Face-selective spectral changes in the human fusiform gyrus

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Abstract

Objective: To characterize ventral occipitotemporal and prefrontal EEG during cognitive processing.

Methods: Depth probes were implanted for seizure localization in 16 pharmaco-resistant epileptics. Probes penetrated from middle temporal through fusiform to lingual gyrus, and from inferior frontal to anterior cingulate gyrus. Event-related potentials (ERPs) and event-related spectral power (ERSP) were calculated during delayed recognition for faces or words.

Results: Face stimuli evoked a broadband fusiform ERSP increase from 5 to 45 Hz at 150–210 ms after stimulus onset. This ERSP increase was immediately followed by an ERSP decrease in the same region from 300 to 1000 ms. Both the early increased ERSP and the late decreased ERSP, were greater for faces than words. Simultaneous with the late temporal ERSP decrease, the prefrontal depth EEG displayed a low frequency (5–12 Hz) ERSP increase to face and word stimuli.

Conclusion: Early temporal ERSP increases occur at a time when the fusiform gyrus is thought to contribute to face processing. This increase is also reflected in spectral analysis of the ERP, but the late temporal ERSP decrease and frontal ERSP increase are not. Thus, intracranial recordings in humans demonstrate event-related fluctuations in EEG spectral power with clear anatomical, temporal and cognitive specificity. © 1999 Elsevier Science Ireland Ltd. All rights reserved.

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1. Introduction

EEG is thought to be generated by cortical synaptic potentials, and is strongly influenced by cognition. In one view, 'background' EEG waves are considered to be noise; eliminating that noise by time-locked averaging with respect to a cognitive event reveals event related potentials (ERPs). In the other view, EEG waves are the signal, to be analyzed according to their power at different frequencies. The resulting measure is termed event-related spectral power (ERSP). In this view, ERPs are simply EEG waves that are phase-locked to the stimulus.

ERP analysis has been successful in demonstrating a series of synchronous synaptic activations associated with different sensory, cognitive and motor aspects of cerebral function (Halgren, 1990). In contrast, early studies suggested that increased EEG power within certain frequency ranges indicated decreased mentation. For exam-

ple, the alpha rhythm increases when the eyes are closed (Berger, 1929), and delta activity increases during non-dreaming sleep (Loomis et al., 1936). Recently, however, it has been suggested that some EEG rhythms, especially in the gamma band, may play a critical role in synchronizing cognitive processing in widespread cortical areas (Basar and Bullock, 1992). Acceptance of this view has been limited by the lack of interlocking cognitive, temporal and anatomical specificity in the spectral responses; specific functional activation should occur only in response to a particular cognitive stimulus, only in the particular structure specialized for analyzing that stimulus, and only at the time when that structure is making its particular contribution.

