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Electrical neuroimaging reveals early generator modulation to emotional words

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Functional electrical neuroimaging investigated incidental emotional word processing. Previous research suggests that the brain may differentially respond to the emotional content of linguistic stimuli pre-lexically (i.e., before distinguishing that these stimuli are words). We investigated the spatiotemporal brain mechanisms of this apparent paradox and in particular whether the initial differentiation of emotional stimuli is marked by different brain generator configurations using high-density, event-related potentials. Such would support the existence of specific cerebral resources dedicated to emotional word processing. A related issue concerns the possibility of right-hemispheric specialization in the processing of emotional stimuli. Thirteen healthy men performed a go/no-go lexical decision task with bilateral word/non-word or non-word/non-word stimulus pairs. Words included equal numbers of neutral and emotional stimuli, but subjects made no explicit discrimination along this dimension. Emotional words appearing in the right visual field (ERVF) yielded the best overall performance, although the difference between emotional and neutral words was larger for left than for right visual field presentations. Electrophysiologically, ERVF presentations were distinguished from all other conditions over the 100–140 ms period by a distinct scalp topography, indicative of different intracranial generator configurations. A distributed linear source estimation (LAURA) of this distinct scalp potential field revealed bilateral lateral-occipital sources with a right hemisphere current density maximum. These data support the existence of a specialized brain network triggered by the emotional connotation of words at a very early processing stage.

Keywords: Event-related potentials, ERPs; Topographic mapping; Source estimation; LAURA; Lexical decision; Hemispheric specialization; Visual field

Introduction

Investigations of the time course of visual perceptual processes reveal that relatively high level functions may occur within the initial approximately 150 ms following stimulus presentation. Such functions include the rapid recognition and categorization of faces (e.g., Braeutigam et al., 2001; Halgren et al., 1994a; Landis et al., 1984; Liu et al., 2002; Seeck et al., 1997; Pizzagalli et al., 1999, 2002), of objects (e.g., Landis et al., 1984; Murray et al., 2002; Rousselet et al., 2002), as well as words (see, e.g., Pulvermüller, 1999, 2001 for review). Typically, this early event-related potential (ERP) modulation to words vs. non-words has been interpreted to reflect visual perceptual processes related to lexical decision, with later modulations (the early left anterior negativity: e.g., Friederici, 1997; and N400: e.g., Brandeis et al., 1995; Kutas and Hillyard, 1980; Lavric et al., 2001) thought to index response to their syntactic and semantic attributes. More recently, however, response modulations have been observed to such "post-lexical" attributes at latencies preceding that typically associated with lexical decision, raising the possibility that there may be linguistic features that are processed before (or in parallel with) their lexical distinction—that is, pre-lexically. In particular, early (before approximately 150 ms post-stimulus) ERP effects have been observed as a function of words' meaning (e.g., Pulvermüller, 2001; Skrandies, 1998), class (see, e.g., Koenig and Lehmann, 1996; Pulvermüller, 1996, 2001 for review), syntax (e.g., Pulvermüller, 2001), length (e.g., Assadollahi and Pulvermüller, 2001), and emotional valence (Begleiter and Platz, 1969; Bernat et al., 2001). However, interpretation of these latter studies of emotional processes is limited by the fact that analyses only identified the timing of ERP modulations.

Such early electrophysiological differences implicate that the neural representation of words' linguistic features can be selectively activated at early processing stages. However, the precise nature of these neural representations remains largely unresolved. One possibility is that words of all varieties share a common brain network, whose activity modulates in strength or latency with different linguistic features. Alternatively, it may be the case that words with particular linguistic features rapidly and selectively access specialized brain networks that may be unevenly distributed between the cerebral hemispheres.

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A large body of psychophysical and neuropsychological literature provides some insights on these alternatives, particularly concerning possible hemispheric specialization in language processes. Such evidence has largely been gleaned from bilateral hemifield presentations, which are believed to maximize hemispheric independence (Boles, 1983; Iacoboni and Zaidel, 1996; McKeever and Hulling, 1971; Wey et al., 1993). On the one hand, behavioral studies have repeatedly demonstrated that presentations of words to the right visual field (RVF) during a lexical decision task result in faster and more accurate performance than words presented to the left visual field (LVF), which has been interpreted as reflecting the left hemisphere's general dominance in language functions (review Bryden, 1982; Graves et al., 1981; Regard et al., 1985a,b,c; Pulvermüller, 1999, 2001). This proposition receives further support from functional neuroimaging investigations (e.g., Cohen et al., 2000). However, parallel evidence would indicate that the right hemisphere also subserves particular language functions. Despite global aphasia resulting from lesions within the left hemisphere, emotional word output is astonishingly intact in such patients during emotionally stressful situations (Hughlings-Jackson, 1874, reprinted 1915). Later studies have shown that aphasic patients with focal left hemisphere damage have better performance in reading aloud and writing emotional than neutral words (Borod, 1992; Borod et al., 1992; Cicero et al., 1999; Landis et al., 1982, 1983). The implication of these neuropsychological studies is that the right hemisphere may play a specialized role in processing emotional linguistic stimuli. More generally, these data raise the possibility that there are cerebral resources dedicated (at least in part) to emotional word processes.

Similar conclusions are also drawn from behavioral studies of healthy individuals. When emotional words are shown during a bilateral lexical decision paradigm, there is both an overall advantage of emotional over neutral words, and an overall better performance for emotional and neutral words in the RVF than the LVF. However, there is also a particular advantage for LVF presentations of emotional over neutral words in that emotional words are recognized quite well, while neutral word detection is at chance level (Graves et al., 1981; Strauss, 1983). Moreover, when the same emotional and neutral words were presented to aphasic patients (Landis et al., 1982), and to healthy control subjects (Graves et al., 1981), there was a highly significant correlation between the LVF performance in controls and that of aphasic patients, while there was no significant correlation between in the case of RVF performance (Goodglass et al., 1980). These results might indicate that both hemispheres detect lexical meaning, but that for the left hemisphere emotional tone plays a minor role, while for the right hemisphere emotional tone is a major prerequisite to access lexical decision. More generally, these results suggest that two different "reading strategies" are at work in the two hemispheres, probably in parallel. The first is the overall specialization of the left hemisphere in language functions. The second is the specialization of the right hemisphere in emotional processing (e.g., Benson and Zaidel, 1985; Borod, 1992; Borod et al., 1992; Làdavas et al., 1984; Landis et al., 1990; Ledoux, 1995; Rolls, 1995).

The aim of the present study was to identify the spatiotemporal dynamics of incidental emotional word processing. To do this, we applied functional electrical neuroimaging techniques during completion of a go/no-go lexical decision task comprised of bilateral presentations of letter strings.

Statistical analyses sensitive to topographic strength and configuration changes in the scalp electric field were conducted on the ERPs in response to emotional and neutral words appearing in each visual field. These analyses revealed if and when there were periods of stable scalp topography and periods when different scalp topographies accounted for specific experimental conditions. Since topographic changes are indicative of alterations in the configuration of the underlying cerebral generators (see, e.g., Fender, 1987; Lehmann, 1987), these analyses provide a means for the statistical assessment of when different experimental conditions engage distinct brain networks. In addition, the LAURA (Grave de Peralta et al., 2001) distributed source localization method was applied to the topographic configurations identified in the ERPs across conditions to define both the common and differential brain areas activated over time.

