

Synchronization Between Temporal and Parietal Cortex During Multimodal Object Processing in Man

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A series of recordings in cat visual cortex suggest that synchronous activity in neuronal cell ensembles serves to bind the different perceptual qualities belonging to one object. We provide evidence that similar mechanisms seem also to be observable in human subjects for the representation of supramodal entities. Electroencephalogram (EEG) was recorded from 19 scalp electrodes (10/20 system) in 19 human subjects and EEG amplitude and coherence were determined during presentation of objects such as house, tree, ball. Objects were presented in three different ways: in a pictorial presentation, as spoken words and as written words. In order to find correlates of modality-independent processing, we searched for patterns of activation common to all three modalities of presentation. The common pattern turned out to be an increase of coherence between temporal and parietal electrodes in the 13–18 Hz beta1 frequency range. This is evidence that population activity of temporal cortex and parietal cortex shows enhanced coherence during presentation of semantic entities. Coherent activity in this low-frequency range might play a role for binding of multimodal ensembles.

Introduction

Many studies have concentrated on sensory processing in one modality. But what happens if an object is perceived with different sensory receptors, a more realistic way to be confronted with objects? Do the different sensory paths converge somewhere to form a uniform representation of the object, a *conceptual object-representation*? Is there a specialized area in the brain, a module, responsible for concept representation? Or is association of all sensory representations of an object into a widely distributed network enough? Integration among different sensory systems has rarely been investigated by animal research. There are some known supramodal, or multimodal areas, established by intracortical investigation (e.g. cat polysensory areas: Clare and Bishop, 1954; area PG: Mesulam, 1990; prefrontal cortex: Goldman-Rakic, 1988), but multimodal representations of objects have not been systematically investigated. Apparently, this topic can be better examined in human subjects. Supramodal representations in the literal sense have mostly been examined through language studies, e.g. the Geschwind model on word-sound integration (Geschwind, 1972). The angular gyrus, a cortical area where lesions lead to the classical Gerstman syndrome (Gerstman, 1957), was considered to be an integrative area where different semantic and verbal entities are integrated and stored as *symbols*. Neuropsychological and imaging results have since then supported but have also questioned the Geschwind model (e.g. Peterson *et al.*, 1988). Since the concept of distributed representation has been developed (e.g. Braitenberg, 1978; Rumelhart *et al.*, 1986), an explicit integration of entities from different modalities into a unitary supramodal representation, however, is no longer needed in theory. There is no need for a site of a 'lexicon'; concepts might be simply represented by associations between different sensory

networks, thus forming an intermodal network distributed over the whole cortex. A question intimately related to supramodal representation is the classical 'binding problem', i.e. the question of how the different characteristics of an object – its visual appearance, its sound, its smell, etc. – are integrated to form a uniform conscious experience. Cortical oscillations have been proposed to play a role in binding the different perceptual qualities belonging to one object (von der Malsburg *et al.*, 1986; Eckhorn *et al.*, 1988; Gray *et al.*, 1989; König, 1995). Empirical evidence for binding by synchrony or, in general, representation by neuronal ensembles, however, has mostly been gained in modality-specific areas, e.g. ensembles representing bars in V1 (Gray *et al.*, 1989), odors in the olfactory bulb (Freeman, 1983), tones in A1 (Espinosa and Gerstein, 1988), or movements in frontal cortex (Abeles *et al.*, 1993), but not between different modalities. The question thus is whether there is a specific area for this higher integrative part of processing, or whether there is evidence for a distributed ensemble of neurons from the different sensory areas.

To address the question of supramodal object representation, an ideal method should be one that, on one hand, measures synchronization of distributed neuronal ensembles and, on the other, can also be applied to humans. Electroencephalographic (EEG) spectral analysis analyzes the dynamics of large neuronal populations and their interactions directly in humans. By analyzing the EEG in the frequency domain, oscillatory activity and synchronization can be measured. The EEG, i.e. the macroscopic potentials measured at scalp electrodes, is constituted by the fluctuating pattern of synchronization and desynchronization of different groups of neurons within the tissue underneath the electrode (Elul, 1972). Since a scalp electrode picks up the summed activity of some square centimeters of cortical tissue (Cooper *et al.*, 1965), EEG measures mostly concerted activity of large-scale cell ensembles. Indeed, with EEG recordings above human visual cortex, there is evidence that EEG amplitude reflects the state of synchronization within functional visual cell ensembles (Lutzenberger *et al.*, 1995; Tallon *et al.*, 1995; von Stein and Petsche, 1995; von Stein *et al.*, 1995a; Müller *et al.*, 1996). This relationship between scalp EEG and intracortical synchronization may explain why EEG analysis has been successfully applied to study cognitive processes in humans such as language processing, spatial reasoning and motor activity (e.g. Giannitrapani, 1975; Pfurtscheller and Aranibar., 1977; Duffy *et al.*, 1981; Rappelsberger *et al.*, 1991; Klimesch *et al.*, 1993; von Stein *et al.*, 1993; Joliot *et al.*, 1994; Gevins *et al.*, 1997). The correlation between EEG channels, however, is usually not analyzed. This is surprising in view of the success of cross-correlation analysis in intracortical recordings (for review, see e.g. Aertsen and Arndt, 1993). In this paper, we have applied spectral coherence analysis to human EEG. Coherence gives information about the