Lesions of a small region in the fusiform gyrus, located bilaterally at the junction of the ventral temporal and occipital lobes, can produce profound and specific deficits in face processing (Damasio et al., 1990). This region is anterior to the retinotopic visual areas, and posterior to the memory-related regions of the ventral temporal lobe. It is specifically activated by faces, according to PET (Haxby et al., 1996) and fMRI (Halgren et al., 1999), with a peak response about 170 ms after face onset according to MEG
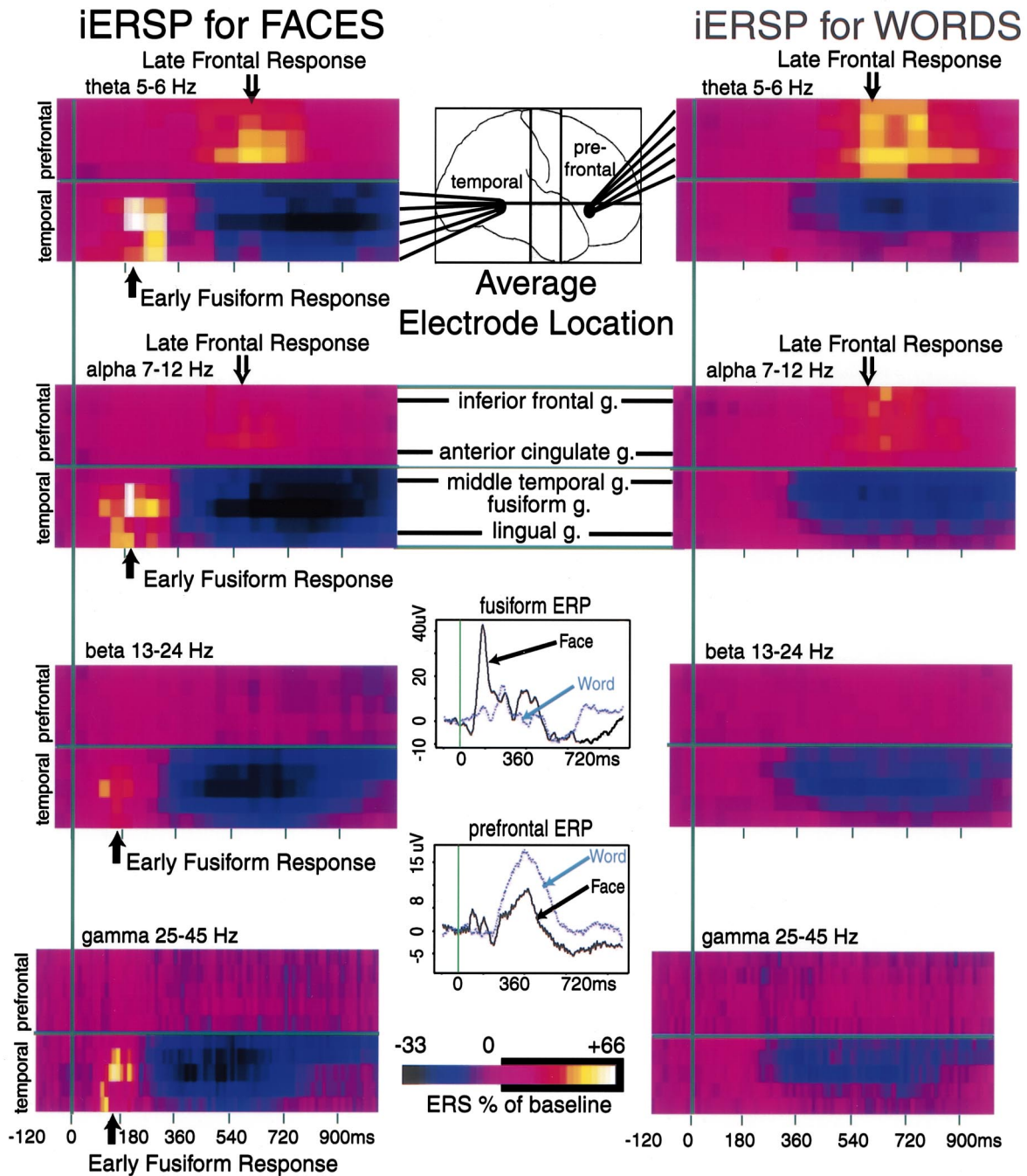
Fig. 1. iERSP averaged across 16 subjects recognizing words or faces. Each color panel presents results from 5 intracranial EEG electrode contacts from each of two depth probes. Depth probes were inserted perpendicular to the vertical mid-line and passed from lateral-to-medial (top-to-bottom in the figure). One probe penetrated the ventral prefrontal cortex, passing from the inferior frontal to the anterior cingulate gyrus (upper half of each color panel). The other probe penetrated the tempo-occipital cortex, passing from middle temporal through the fusiform to the lingual gyrus (lower half of each panel). ERSP values were normalized by baseline values (− 120 to 80 ms for theta, − 120 to 60 ms for alpha and beta and − 120 to 0 ms for gamma). A broadband iERSP increase occurs at about 180 ms after stimulus onset in the fusiform gyrus to faces (→). Lower-frequency iERSP increases at about 600 ms, occur in ventral prefrontal cortex to both faces and words (⇒). During this prefrontal iERSP increase, the temporal EEG displays a strong decrease in iERSP. In contrast to these opposite reactions in iERSP, ERPs in the same latency range from the same subjects and tasks consistently showed long-latency components of comparable amplitude in both temporal and frontal cortices (lower center of figure).

(Sams et al., 1997; Halgren et al., in preparation) and intracranial EEG (Allison et al., 1994; Halgren et al., 1994a). This peak immediately follows processing in retinotopic cortex, and immediately precedes more cognitive processing in ventral temporal areas that occurs from 240 to 600 ms (Halgren et al., 1994a).