Materials and methods

Subjects

Thirteen healthy Caucasian men, aged 18–36 years (mean 26 years), provided written consent and were paid to participate in the experiment, which was approved by the Medical Ethics Committee at the University Hospital of Geneva. All were right-handed (Edinburgh Inventory; Oldfield, 1971), native French speakers, with normal or corrected-to-normal vision and no neurological or psychiatric illnesses. All participants were graduate or medical students at the University of Geneva.

The rationale to restrict our study sample to male participants was to avoid obscuring sex differences in brain responses, which are likely to occur when using the present (Graves et al., 1981) or related (Haussman and Güntürkün, 2000; Heister et al., 1989) paradigms. Moreover, the possible impact of hormonal fluctuations in women on lateralized functioning remains yet to be fully resolved (see, e.g., Hampson and Kimura, 1988; Haussman and Güntürkün, 2000; Heister et al., 1989, for discussion).

Stimuli and procedure

The 112 letter-string stimuli (four to seven characters long) included eight emotional French abstract nouns (of both positive and negative valence, refer to word list in Table 1), eight French neutral abstract nouns, a set of 48 pronounceable non-words (following the same consonant–vowel structure as words), and another set of 48 pronounceable non-words (each non-word was created according to the same consonant–vowel structure as its associated contralaterally presented non-word constituting 24 non-word/non-word pairs). The first 48 non-words were used to create word/non-word pairs. Since words were repeated three times per block, a different non-word was presented for each word/non-word pair. Word selection was done in the following way. To ensure that neutral and emotional words were all of high frequency of usage, 215 words were selected from the table of French words (Content et al., 1990). Thirty volunteers, comprised of nurses and medical doctors from the University of Geneva Hospital and who did not participate in the EEG experiment, then rated each word's emotional content on a scale from 0 to 7 (0 = unemotional; 7 = very emotional). The eight words with the highest and lowest ratings were used in the EEG experiment (see Table 1). The selected emotional and neutral words had a mean usage frequency of 186

Table 1
List of the eight neutral and eight emotional French words used during the lexical decision task

Neutral words	Emotional words
actuel (actual)	colère (anger)
bout (end)	espoir (hope)
cause (cause)	joie (joy)
chose (thing)	mort (death)
fait (fact)	plaisir (pleasure)
ligne (line)	rêve (dream)
sorte (sort)	sexe (sex)
truc (trick)	viol (rape)

Their English translation is provided in parentheses.

and 226 occurrences per million words, respectively. No significant difference in word frequency existed between the emotional and non-emotional words [$t_{(7)} = -0.14$; $P = 0.89$; paired t test]. Subjects participating in the EEG experiment were not informed about the emotional content of the stimuli.

Letter-strings were presented in pairs—one on either side of central fixation (spanning approximately 2–5° eccentricity) in the left or right visual field (LVF and RVF, respectively). Words, when present, were always paired with non-words and could appear randomly on either side of fixation, but with equal overall likelihood across the experiment. Each word appeared three times in each visual field per block of trials. The order of experimental trials was pseudorandom. No more than three consecutive trials with the same word type appeared in the same visual field. Stimuli appeared white on black for 13 ms, which was confirmed by photocell measurements (E-prime Psychology Software Tools Inc., Pittsburgh, USA) on a computer monitor located 140 cm from the subject, whose head position was stabilized in a chin rest. For each trial, subjects were instructed to centrally fixate and judge whether a word was present and, if so, on which side it appeared. That is, if they believed a word was presented, they pressed a button as quickly as possible with their index finger of the hand on the same side of the fixation cross as the word (e.g., right hand for RVF presentations; Fig. 1A). Catch trials involved presentation of two non-words and required no button-press. Subjects were not explicitly asked to judge the emotional tone of the words. However, for analysis purposes, conditions containing words were further and equally subdivided into those containing emotional or neutral words. This resulted in four experimental conditions: emotional words presented in the RVF or LVF (hereafter ERVF and ELVF, respectively) and neutral words presented in the RVF or LVF (hereafter NRVF and NLVF, respectively). The interstimulus interval varied randomly from 1500 to 2000 ms. Subjects completed five blocks, each containing 120 trials. As such, each subject's participation required approximately 40 min, including time for electrode cap application and clean up. Before inclusion in this study, potential subjects completed a training session comprised of a shortened version of the five blocks of stimuli described above, but with different word and non-word stimuli. Inclusion in the experiment required a minimum of 50% accuracy on each condition. The 13 subjects described herein all met this criterion.

Mean reaction time and percentage of correct responses from the five experimental blocks were calculated for each subject and condition and were submitted to an ANOVA with stimulus class (emotional vs. neutral) and visual field of the word (left vs. right) as within-subject factors. Moreover, to account for the previously reported emotional word advantage between visual fields (Graves et al., 1981), we calculated a conventional laterality index score (Marshall et al., 1975) for percentage of correct responses for each visual field separately (emotional words − neutral words) / (emotional words + neutral words). Thus, positive values indicate an emotional word advantage and negative values a neutral word advantage. The laterality index scores for each visual field were compared using a paired t test.

EEG acquisition and analysis

Continuous EEG was acquired with a Geodesics Netamps system (Electrical Geodesics, Inc., USA) from 123 scalp electrodes (impedances <50 kΩ; vertex reference; 500-Hz digitization; band-pass filtered 0.1–200 Hz) as subjects sat in a darkened,

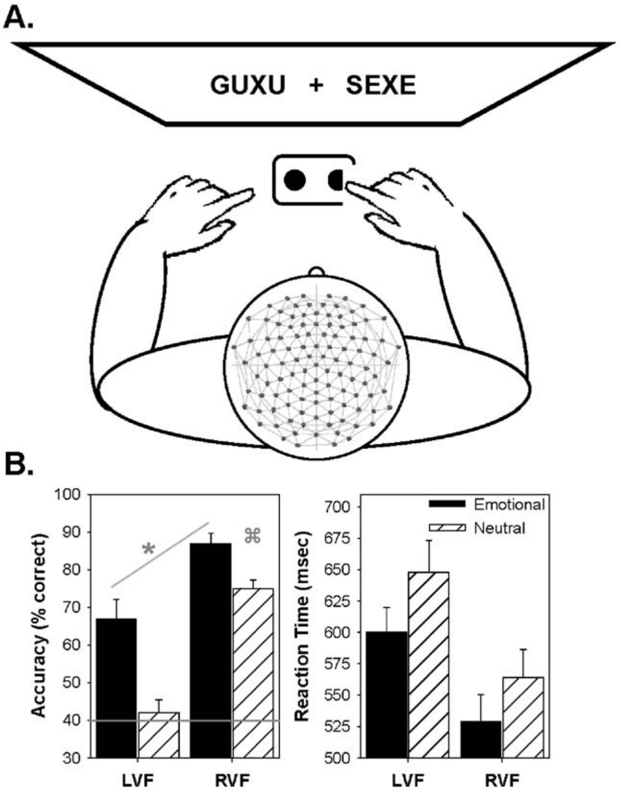


Fig. 1. (A) Experimental paradigm. Letter-string stimuli were presented bilaterally for 13 ms as subjects centrally fixated. Their task was to indicate if either letter-string constituted a French word and, if so, to press the button with the index finger of the hand on the same side as the word. They were instructed to withhold responses on trials not containing words in either visual field. High-density EEG was acquired during performance of this task, and the montage is displayed in the inset. Further details of the experimental procedure can be found in Materials and methods. (B) Behavioral results. Mean (SEM shown) percentage correct (left) and reaction time in milliseconds (right) for each of the four experimental conditions is shown according to the visual field where the word appeared. Solid bars display results from trials containing emotional words, and striped bars those from neutral words. The gray line in the plot of accuracy indicates chance level (= 40%). Both performance measures indicate an advantage for RVF presentations as well as for emotional words (see Results for full details).