amount of correlated activity between electrodes and thus about inter-areal synchronization. In several studies we measured coherence between signals at different scalp locations and found that EEG coherence is a good and more sensitive measure for higher cognitive processes than EEG amplitude (Rappelsberger and Petsche, 1988; Petsche *et al.*, 1992, 1996; von Stein *et al.*, 1993; von Stein, 1994a; Johnson *et al.*, 1996; Sarthein *et al.*, 1998). In particular, coherence was found to be sensitive to different language-related tasks (Weiss and Rappelsberger, 1996). With respect to the new concepts on distributed representation and to multimodal representations in particular, coherence seems to be specifically important as it does not detect local activity but the correlated signal components between distant cortical sites. In this paper, we used coherence and amplitude analysis to study in detail whether multimodal object representation is reflected in human EEG.

EEG was recorded in 19 human subjects during presentation of different semantic stimuli: high imagery objects of daily life – hammer, table, dog, etc. – were presented as pictorial representations, as written words and as spoken words (Fig. 1a). The aim was to analyze whether a common activation can be determined in all three modalities, a correlate of *supramodal object-representation*. As control conditions, non-sense pictures, visually presented non-sense words and spoken non-sense words were presented. Correlates of semantic representations could thus be determined by looking for EEG patterns common to the three semantic ('sense') conditions, and by looking for differences between the sense and the non-sense condition in each modality.

We found that a common activation was present in all three modalities in which objects have been perceived: an enhanced coherence between temporal and parietal electrodes, appearing in the 13–18 Hz frequency range. We see this as evidence that neuronal ensembles in temporo-parietal cortex may be responsible for supramodal concept representation.

Materials and Methods

Experimental Design and Procedure

In our study we examined 23 healthy, right-handed subjects (25.9 ± 2.0 years old, 12 males). EEG was recorded while subjects were seated comfortably in an acoustically shielded room perceiving stimuli. Stimuli were presented on a black and white computer screen (70 Hz frame rate) at a distance of 50 cm from the subjects. Contrast and luminance were adjusted individually to minimize subject's eye strain and to reduce muscle artefacts. Stimuli were presented in consecutive blocks of nine different conditions. Conditions 1, 3 and 7 were chosen to induce semantical processing, the other conditions served as controls. (The experimental design is shown in Fig. 1a–c.)

(1) (*pictorial*): Forty pictures describing daily life objects such as house, ball, tree were presented for 2 s each with an interval of 2–3 s between them. The pictures were simple pictograms sized $4 \times 5 \text{ cm}^2$.

(2) (*non-sense pictorial*): Non-sense pictures (line drawings consisting of the same graphical elements and size as the 'sense' pictures, but not depicting existing objects) were presented in the same manner.

(3) (*written*): Forty words denoting daily life objects (with 50% of the objects overlapping with those presented in the pictures) were presented with a letter size of $\sim 0.8 \text{ cm}$ black on white on the same screen and with the same duration.

(4) (*non-sense written*): Pronounceable non-sense words were presented at the same letter size on the same screen.

(5) (*letter strings*): Non-pronounceable letter strings were presented also in the same manner.

(6) (*abstract*): Abstract words were presented written.

(7) (*auditory*): Forty concrete words were presented auditorily, binaurally via headphones (again with 50% of the denoted objects