Evidence for the presence and location of a prefrontal area that participates in face processing is less well estab-

lished. In the macaque monkey, face-specific unit-firing has been reported in the ventrolateral prefrontal cortex (Pigarev et al., 1979; Skelly et al., 1992). In humans, using iEEG, Halgren et al. (1994b) showed large ERPs in the ventrolateral prefrontal cortex from 300 to 700 ms after the presentation of faces in a declarative recognition memory task. Words evoked similar potentials, but simple visual and auditory stimuli in signal detection tasks did not (Baudena et al., 1995). Using PET and fMRI, Courtney et al. (Courtney et al., 1996, 1997) found that ventrolateral prefrontal cortex showed sustained activation in a working memory task involving faces. More generally, these techniques frequently find bilateral ventrolateral prefrontal cortex activation, during a variety of semantic word-processing tasks (Gabrieli et al., 1998). In addition, direct electrical stimulation of the right anterior inferior frontal gyrus may evoke hallucinations of faces (Vignal et al., 1999).

The current study measured temporal specificity by analyzing spectra in several frequency bands, during brief time-periods following stimulus presentation. Cognitive specificity was probed by comparing ERSP elicited by faces versus words in the same task. Comparison of intracranial EEG recordings across multiple structures, including the fusiform gyrus and ventral prefrontal cortex, provided anatomical specificity.

2. Methods and materials

Subjects ($n = 16$) suffered from medically resistant complex partial epilepsy and were candidates for surgical therapy. Depth probes were recommended only if non-invasive measures were inadequate to identify the seizure focus (Chauvel et al., 1996). Subjects gave fully informed consent and were monitored by institutional review boards. Depth probes were 0.8 mm in diameter, blunt-tipped, and had 5, 10 or 15 recording electrode contacts. Each contact was 2.0 mm in length, and successive contacts were separated by 1.5 mm. The middle contact of the prefrontal probes ($n = 10$) had average Talairach coordinates of ± 27, $+37$, -4; the middle (fusiform gyrus) contact of the temporal probes ($n = 17$) had average coordinates of ± 31, -55, -1 (Talairach and Tournoux, 1988). In all, ERSP measures from 135 intracranial EEG contacts are reported here.

No systematic differences were noted between left and right recordings, which were therefore combined in subsequent analyses (one subject had fusiform recordings in both hemispheres). The results illustrated in Fig. 1 are essentially identical to those that were obtained from a population subset ($n = 5$) where both temporal and frontal regions from the right hemisphere were recorded in both face and word tasks for each individual.

Subjects performed delayed recognition tasks for either faces or written words. One hundred and twenty to 280 trials were presented per condition. In 11 cases, the subject performed only one task. Faces were shown using color slides on a back projection screen, and words using a video monitor. Stimuli were presented every 3 s for a duration of 300 ms. Faces subtended a visual angle of 5.5° horizontal by 8.3° vertical. The face stimuli were photographs of previously unfamiliar young adults of European descent who lacked beards or mustaches. Words subtended a visual angle of 1.2–1.5° horizontal by 0.4° vertical and were sampled from both low and high lexical frequency lists (for complete methodological details, see Halgren et al., 1994a,b).

Waveforms were digitized every 6 ms at 12 bit resolution for 1200 ms beginning 120 ms before stimulus onset, and referenced to the tip of the nose. Trials were rejected if eye movements, epileptiform EEG spikes or other large transients contaminated them. Contacts were also excluded if they were in an epileptogenic area. On average, 6% of the electrode contacts were rejected as lying in epileptogenic areas, and in the remaining areas 16% of the trials were rejected on amplitude criteria.

ERSP was measured as the square root of power in 4 frequency bands, including theta (5–6 Hz), alpha (7–12 Hz), beta (13–24 Hz) and gamma (25–45 Hz), and then baseline-normalized. EEG epochs were 198 ms long for theta band measures, 180 ms for alpha and beta, and 36 ms for gamma. A sliding window was used to attain a higher temporal resolution, i.e. ERSP was re-calculated after shifting the window an increment smaller than the analysis epoch length. This increment was 60 ms for the theta band, 30 ms for both alpha and beta and 12 ms for gamma. For individual trial-based ERSP (iERSP), these calculations were performed on the EEG from each trial, and then averaged across trials for a given subject, task, electrode contact and trial type. For average-based ERSP (aERSP), the EEG was first averaged across trials for a given subject, task, electrode contact and trial type, and then the ERSP calculations were performed on this averaged EEG (i.e. on the ERP).