electrically shielded booth. Epochs of EEG (from 0 to 600 ms post-stimulus onset) from trials yielding correct responses were averaged for each of the four experimental conditions and from each subject to calculate the event-related potential (ERP). In addition to the rejection of sweeps where any channel exceeded the amplitude of ±100 μV, the data were visually inspected to reject epochs with blinks, eye movements, or other sources of transient noise. The mean number of accepted epochs per condition was 68 for ERVF, 50 for ELVF, 59 for NRVF, and 30 for NLVF.

For each subject's ERPs, the electrodes on the outermost circumference (chin and neck) as well as other artifact channels were excluded and interpolated to a standard 111-channel electrode array (two-dimensional spherical spline; Perrin et al., 1987). ERPs were band-pass filtered (1–30 Hz), recalculated against the average reference, and normalized to their mean global field power (GFP; Lehmann and Skrandies, 1980) before group averaging. This measure is equivalent to the spatial standard deviation of the scalp electric field, yields larger values for stronger electric fields, and is calculated as the square root of the mean of the squared value recorded at each electrode (vs. the average reference).

Based on the electrophysiological evidence for early differences in word categorization (e.g., Bernat et al., 2001; Koenig and Lehmann, 1996; Pulvermüller, 2001), we restricted our analyses to the initial 250 ms post-stimulus period in terms of the spatio-temporal characteristics of the global electric field on the scalp (maps). The topography (i.e., the spatial configuration of these maps) was compared over time within and between conditions. Changes in the map configuration are indicative of differences in the active neuronal populations in the brain (e.g., Fender, 1987; Lehmann, 1987). This analysis approach has been used in several previous studies both from our laboratory (see, e.g., Michel et al., 1999, 2001 for reviews; Ducommun et al., 2002; Morand et al., 2000) as well as from those of others (e.g., Brandeis and Lehmann, 1989; Koenig and Lehmann, 1996; Koenig et al., 2002; Lavric et al., 2001; Pizzagalli et al., 2000, 2002). The method applied here consisted of the following steps.

First, a spatial cluster analysis (Pascual-Marqui et al., 1995) identified the most dominant scalp topographies appearing in the group-averaged ERPs from each condition over time. This approach is based on the observation that scalp topographies do not change randomly, but rather remain for a period of time in a certain configuration and then switch to a new stable configuration (e.g., Lehmann, 1987; Michel et al., 1999, 2001 for reviews). We further applied the constraint that a given scalp topography must be observed for at least five consecutive data points (>10 ms at a 500-Hz digitization rate) in the group averaged data. This criterion is effectively similar to that frequently applied in the analysis of ERP waveform modulations (e.g., Picton et al., 2000). From such pattern analysis, it is possible to summarize ERP data by a limited number of scalp potential fields, which we refer to here as "segmentation maps". Each such segmentation map is thought to represent a given "functional microstate" of the brain or a given computational step during information processing (Lehmann, 1987; Michel et al., 1999, 2001 for reviews). This method is independent of the reference electrode and is insensitive to amplitude modulation of the same scalp potential field across conditions, since topographies of normalized maps are compared (Lehmann, 1987). The optimal number of segmentation maps that explains the whole group-averaged data set (i.e., the group-averaged ERPs from all four experimental conditions, collectively) is determined by a modified cross-validation criterion (Pascual-Marqui et al., 1995).

Second, the appearance and sequence of the segmentation maps identified in the group-averaged data was statistically verified in the ERPs of the individual subjects. To do this, each segmentation map was compared with the moment-by-moment scalp topography of the individual subjects' ERPs from each condition by strength-independent spatial correlation (see, e.g., Michel et al., 2001 for review). That is, for each time point of the individual subject's ERPs (note that the 10-ms criterion was not applied to the individual subject data), the scalp topography was compared to all segmentation maps and was labeled according to the one with which it best correlated. From this "fitting" procedure, we determined the onset and offset as well as the total amount of time a given topography was observed for a given condition across subjects (e.g., Brandeis et al., 1992). These latter values, which represent the frequency with which a given segmentation map was observed within a given time period for each experimental condition, were then subjected to a repeated measures ANOVA. It is important to note that this labeling procedure is not exclusive, such that a given period of the ERP for a given subject and stimulus condition is often labeled with multiple segmentation maps. As such, the results of the labeling reveal if the ERP from a given experimental condition is more often described by one segmentation map vs. another, and therefore if different generator configurations better account for particular experimental conditions. If the processing of emotional stimuli relies on a distinct cortical network, this analysis should reveal that different scalp topographies explain the ERPs to the different word classes.

