordinates.

The evidence of information integration reported here also suggests a progressive integration of information over the left and right occipitotemporal region. For control, we would predict a strongly overlapping fronto-occipitotemporal network responsible for the implementation of top-down expectations that allow for the effective integration (i.e., encoding and retention) of visual categorization information over short periods of time.

Implications of Diagnostic Information

We demonstrated that the integration of the expression-specific diagnostic information occurs just before the N170 peaks, on the left and right occipitotemporal electrodes (see Figure 4). Consequently, in a time window ranging from approximately 160–205 ms, there is enough information in the brain (though split between two hemispheres), to determine the emotional category of the input stimulus, a category-specific effect. The idea of category-specific effects on the N170 has never been conclusively associated with the specific information of a behavioral categorization response (e.g., the left corner of the nose on OTL and the right corner of the nose on OTR for "disgust," see Figure 2). Our findings extend those demonstrating that inferior temporal-cortex neurons in nonhuman primates are sensitive to diagnostic object properties [29–32]. They also open the interesting prospect of predicting behavior from a brain signal measured as early as 160–200 ms after stimulus onset, a critical finding for "mind reading" [33].

However, there is considerable lateralization of the diagnostic information observed over the N170 (e.g., see "disgust" in Figure 2). This raises the question of whether interhemispheric integration of diagnostic information, after its extraction over the N170 time course, is required for perceptual decision [23]. A better understanding of the dynamics of information processing, from its lateralized extraction to its integration for perceptual decision, will be critical for understanding categorization processes.

Experimental Procedures

Subjects, Stimuli, and Task

We used *Bubbles* to synthesize sparse versions of the original stimuli by randomly sampling facial information from five one-octave nonoverlapping SF bands (see Figure 1 and [19, 20]). During the experiment, three observers categorized by expression 21,000 of these sparsely sampled expressive images while we concurrently recorded their EEG. Online calibration of sampling density ensured 75% accuracy per expression.

Data Collection

We used sintered Ag/AgCl electrodes mounted in a 62-electrode cap at scalp positions including the standard 10-20 system positions along with intermediate positions and an additional row of low occipital electrodes. Linked mastoids served as initial common reference, and electrode AFz served as the ground. Analysis epochs for correct, nonartifact trials were generated beginning 500 ms prior to stimulus onset for 1500 ms and were rereferenced to average reference. For each observer, we selected a left and right occipitotemporal electrode on the basis of those electrodes recording the highest amplitude of the N170 peak.

Computations

We reverse correlated the location of the sampled information with behavioral response to represent in the three dimensions of image sampling the combination of SF bands and image features diagnostic for the categorization of each expression (see [19–21] for further details and see [21, 24, and 34] for discussions of Spatial Frequency integration for perception and recognition). Similarly, we applied *Bubbles* to the single-trial raw electrode amplitudes to ascertain the facial information systematically correlated with modulations of the EEG signal [22–24] over the time course of the N170. From the EEG classification images, we inferred the information processing function of the N170.

Supplemental Data

Additional Experimental Procedures and seven figures are available at http://www.current-biology.com/cgi/content/full/17/18/1580/DC1/.

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