Levels of significance are based on t tests of iERSP levels in post-stimulus epochs versus baseline. Statistical comparisons between tasks were performed in a similar manner on the difference between the face and word conditions. Significance levels are corrected for multiple comparisons by multiplying them by the window length divided by epoch length, and the number of intracranial EEG contacts analyzed.

3. Results

3.1. Fusiform gyrus

Faces evoked a powerful wide band iERSP increase of the intracranial EEG, that was recorded directly from the fusiform gyrus during the critical period of 150–210 ms after stimulus onset (Fig. 1). Examination of the change in power

Table 1
ERSP percentage changes from baseline across all subjects. Latency was derived from the window center for a given peak iERSP response. $*P < 10^{-3}$; $**P < 10^{-5}$; $^{\triangledown}P < 10^{-7}$; $^{\triangledown\triangledown}P < 10^{-9}$; ns$P > 10^{-3}$, after correction.

Frequency range		Theta 5–6 Hz		Alpha 7–12 Hz		Beta 13–24 Hz		Gamma 25–45 Hz	
Deviation from baseline		% Base	Latency (ms)	% Base	Latency (ms)	% Base	Latency (ms)	% Base	Latency (ms)
Faces									
Temporal	↑ ERSP	$+60^{*}$	190	$+67^{*}$	190	$+29^{*}$	180	$+40^{**}$	180
Temporal	↓ ERSP	-30^{*}	550	$-33^{\triangledown\triangledown}$	650	$-27^{\triangledown\triangledown}$	600	$-29^{\triangledown\triangledown}$	500
Prefrontal	↑ ERSP	$+37^{*}$	500	$+27^{*}$	550	$+10^{ns}$	190	$+15^{ns}$	190
Words									
Temporal	↑ ERSP	$+20^{ns}$	180	$+15^{*}$	200	$+6^{ns}$	180	$+12^{*}$	200
Temporal	↓ ERSP	-23^{*}	500	-21^{**}	650	-17^{**}	700	$-16^{\triangledown\triangledown}$	600
Prefrontal	↑ ERSP	$+37^{*}$	600	$+24^{\triangledown}$	600	$+7^{ns}$	550	$+7^{ns}$	550

spectrum between baseline recordings and the peak iERSP response failed to reveal any clear peaks that were confined within a narrow frequency range. Instead, significant increases in spectral power were seen in response to face stimuli between 150 and 210 ms, in all examined frequency ranges (theta, alpha, beta and gamma) (Table 1). Fusiform iERSP from 150 to 210 ms was significantly less in response to words delivered to the same subjects, in the same task ($P < 0.001$ across all subjects with fusiform recordings ($n = 16$)). This comparison was also significant at $P < 0.025$ in 4 of 6 subjects when considering individual subjects that had both face and word data.

Face-specific, early broadband increases in iERSP were followed by a prolonged iERSP decrease that began at 300 ms and lasted until 1000 ms after the stimulus (Table 1). This profound iERSP decrease was present in all frequency bands examined (encompassing 3–45 Hz), and the decrease was again larger to faces than to words ($P < 0.001$ across all subjects with fusiform recordings ($n = 16$)). When considering only the individual subjects with both face and word data, this comparison was significant ($P < 0.01$) in all 6 subjects.

3.2. Ventrolateral prefrontal cortex

Following the brief burst of oscillating waveforms in the fusiform gyrus, the ventrolateral prefrontal cortex produced a large increase in iERSP starting at 360 and continuing until 700 ms after stimulus onset. In contrast to the fusiform iERSP, the prefrontal iERSP was limited to the lower frequency bands (5–12 Hz), and was greater to words than faces ($P < 0.001$ across all subjects with frontal recordings ($n = 10$)). When considering only the individual subjects with frontal recordings and both face and word data, this comparison was significant ($P < 0.01$) in 4 of 5 subjects.

3.3. ERP averages

The ratio of spectral power values derived from the ERPs (aERSP) to the spectral values derived from individual trials (iERSP) should be equal to one, when perfect phase-locking to the stimulus occurs and should decrease to zero as phase becomes random, according to the square root of the number of trials. This ratio, aERSP/iERSP (a/i) is thus a measure of phase-locking. The baseline of aERSP will tend toward zero given that the phase before stimulus onset is typically random. Indeed, the a/i ratios for the baseline period were on average $9 \pm 3\%$ (mean, standard deviation), as one would expect given that about 120 trials were included in the averages. Since the aERSP of the baseline period is near minimal, it should not be possible to observe decreases relative to the baseline in the aERSP. As a result of these technical considerations, the decreases in spectral values reported above for iERSP were not observed with the aERSP measure (Fig. 2).