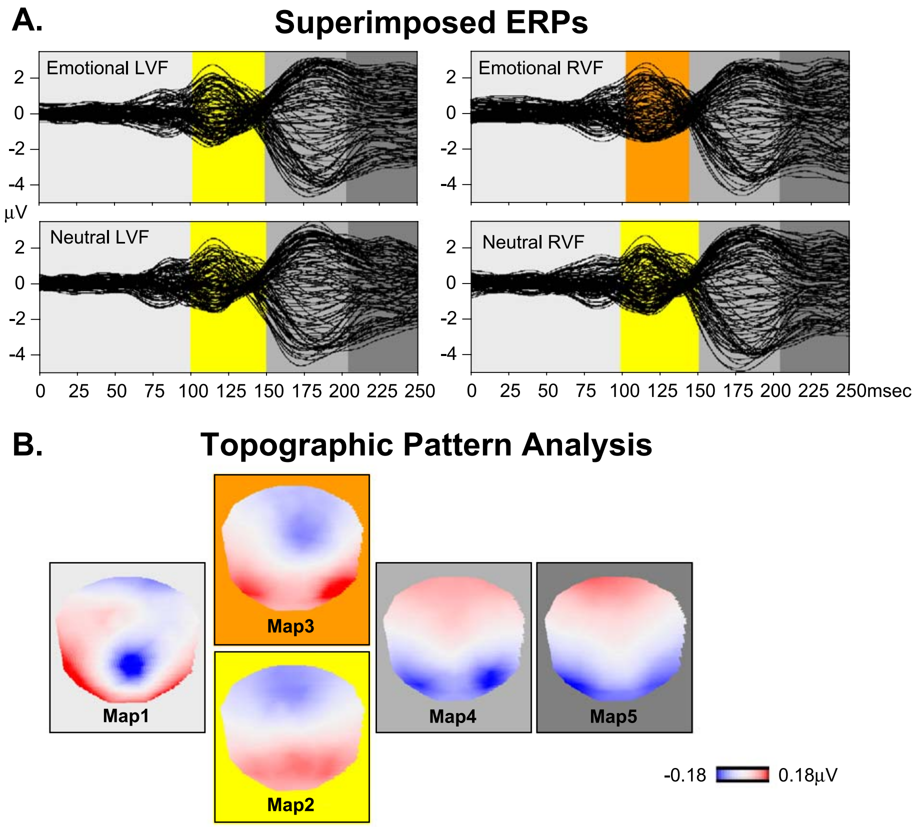
Source estimation

As a final step, we estimated the sources in the brain that gave rise to each of the segmentation maps, using a distributed linear inverse solution. The inverse matrices applied here were based on a Local Auto-Regressive Average (LAURA) model of the unknown current density in the brain (Grave de Peralta et al., 2001). This linear distributed inverse solution selects the source configuration that better mimics the biophysical behavior of electric vector fields. That is, the estimated activity at one point depends on the activity at neighboring points according to electromagnetic laws. Since LAURA belongs to the class of distributed inverse solutions, it is capable of dealing with multiple simultaneously active sources of a priori unknown location. This solution increases the amount of sources with zero localization error while reducing the maximum error when compared with other available inverse solutions (Grave de Peralta and Gonzalez Andino, 2002). The lead field (solution space) was calculated on a realistic head model that included 4024 nodes, selected from a 6 × 6 × 6 mm grid equally distributed within the gray matter of the average brain provided by the Montreal Neurological Institute (MNI). Source estimations are rendered on a brain supplied by MRIcro (Rorden and Brett, 2000). Transformation between the MNI coordinate system and that of Talairach and Tournoux was performed using the MNI2TAL formula (available at , www.mrc-cbu.cam.ac.uk/imaging) devised by Matthew Brett (Medical Research Council Cognition and Brain Sciences Unit, Cambridge, UK). It is important to note that these estimations provided visualization of the likely underlying sources of each segmentation map and, in contrast to the derivation of the segmentation maps, do not represent a statistical analysis.

Results

Behavioral results

Fig. 1B displays mean accuracy and reaction time data from each of the four experimental conditions requiring responses. These values were submitted to an ANOVA using word class (emotional, neutral) and word location (LVF, RVF) as within-subjects factors. The analysis of subject's accuracy revealed significant main effects of word class [$F_{(1,12)} = 39.88$; $P < 0.0001$; emotional > neutral: 77 ± 17% > 58 ± 10%] and word location [$F_{(1,12)} = 55.14$; $P < 0.0001$; RVF > LVF: 81 ± 7% > 55 ± 14%], indicating that subjects performed better with emotional words and with words appearing in the RVF. There was also a significant interaction between these factors [$F_{(1,12)} = 13.73$; $P < 0.003$], indicating that lexical decisions with neutral words were more affected by word position than those with emotional words. Post hoc comparisons (Bonferroni corrected) revealed that performance with neutral words presented to the LVF was lowest (at chance level) as compared to performance with neutral words presented to the RVF ($P < 0.0001$) and emotional words presented to the LVF ($P < 0.0001$; see Fig. 1B). Moreover, performance with emotional words presented to the RVF was highest as compared to performance with neutral words presented to the RVF ($P = 0.001$, see in Fig. 1B) and emotional words presented to the LVF ($P < 0.0001$, see * in Fig. 1B). The paired t test on the laterality index score confirmed previous observations (Graves et al., 1981) that the "emotional word advantage" was significantly larger for LVF (0.23 ± 0.10) than for RVF (0.08 ± 0.07) presentations [$t_{(12)} = -4.94$, $P = 0.0003$].



Condition	Map1	Maps2/3	Map4	Map5
Emotional RVF	0-104	106-140	142-206	208-250
Neutral RVF	0-98	100-144	146-206	208-250
Emotional LVF	0-102	104-146	148-204	206-250
Neutral LVF	0-100	102-146	148-204	206-250msec

Fig. 2. Electrophysiological results. (A) Group-averaged ($N = 13$) event-related potentials are shown for each experimental condition superimposed across scalp electrodes. Colored sections indicate the segmentation map that best correlated with each data point in the group-averaged data. (B) The segmentation maps revealed by the topographic pattern analysis across the group-averaged ERPs of all four experimental conditions are shown on the left side. Maps are plotted with the nasion upward and right ear on the right side (scale indicated). Those segmentation maps framed in shades of gray were common to all conditions, whereas those framed in orange or yellow dominated particular conditions. The time period over which each segmentation map was observed in the group-averaged data is listed in the table and is also displayed with the same color scheme in A.

Analysis of reaction times yielded significant main effects of both word class [$F_{(1,12)}$ = 101.44; P < 0.0001: neutral > emotional: 606.04 ± 109.11 > 564.58 ± 101.34] and word location [$F_{(1,12)}$ = 19.36; P < 0.0009: LVF > RVF: 623.88 ± 119.56 > 546.73 ± 106.62]. However, the interaction between these factors did not reach our significance criterion [$F_{(1,12)}$ = 1.21; P > 0.05]. Thus, irrespective of the visual field of stimulus presentation, emotional words were detected faster than neutral words.

Electrophysiological results

The group-averaged ERPs from the four conditions containing words in either visual field and yielding correct responses are shown in Fig. 2A with traces across scalp sites superimposed. Archetypal ERP components (e.g., P1 and N1) are readily observed for each condition. Since our primary objective was to determine if the initial differentiation of emotional word stimuli is marked by a change in the brain's generator configuration, we submitted the initial 250 ms of the ERP from these conditions to tests of the scalp electric field.

This pattern analysis (see Materials and methods for details) revealed that five different scalp topographies (segmentation maps) optimally described the cumulative 250 ms post-stimulus periods across all four conditions. These were labeled as Maps 1–5 (Fig. 2C). While most of these segmentation maps were observed in the group-averaged ERPs of all conditions, one was observed in one condition and not the others over the approximately 100–140 ms period (Fig. 2). That is, Map 3 was observed in the case of emotional words presented in the RVF, whereas Map 2 was observed for all other stimulus conditions. To statistically test this observation in the group-averaged data, the appearance of these segmentation maps was quantified in the ERPs of the individual subjects using a strength-independent spatial correlation fitting procedure, wherein each time point of each subject's ERP was labeled with the segmentation map with which it best correlated. From this fitting procedure, we determined the total amount of time a given topography was observed in a given condition across subjects (Fig. 2C, inset table and Fig. 3). These values from the 100 to 140 ms period were subjected to a 4 × 2 repeated measures ANOVA using experimental condition and segmentation map as within-subject factors. Neither main effect reached our significance criterion. Critically, the interaction between factors of experimental condition and segmentation map was significant [$F_{(3,36)}$ = 9.02; P < 0.00015], indicating that some experimental conditions were better represented by Map 2 and other conditions by Map 3. Follow-up comparisons (paired *t* tests) confirmed the observations in the group-averaged data (asterisks in Fig. 3, left), and indicate that Map 3 was significantly more often observed in the case of ERVF than any of the other three experimental conditions and conversely that Map 2 was significantly less often observed in the case of ERVF than any of the other three experimental conditions. Thus, we observe a change in the scalp field configuration that corresponds with the behavioral advantage found for the ERVF condition. No differences were observed in the frequency of map presence among these other three experimental conditions. As such, the chance level performance for the NLVF condition failed to yield a corresponding scalp electric field modulation over the initial 250-ms period.