The a/i ratio was, however, useful in evaluating the degree to which transient phase-locking occurred during the increases in iERSP. Specifically, there was a striking difference in the a/i ratio between the early temporal and the later frontal responses (Fig. 2). At a latency of 150–210 ms the a/i ratio was high in the fusiform gyrus ($29 \pm 9\%$ for theta, $59 \pm 18\%$ for alpha, $47 \pm 17\%$ for beta and $50 \pm 18\%$ for gamma), indicating strong phase-locking across trials. At a latency of 360–510 ms, when the ventral prefrontal cortex shows an iERSP increase, the a/i ratio was low ($7 \pm 2\%$ for theta, $14 \pm 9\%$ for alpha, $14 \pm 7\%$ for beta and $12 \pm 6\%$ for gamma). This latter response was near baseline levels, indicating random phase.

The above a/i ratios were derived across subjects and multiple electrode contacts. Individual electrode contacts located closest to the fusiform gyrus tended to produce higher a/i ratios. One subject produced a fusiform a/i ratio at 150–210 ms of 48% for theta, 92% for alpha, 56% for beta and 80% for gamma frequencies. This indicates a remarkably powerful stimulus induced phase-locking of the EEG signal.

4. Discussion

Three major task-related changes in iERSP were found in this study: an early fusiform increase, a late fusiform decrease and a late ventral prefrontal increase. The early fusiform increase showed evidence for temporal, anatomical
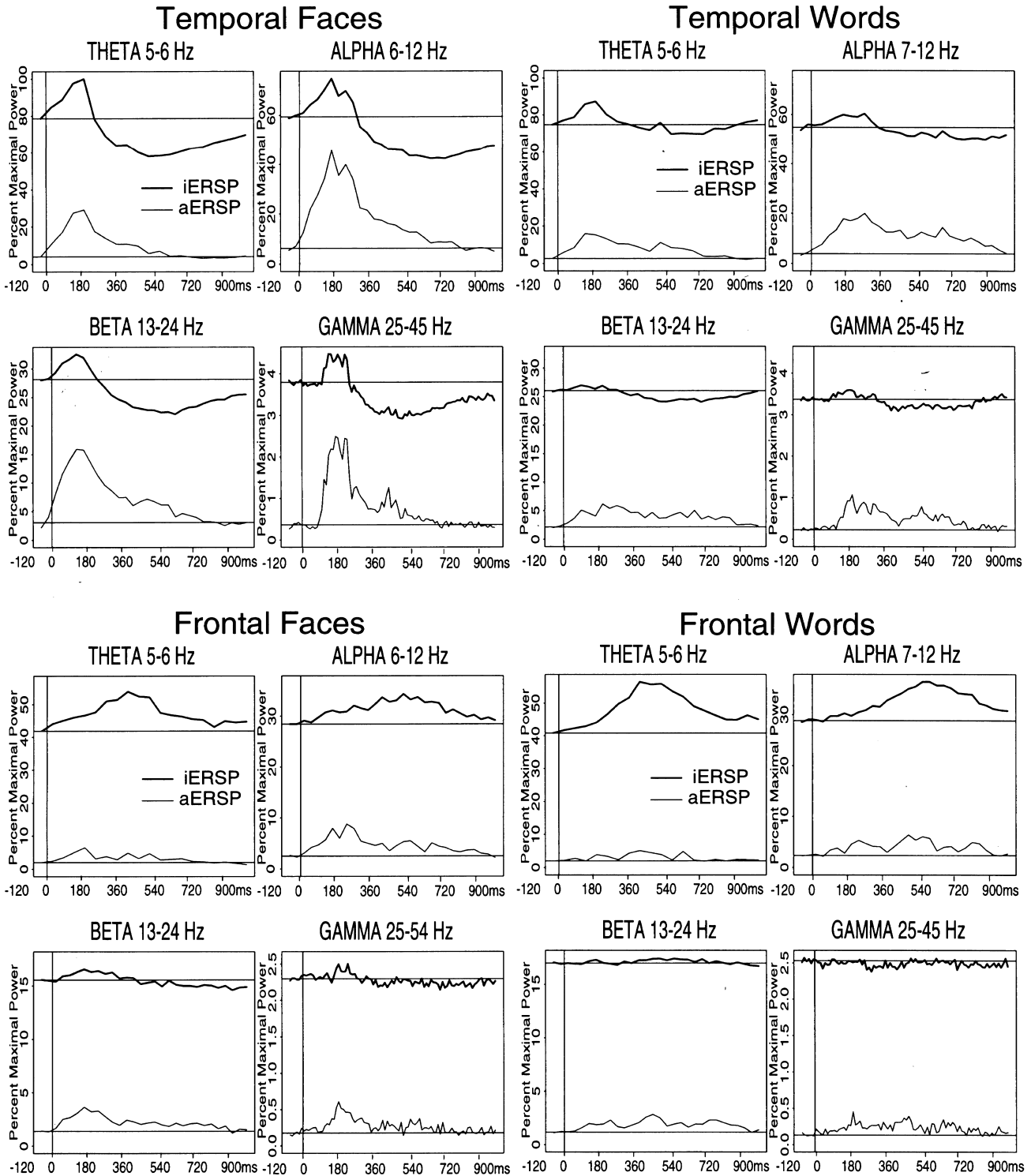
Fig. 2. Comparison of ERSP calculated on the averaged EEG (aERSP, thin lines) versus on the individual trials and then averaged (iERSP, thick lines). ERSP was averaged across 5 electrode contacts in both the tempo-occipital and ventral prefrontal regions. Each frequency range for each stimulus type is shown. The solid horizontal line in each plot indicates the mean baseline ERSP values. Power values are normalized to show percent of the maximal ERSP measure. This maximal value occurred in the tempo-occipital cortex from 5 to 6 Hz during the face task.