The analyses thus far indicate that presentation of emotional words to the RVF result both in enhanced performance as well as in a distinct scalp topography over the approximately 100–140 ms period. Since different topographic configurations are indicative of different brain generator configurations, we applied the LAURA (Grave de Peralta et al., 2001) distributed linear inverse solution estimation algorithm to visualize the brain sources underlying Map 3 and Map 2 (Fig. 3, right). This source estimation reveals bilateral lateral-occipital sources for Map 3

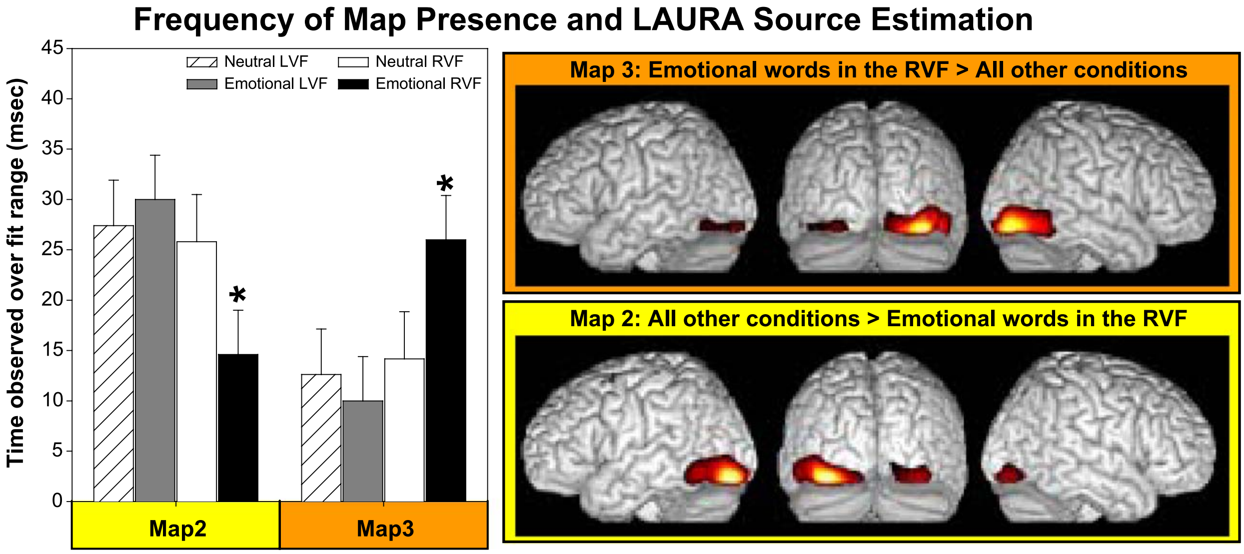


Fig. 3. Frequency of map presence and LAURA source estimation. The bar graph depicts the results of the fitting procedure for Map 2 and Map 3 over the 100–140 ms period, which indicates the frequency that each of these segmentation maps was observed in each experimental condition. Asterisks indicate that one segmentation map (Map 3) better represented responses to emotional words presented in the RVF, whereas a different segmentation map (Map 2) better represented all other conditions. Cortical sources associated with each of these segmentation maps were estimated using LAURA (Grave de Peralta et al., 2001) and are rendered on the average brain supplied by MRIcro as shown from the left, back, and right. Talairach and Tournoux (1988) coordinates of the current density maximum are detailed in Results.

as well as Map 2. However, there is a striking visual difference between these inverse solution estimations in the laterality of these sources' strengths. The current density maximum for Map 3 was in the right hemisphere ($x, y, z = 35, -82, -6$ mm), whereas that for Map 2 was in the left hemisphere ($-36, -82, -6$ mm; Talairach and Tournoux, 1988).

Discussion

This study elucidates the spatiotemporal dynamics of incidental emotional word discrimination following brief presentation of bilateral letter strings. We provide evidence supporting a distinct cortical mechanism for the treatment of emotional words. The behavioral data indicate two ways in which subjects treated emotional word stimuli distinctly. First, there was an overall advantage for emotional words over neutral words. Second, this emotional word advantage was much bigger in the case of LVF presentations. This advantage is due to a drop at chance level in accuracy of neutral word detection when presented to the LVF. This suggests that words presented to the LVF (right hemisphere) are detected predominantly when they have an emotional connotation, whereas emotional and neutral words are both detected when presented to RVF (left hemisphere). These behavioral data support the notion that there are different reading processes activated when words are entering the left and right visual cortex, respectively.

The electrophysiological data provide further, complementary support. Over the 100–140 ms post-stimulus period, a distinct scalp topography (Map 3) better characterized the ERPs in response to ERVF relative to all other experimental conditions, which were characterized instead by a different scalp topography (Map 2). Since different scalp topographies are indicative of changes in the underlying generator configuration, we applied the LAURA distributed linear source estimation to these distinct topographies. The scalp topography that better characterized responses to ERVF (Map 3) yielded bilateral lateral-occipital sources with a right hemisphere current density maximum, whereas the scalp topography predominating all other conditions (Map 2) yielded similar sources with a left hemisphere current density maximum. These collective observations support a model of (emotional) word processing that includes a network within the right hemisphere that can be selectively activated at early stages of visual processing when emotional words have been projected to the contralateral hemisphere (RVF presentation).

At just 100–140 ms, a distinct scalp topography was evident between ERVF and all other experimental conditions, indicative of an intracranial generator configuration that better describes responses to these stimuli than to all others. Two observations in this data set attest to the specificity of this effect. The first is the parallel pattern observed in subjects' performance, wherein responses to emotional words were best for ERVF relative to all other conditions. Second, and more critically, no other electrophysiological difference was observed over the initial 250 ms post-stimulus epoch. Moreover, the LAURA inverse solution localized this selective scalp topography to bilateral regions of the visual cortex, including the lateral-occipital complex (LOC; e.g., Malach et al., 1995; Murray et al., 2002), with a right hemisphere current density maximum.

This localization would support previous claims that the right hemisphere plays an integral role in emotional word processing (e.g., Borod et al., 1992; Graves et al., 1981), albeit these claims would also implicate that the right hemisphere plays a specific role in ELVF. Although enhanced treatment of these stimuli (vs. their neutral counterparts) was observed behaviorally, the electrophysiological data provide no indication of differential processing of these stimuli over the initial 250 ms post-stimulus onset. Whereas some hemodynamic neuroimaging studies of emotional processing (e.g., Crosson et al., 2002; Maddock et al., 2003) have demonstrated significant activity either in the anterior frontal or medial-limbic cortices lobe in emotional word processing, the present selective topography did not reveal such sources. We would note, however, that such does not preclude their selective activation at later time periods. Nonetheless, under the conditions of the present paradigm, there is apparently functional specialization in the form of a distinct generator configuration for the processing of emotional words appearing in the RVF.

Despite this evidence for functional specialization, neither the specificity of this topographic difference for ERVF condition nor the observed loci of current density maxima in the inverse solution estimation can be readily explained by a single, simple mechanism of hemispheric specialization. Rather, the specificity of this effect invokes the combination of one mechanism specialized for language processes, which previous research would lateralize to the left hemisphere, and a second specialized for the processing of emotional content, which is hypothesized to be lateralized to the right hemisphere. Thus, even in an overly simplified model as the above, interhemispheric interactions would be required to account for both the specificity as well as the right-hemisphere laterality of the responses to ERVF stimuli. However, we would emphasize that this proposed interhemispheric sharing of lexical resources is earliest for emotional words in the RVF vs. all other conditions, and not necessarily exclusive at later times. Within such a framework, direct-projection to the left and language-dominant hemisphere would facilitate "coarse" reading of emotional stimuli by selectively activating an interhemispheric pathway specialized for emotional word processing. By extension, then, emotional word processing would rely on a specialized bilateral network.

In agreement, recent modeling of cortical language representation has applied Hebbian principles (see Pulvermüller, 1996, 1999, 2001 for review) to posit that words' representations may be segregated throughout cerebral hemispheres by their "conceptual structure" (see Pulvermüller, 1996, 2001). This structure is considered to include not only words' visual forms, but also their meanings, sounds, and related memories. Of importance for the interpretation of the present results, this model and the data at its foundation would suggest that various classes of words have differentially distributed neural representations. The emotional vs. neutral distinction evaluated in the present study would thus constitute another instantiation of this model's predictions, in that we provide evidence for topographically distinct neural representations of these different word classes. In addition, we demonstrate how the spatial location of word stimuli influences at an early latency the time course, and perhaps also the spatiotemporal mechanism, by which the neural representations of particular word classes are activated.

Indeed, the time frame for the activation of a specialized cortical network in emotional word processing is of particular importance for the conceptualization of linguistic processes. Here, we show that already at approximately 100–140 ms post-stimulus onset there is discrimination of the letter-string stimuli according to their emotional content. This timing is earlier than that typically ascribed to the discrimination of words from non-words (see, e.g., Allison et al., 1994; Halgren et al., 1994a,b; Nobre et al., 1994; Pulvermüller, 1999, 2001 for review). However, we are hesitant to interpret the present findings as evidence of "pre-lexical" reading abilities for emotional stimuli, particularly since recent electrophysiological studies have suggested that information about word's meaning can be accessed near-simultaneously with information about its form, reporting response modulations at similar latencies to those observed here (Begleiter and Platz, 1969; Pulvermüller, 2001; Skrandies, 1998 for review; but see Windmann et al., 2002). This timing is in accordance with recent studies showing rapid visual categorization within the initial approximately 150 ms post-stimulus onset (e.g., Landis et al., 1984; Murray et al., 2002; Rousselet et al., 2002). It may thus be the case that like faces (e.g., Braeutigam et al., 2001; Eger et al., 2003; Kanwisher et al., 1997; Landis et al., 1984; Liu et al., 2002; Seeck et al., 1997) emotional words, although used with equal frequency as neutral words, constitute a specialized form representation.[1]

In summary, the present study provides evidence for a specialized cortical network (vis à vis a distinct scalp topography) facilitating emotional word processing when such stimuli were presented to the RVF. This may reflect the existence of a specialized reading mechanism/strategy, engaging not only the language-dominant system, but also "emotion-dedicated" networks that likely involve the right hemisphere in parallel. This notion, namely that sensory–cognitive functions are subserved by networks throughout rather than discrete regions within the brain, is supported by both anatomical (e.g., Felleman and Van Essen, 1991) and functional data (e.g., Kim et al., 2001; Pulvermüller, 1996, 1999, 2001). We propose that the present behavioral facilitation and specific electrophysiological effect at just 100 ms are most parsimoniously explained as the rapid activation of neural representations—mnemonic templates—for emotional word stimuli, rather than pre-lexical semantic processes per se (Pulvermüller, 1996, 1999, 2001). A similar proposition has recently been applied to the rapid discrimination of face stimuli (Mouchetant-Rostaing et al., 2000), where the authors raise the possibility of more direct neural pathways/networks for stimuli with strong behavioral significance or associated memories/actions (see also Pulvelmüller et al., 2001). In using the term, 'mnemonic template', we wish to highlight the likely influence of learned associations and past experiences on the rapid processing and discrimination of incoming sensory stimuli.

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References

Allison, T., McCarthy, G., Nobre, A., Puce, A., Belger, A., 1994. Human extrastriate visual cortex and the perception of faces, words, numbers, and colors. Cereb. Cortex 4, 544–554.

Assadollahi, R., Pulvermüller, F., 2001. Neuromagnetic evidence for early access to cognitive representations. NeuroReport 12, 207–213.

Begleiter, H., Platz, A., 1969. Cortical evoked potentials to semantic stimuli. Psychophysiology 6, 91–100.

Benson, D.F., Zaidel, E., 1985. The Dual Brain. The Guilford Press, New York.

Bernat, E., Bunce, S., Shevrin, H., 2001. Event-related brain potentials differentiate positive and negative mood adjectives during both supraliminal and subliminal visual processing. Int. J. Psychophysiol. 42, 11–34.

Boles, D.B., 1983. Hemispheric interaction in visual field asymmetry. Cortex 19, 99–113.

Borod, J.C., 1992a. Interhemispheric and intrahemispheric control of emotion: a focus on unilateral brain damage. J. Consult. Clin. Psychol. 60, 339–348.

Borod, J.C., Andelman, F., Obler, L.K., Tweedy, J.R., Welkowitz, J., 1992b. Right hemisphere specialization for the identification of emotional words and sentences: evidence from stroke patients. Neuropsychologia 30, 827–844.

Bub, D.N., Lewine, J., 1988. Different modes of word recognition in the left and right visual fields. Brain Lang. 33, 161–188.

Braeutigam, S., Bailey, A.J., Swithenby, S.J., 2001. Task-dependent early latency (30–60 ms) visual processing of human faces and other objects. NeuroReport 12, 1531–1536.

Brandeis, D., Lehmann, D., 1989. Segments of event-related potential map series reveal landscape changes with visual attention and subjective contours. Electroencephalogr. Clin. Neurophysiol. 73, 507–519.

Brandeis, D., Naylor, H., Halliday, R., Callaway, E., Yano, L., 1992. Scopolamine effects on visual information processing, attention, and event-related potential map latencies. Psychophysiology 29, 315–336.

Brandeis, D., Lehmann, D., Michel, C.M., Mingrone, W., 1995. Mapping event-related brain potential microstates to sentence endings. Brain Topogr. 8, 145–159.

Bryden, M.P., 1982. Laterality: functional asymmetry in the intact brain. Academic Press, New York.

Cicero, B.A., Borod, J.C., Santschi, C., Erhan, H.M., Obler, L.K., Agosti, R.M., Welkowitz, J., Grunwald, I.S., 1999. Emotional versus nonemotional lexical perception in patients with right and left brain damage. Neuropsychiatry Neuropsychol. Behav. Neurol. 12, 255–264.

Chiarello, C., 1988. Right Hemisphere Contributions to Lexical Semantics. Springer-Verlag, New York.

Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M.A., Michel, F., 2000. The visual word form area. Brain 123, 291–307.

Content, A., Mousty, P., Radeau, M., 1990. L'année psychologique 90, 551–566.

Crosson, B., Cato, M.A., Sadek, J.R., Gokcay, D., Bauer, R.M., Fischler, I.S., Maron, L., Gopinath, K., Auerbach, E.J., Browd, S.R., Briggs, R.W., 2002. Semantic monitoring of words with emotional connotation during fMRI: contribution of anterior left frontal cortex. J. Int. Neuropsychol. Soc. 8, 607–622.

Day, J., 1977. Right-hemisphere language processing in normal right-handers. J. Exp. Psychol. Hum. Percept. Perform. 3, 518–528.

Ducommun, C.Y., Murray, M.M., Thut, G., Bellmann, A., Viaud-Delmon, I., Clarke, S., Michel, C.M., 2002. Segregated processing of auditory motion and auditory location: an ERP mapping study. NeuroImage 16, 76–88.

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[1] We would also like to note that the finding of distinct scalp topographies to linguistic stimuli early in sensory-cognitive processing need not be limited to the case of emotional words. Indeed, given the different roles of the hemispheres in "reading" (see Chiarello, 1988 for overview), it may be the case that other stimulus categories or word categories might exhibit similar phenomena, as suggested by many behavioral studies using metaphors (Shields, 1991), stenography (Regard et al., 1985b,c), width of association (Rodel et al., 1992), imaginable words (Bub and Lewine, 1988; Day, 1977), or brand name recognition (Gontijo et al., 2002).

Eger, E., Jedynak, A., Iwaki, T., Skrandies, W., 2003. Rapid extraction of emotional expression: evidence from evoked potential fields during brief presentation of face stimuli. Neuropsychologia 41, 808–817.

Felleman, D.J., Van Essen, D.C., 1991. Distributed hierarchical processing in the primate cerebral cortex. Cereb. Cortex 1, 1–47.

Fender, D.H., 1987. Source localisation of brain electrical activity. In: Gevins, A.S., Remond, A. (Eds.), Handbook of Electroencephalography and Clinical Neurophysiology, vol. 1. Elsevier, Amsterdam, pp. 355–399.

Friederici, A.D., 1997. Neurophysiological aspects of language processing. Clin. Neurosci. 4, 64–72.

Gontijo, P.F., Rayman, J., Zhang, S., Zaidel, E., 2002. How brand names are special: brands, words, and hemispheres. Brain Lang. 82, 327–343.

Goodglass, H., Graves, R., Landis, T., 1980. The role of the right hemisphere in reading. Rev. Neurol. 136, 669–673.

Grave de Peralta, R., Gonzalez Andino, S., 2002. Comparison of algorithms for the localization of focal sources: evaluation with simulated data and analysis of experimental data. Int. J. Bioelectromagn. 4 (1).

Grave de Peralta, R., Gonzalez, S.L., Lantz, G., Michel, C.M., Landis, T., 2001. Noninvasive localization of electromagnetic epileptic activity. I Method descriptions and simulations. Brain Topogr. 14, 131–137.

Graves, R., Landis, T., Goodglass, H., 1981. Laterality and sex differences for visual recognition of emotional and non-emotional words. Neuropsychologia 19, 95–102.

Halgren, E., Baudena, P., Heit, G., Clarke, M., Marinkovic, K., 1994a. Spatio-temporal stages in face and word processing: 1. Depth recorded potentials in the human occipital and parietal lobes. J. Physiol. 88, 1–50.

Halgren, E., Baudena, P., Heit, G., Clarke, M., Marinkovic, K., 1994b. Spatio-temporal stages in face and word processing. 2. Depth recorded potentials in the human frontal and Rolandic cortices. J. Physiol. 88, 51–80.

Hampson, E., Kimura, D., 1988. Reciprocal effects of hormonal fluctuations on human motor and perceptual spatial skills. Behav. Neurosci. 102, 456–459.

Haussman, M., Güntürkün, O., 2000. Steroid fluctuations modify functional cerebral asymmetries: the hypothesis of progesterone-mediated interhemispheric decoupling. Neuropsychologia 38, 1362–1374.

Heister, G., Landis, T., Regard, M., Schroeder-Heister, P., 1989. Shift of functional cerebral asymmetry during the menstrual cycle. Neuropsychologia 27, 871–880.

Hughlings-Jackson, J., 1874. On the nature of duality of the brain. Med. Press Circ. 17, 19 (reprinted in Brain 38 (1915) 80–103).

Iacoboni, M., Zaidel, E., 1996. Hemispheric independence in word recognition: evidence from unilateral and bilateral presentations. Brain Lang. 53, 121–140.

Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci. 17, 4302–4311.

Kim, M., Kim, J., Kwon, J.S., 2001. The effect of immediate and delayed word repetition on event-related potential in a continuous recognition task. Brain Res. Cogn. Brain Res. 11, 387–396.

Koenig, T., Lehmann, D., 1996. Microstates in language-related brain potential maps show noun-verb differences. Brain Lang. 53, 169–182.

Koenig, T., Prichep, L., Lehmann, D., Sosa, P.V., Braeker, E., Kleinlogel, H., Isenhart, R., John, E.R., 2002. Millisecond by millisecond, year by year: normative EEG microstates and developmental stages. NeuroImage 16, 41–48.

Kutas, M., Hillyard, S.A., 1980. Reading senseless sentences: brain potentials reflect semantic incongruity. Science 207, 203–205.

Làdavas, E., Nicoletti, R., Umilta, C., Rizzolatti, G., 1984. Right hemisphere interference during negative affect: a reaction time study. Neuropsychologia 22, 479–485.

Landis, T., Graves, R., Goodglass, H., 1982. Aphasic reading and writing: possible evidence for right hemisphere participation. Cortex 18, 105–112.

Landis, T., Regard, M., Graves, R., Goodglass, H., 1983. Semantic paralexia: a release of right hemispheric function from left hemispheric control? Neuropsychologia 21, 359–364.

Landis, T., Lehmann, D., Mita, T., Skrandies, W., 1984. Evoked potentials of figure and ground. Int. J. Psychophysiol. 1, 345–348.

Landis, T., Regard, M., Weniger, D., 1990. The right cerebral hemisphere. Schweiz. Med. Wochenschr. 120, 433–439.

Lavric, A., Pizzagalli, D., Forstmeier, S., Rippon, G., 2001. Mapping dissociations in verb morphology. Trends Cogn. Sci. 5, 301–308.

Ledoux, J.E., 1995. In search of an emotional system in the brain: leaping from fear to emotion and consciousness. In: Gazzaniga, M.S. (Ed.), The Cognitive Neurosciences. Cambridge, Bradford, pp. 1049–1061.

Lehmann, D., 1987. Principles of spatial analysis. In: Gevins, A.S., Remond, A. (Eds.), Methods of Analysis of Brain Electrical and Magnetic Signals. Handbook of Electroencephalography and Clinical Neurophysiology, vol. 1. Elsevier, Amsterdam, pp. 309–354.