and cognitive selectivity (Fig. 1). First, the fusiform iERSP increase was highly delimited temporally, rising abruptly from baseline at about 150 ms and terminating within about 60 ms, close to the resolution of this technique. The fusiform iERSP increase was also highly focal. No significant response of this kind has been seen in most other cortical sites sampled including frontal, rolandic and parietal electrode contacts (Klopp et al., in preparation). In this study,

early iERSP increases were observed in the ventrolateral temporal cortex as well as in the lingual gyrus, but they were in all cases much weaker than those observed in the fusiform gyrus. In another study, we found that mesial anterior temporal sites, especially in the parahippocampal gyrus, may also respond at this latency, but again much more weakly than the fusiform gyrus. Finally, the fusiform increase was selective to faces versus words. Although the specificity of the iERSP measure needs to be further explored, previous PET (Haxby et al., 1996), fMRI (Kanwisher et al., 1997), MEG (Halgren et al., in preparation) and iEEG (Allison et al., 1994) studies, have shown that fusiform activation is highly specific for human faces, in comparison with sensory controls, objects, animal faces, scrambled faces, etc. Similarly, lesions of this area can produce highly specific deficits in face processing, with object processing, for example, preserved (Bruce and Humphreys, 1994; Farah, 1995; Sergent and Signoret, 1992).

Fusiform ERSP was found to be highly phase-locked to stimulus onset (Fig. 2). Transient phase-locking could be a mechanism, whereby environmental elements are bound into a cognitive representation. However, unlike some theories that suggest such binding occurs within narrow frequency bands (Gray et al., 1989; Llinas and Ribary, 1993), the current results demonstrate phase-locking across a broadband of frequencies from 5 to 45 Hz.

The second task-related change observed was a strong iERSP decrease in lateral temporal, fusiform and lingual sites from 300 to 1000 ms (Fig. 1). The greatest iERSP decrease at this latency occurred during the face task. This iERSP decrease also occurred during the word task; however, it was weaker and was not consistently present over all temporal lobe electrode contacts. This iERSP decrease was strongest in the fusiform gyrus, but was less focal than the earlier iERSP increase. Thus, the late fusiform iERSP decrease showed less temporal and material specificity than the preceding increase.

The third and final task-related change was a late ventrolateral prefrontal iERSP increase from 360 to 700 ms (Fig. 1). Unlike the wide band fusiform iERSP increase, this iERSP increase was limited to a lower frequency range of 5–12 Hz, and was not as anatomically localized. In addition, the late frontal iERSP increase is not evident in the aERSP and a/i values are similar to those obtained during the pre-stimulus period. This suggests that the ventrolateral prefrontal event-related increases in EEG oscillations are not phase-locked to the stimulus. Finally, whereas the fusiform iERSP increase was highly selective for faces, the ventrolateral prefrontal iERSP increase occurred to both stimulus types, and was actually larger to word stimuli.

The ERSP and ERP measures seem to produce different views of activation. According to ERSP analysis, the fusiform gyrus has a burst of broadband increase in power around 180 ms and then a prolonged and profound depression, during which the ventrolateral prefrontal cortex shows a broadband increase in power. If increases in spectral power denote functional activation, then these ERSP results imply sequential processing in the two areas. Like ERSP, the ERPs show face selective activity localized to the fusiform gyrus at about 180 ms. However, ERPs are seen in the frontal and temporal electrodes from 300 to 900 ms, and are approximately equal in amplitude (Fig. 1: see also Halgren et al., 1994a, b, for example ERPs from individual subjects). If ERPs indicate functional activation, then this implies parallel processing of faces in fusiform and prefrontal cortices during these late responses. In conclusion, at longer latencies the ERSP and ERP measures diverge: at the same time that the fusiform and prefrontal areas are showing opposite ERSP responses, they show similar ERP activity.

Anatomical, imaging, neuropsychological and physiological evidence support a model wherein the fusiform gyrus encodes faces, transforming the sensory code into a format that allows downstream areas, including the ventrolateral prefrontal cortex, to integrate the face with the ongoing cognitive context. As noted above, neuroimaging studies have shown that fusiform activation is highly specific for human faces, and lesions of this area can produce highly specific deficits in face processing. Using fMRI, the face-selective fusiform area has been shown to be anterior to the retinotopic visual area V4v, and ventromedial to the motion-sensitive areas MT/MSTd (Halgren et al., 1999). There is a further retinotopic area encoding both dorsal and ventral visual fields interposed between V4v and the fusiform face area. This topology, as well as this area's cytoarchitectonics and its location relative to gross anatomical landmarks, all imply that it is homologous to area TF (or possibly CITv) of monkeys. These areas receive their main inputs from V4 and PIT, and project heavily to more anteromedial temporal areas, including entorhinal and perirhinal cortices, which in turn project to the ventrolateral prefrontal cortex (Felleman and VanEssen, 1991; Suzuki, 1996).

The 170 ms peak latency of the fusiform activation places it after the exogenous sensory responses that are generated in early visual cortical regions, and before the cognitive responses modulated by mnestic, emotional and high-level contextual variables. Such cognitive responses are most prominent during the ERP component termed N400. The cognitive correlates, timing and generators of N400 suggest that it embodies the cognitive integration of the stimulus, relating it to short-term and remote memories, evaluating it for emotional significance, and placing it into the current cognitive context (Halgren et al., 1994a, b). Lesion studies confirm a role for the ventrolateral prefrontal cortex in the integration of perceptual events with the cognitive and emotional context (Fuster, 1989; Halgren and Marinkovic, 1995). Its activation is not specific for faces or any other specific type of material, but rather, seems to be related to the semantic analysis of stimuli in relation to internally-held comparison criteria or contexts (i.e. during working memory) (Gabrieli et al., 1998).

In conclusion, the fusiform face area is anatomically

located just anterior to the retinotopic visual areas, and is activated at 170 ms just after their activation. This activation is highly specific for faces, and lesions to this area can produce deficits highly selective for faces. In contrast, the ventrolateral prefrontal cortex is anatomically downstream to the fusiform area, and is activated after it (but before the cognitive response). Its activation is not specific for faces but rather to semantic analysis, and lesions there produce general high level cognitive deficits, rather than material-specific impairments. These considerations all argue in favor of the sequential model of fusiform to prefrontal activation, suggested by the ERSP analysis reported here. It may, however, be the case that the view suggested by ERP analysis is also partially correct, with the major processing locus shifting from fusiform to prefrontal (and other association) areas at longer latencies, but some information being fed back to the fusiform area for a prolonged period.

This appears to be the first report of evoked phase-locked increases in spectral power with clear anatomical, temporal and cognitive specificity, identified with intracranial recordings in humans. Our results suggest that functional activation may sometimes be associated with increased EEG spectral power, while functional inactivation may be associated with decreased EEG spectral power.

Acknowledgements

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