Lehmann, D., Skrandies, W., 1980. Reference-free identification of components of checkerboard-evoked multichannel potential fields. Electroencephalogr. Clin. Neurophysiol. 48, 609–621.

Liu, J., Harris, A., Kanwisher, N., 2002. Stages of processing in face perception: an MEG study. Nat. Neurosci. 5, 910–916.

Maddock, R.J., Garrett, A.S., Buonocore, M.H., 2003. Posterior cingulate cortex activation by emotional words: fMRI evidence from a valence decision task. Hum. Brain Mapp. 18, 30–41.

Malach, R., Reppas, J.B., Benson, R.R., Kwong, K.K., Jiang, H., Kennedy, W.A., Ledden, P.J., Brady, T.J., Rosen, B.R., Tootell, R.B., 1995. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc. Natl. Acad. Sci. 92, 8135–8139.

Marshall, J.C., Caplan, D., Holmes, J.M., 1975. The measure of laterality. Neuropsychologia 13, 315–321.

McKeever, W.F., Hulling, M.D., 1971. Bilateral tachistoscopic word recognition as a function of hemispheric stimulated and interhemispheric stimulated and interhemispheric transfer time. Neuropsychologia 9, 281–288.

Michel, C.M., Grave de Peralta, R., Lantz, G., Gonzalez Andino, S., Spinelli, L., Blanke, O., Landis, T., Seeck, M., 1999. Spatiotemporal EEG analysis and distributed source estimation in presurgical epilepsy evaluation. J. Clin. Neurophysiol. 16, 239–266.

Michel, C.M., Thut, G., Morand, S., Khateb, A., Pegna, A.J., Grave de Peralta, R., Gonzales, S., Seeck, M., Landis, T., 2001. Electric source imaging of human brain functions. Review. Brain Res. Rev. 36, 108–118.

Morand, S., Thut, G., Grave de Peralta, R., Clarke, S., Khateb, A., Landis, T., Michel, C.M., 2000. Electrophysiological evidence for fast visual processing through the human koniocellular pathway when stimuli move. Cereb. Cortex 10, 817–825.

Mouchetant-Rostaing, Y., Giard, M.H., Delpuech, C., Echallier, J.F., Pernier, J., 2000. Early signs of visual categorization for biological and non-biological stimuli in humans. NeuroReport 11, 2521–2525.

Murray, M.M., Wylie, G.R., Higgins, B.A., Javitt, D.C., Schroeder, C.E., Foxe, J.J., 2002. The spatiotemporal dynamics of illusory contour processing: combined high-density electrical mapping, sources analysis, and functional magnetic resonance imaging. J. Neurosci. 22, 5055–5073.

Nobre, A.C., Allison, T.A., McCarthy, G., 1994. Word recognition in the human inferior temporal lobe. Nature 372, 260–263.

Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113.

Pascual-Marqui, R.D., Michel, C.M., Lehmann, D., 1995. Segmentation of brain electrical activity into microstates: model estimation and validation. IEEE Trans. Biomed. Eng. 42, 658–665.

Perrin, F., Pernier, J., Bertrand, O., Giard, M.H., Echallier, J.F., 1987. Mapping of scalp potentials by surface spline interpolation. Electroencephalogr. Clin. Neurophysiol. 66, 75–81.

Picton, T.W., Bentin, S., Berg, P., Donchin, E., Hillyard, S.A., Johnson, R.J., Miller, G.A., Ritter, W., Ruchkin, D.S., Rugg, M.D., Taylor, M.J., 2000. Guidelines for using event-related potentials to study cognition: recording standards and publication criteria. Psychophysiology 37, 127–152.

Pizzagalli, D., Regard, M., Lehmann, D., 1999. Rapid emotional face processing in the human right and left brain hemispheres: an ERP study. NeuroReport 10, 2691–2698.

Pizzagalli, D., Lehmann, D., Koenig, T., Regard, M., Pascual-Marqui, R.D., 2000. Face-elicited ERPs and affective attitude: brain electric microstate and tomography analyses. Clin. Neurophysiol. 111, 521–531.

Pizzagalli, D.A., Lehmann, D., Hendrick, A.M., Regard, M., Pascual-Marqui, R.D., Davidson, R.J., 2002. Affective judgments of faces modulate early activity (approximately 160 ms) within the fusiform gyri. NeuroImage 16, 663–677.

Pulvermüller, F., 1996. Hebb's concept of cell assemblies and the psychophysiology of word processing. Psychophysiology 33, 317–333.

Pulvermüller, F., 1999. Words in the brain's language. Behav. Brain Sci. 22, 253–279 (discussion 280–336).

Pulvermüller, F., 2001. Brain reflections of words and their meaning. Trends Cogn. Sci. 5, 517–524.

Regard, M., Landis, T., Wieser, H.G., Hailemariam, S., 1985a. Functional inhibition and release: unilateral tachistoscopic performance and stereoelectroencephalographic activity in a case with left limbic status epilepticus. Neuropsychologia 23, 575–581.

Regard, M., Landis, T., Hess, K., 1985b. Preserved stenography reading in a patient with pure alexia. A model for dissociated reading processes. Arch. Neurol. 42, 400–402.

Regard, M., Landis, T., Graves, R., 1985c. Dissociated hemispheric superiorities for reading stenography vs. print. Neuropsychologia 23, 431–435.

Rodel, M., Cook, N.D., Regard, M., Landis, T., 1992. Hemispheric dissociation in judging semantic relations: complementarity for close and distant associates. Brain Lang. 43, 448–459.

Rolls, E.T., 1995. A theory of emotion and consciousness, and its application to understanding the neural basis of emotion. In: Gazzaniga, M.S. (Ed.), The Cognitive Neurosciences. Cambridge, Bradford, pp. 1091–1106.

Rorden, C., Brett, M., 2000. Stereotaxic display of brain lesions. Behav. Neurol. 12, 191–200.

Rousselet, G.A., Fabre-Thorpe, M., Thorpe, S.J., 2002. Parallel processing in high-level categorization of natural images. Nat. Neurosci. 5, 629–630.

Seeck, M., Michel, C.M., Mainwaring, N., Cosgrove, R., Blume, H., Ives, J., Landis, T., Schomer, D.L., 1997. Evidence for rapid face recognition from human scalp and intracranial electrodes. NeuroReport 8, 2749–2754.

Shields, J., 1991. Semantic–pragmatic disorder: a right hemisphere syndrome? Br. J. Disord. Commun. 26, 383–392.

Skrandies, W., 1998. Evoked potential correlates of semantic meaning—A brain mapping study. Brain Res. Cogn. Brain Res. 6, 173–183.

Strauss, E., 1983. Perception of emotional words. Neuropsychologia 21, 99–103.

Talairach, J., Tournoux, P., 1988. Co-planar Stereotaxic Atlas of the Human Brain. Thieme, New York.

Wey, T.V., Cook, N.D., Landis, T., Regard, M., Graves, R.E., 1993. Lateralized lexical decisions and the effects of hemifield masks: a study of interhemispheric inhibition and release. Int. J. Neurosci. 71, 37–44.

Windmann, S., Daum, I., Güntürkün, O., 2002. Dissociating pre-lexical and post-lexical processing of affective information in the two hemispheres: effects of the stimulus presentation format. Brain Lang. 80, 269–286.