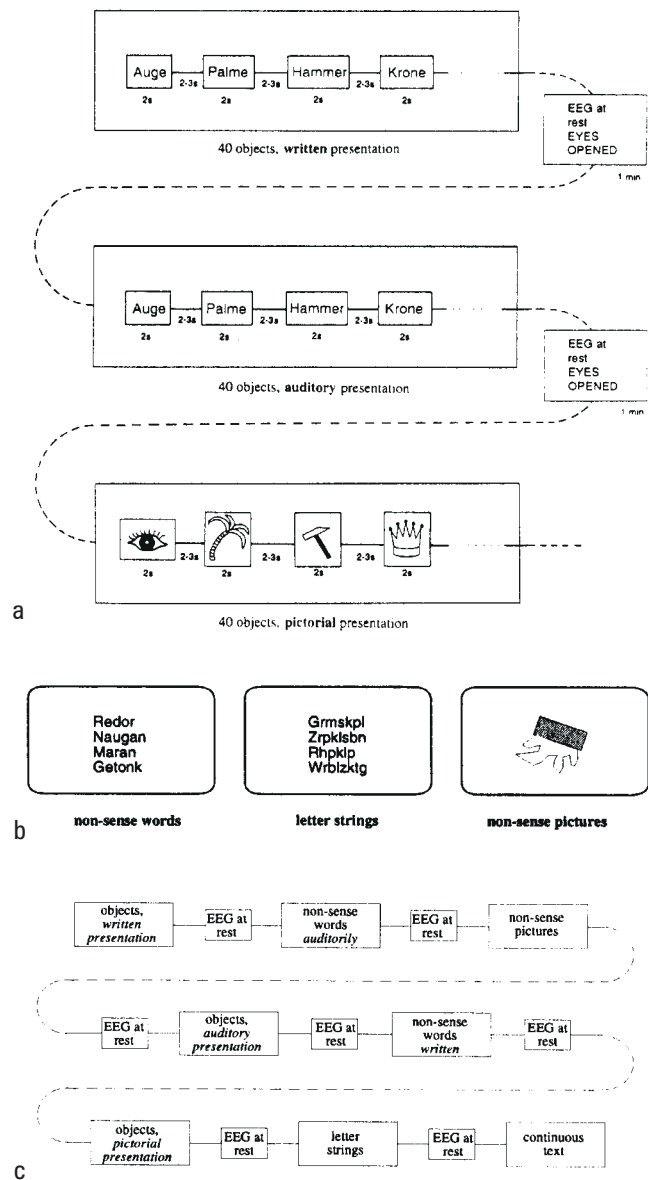


Figure 1. (a) Forty objects of daily life were presented (1) as pictorial representation (*pictorial*), (2) as spoken word (*auditorily*), and (3) as written word (*written*) to 19 human subjects. Each item was presented for 2 s with a 2–3 s interstimulus interval. EEG parameter coherence and amplitude were determined for each condition. The aim was to analyze whether a common activation can be determined in all three modalities, a correlate of *supramodal concept-representation*. (b) As control-conditions, pronounceable non-sense words were presented, both visually and auditorily. Further, letter strings (non-pronounceable strings of consonants) and non-sense pictures were presented. (c) All items were presented blockwise. Blocks containing meaningful entities were intermingled with blocks of the control conditions. The complete sequence of blocks is depicted. Resting conditions of 1 min duration where subjects relaxed with eyes open were dispersed between the blocks and served as a baseline for the analysis.

overlapping with those presented in the pictures). The auditory words were pronounced slowly and lasted 1–1.5 s.

(8) (*non-sense auditory*): Forty non-sense words were presented auditorily.

(9) (*text*): Finally, a continuous text of ~ 300 words was presented visually.

The words were such that the objects they denote were easily represented in a simple pictorial way. They were concrete German nouns two syllables in length that denote objects encountered very frequently in daily life. The non-sense words were pronounceable and had the same

Table 1

Percentage of remembered items

(a) single subjects

Visual subject	Single presentation					Double presentation				
	Episodic	Semantic	None	Imagery	Other	Episodic	Semantic	None	Imagery	Other
304	68	5	26	11	58	77	18	5	0	77
303	21	5	74	0	21	17	83	0	9	9
302	47	5	47	32	16	57	9	35	48	9
301	63	5	32	58	5	78	13	9	61	17
299	79	16	5	68	11	88	13	0	75	13
295	67	11	22	67	0	78	9	13	22	57
293	50	10	40	20	30	70	30	0	5	65
292	47	11	42	47	0	61	30	9	52	9
291	42	11	47	32	11	29	52	19	29	0
290	53	37	11	21	32	43	57	0	30	13
289	53	11	37	26	26	30	13	57	0	30
288	74	5	21	63	11	78	17	4	78	0
287	37	0	63	37	0	39	61	0	39	0
286	68	21	11	63	5	68	27	5	64	5
285	89	0	11	79	11	96	0	4	74	22
283	76	6	18	71	6	91	4	4	83	9
275	65	24	12	47	18	57	35	9	26	30
Ave.	59	11	30	44	15	62	28	10	41	21

(b) Average over subjects

Visual	Average over subjects			
	Episodic	Semantic	None	
59	11	30	single	
62	28	10	double	
50	14	36	single	
52	42	11	double	
41	20	39	single	
53	36	14	double	
Ave.	50	15	35	single
	56	35	12	double

length (two syllables) as the sense words (e.g. 'Naugan', 'Redor'). To imitate German nouns they were written with a capitalized initial letter. The ('sense') pictures showed the same objects denoted by the words. Only 50% of the words were exactly the same in all three modalities; the other 50% were of similar content but not the same.

The 40 items within each block were randomized. Interstimulus intervals were 2–3 s in all conditions. Between each block there was a period of 1 min when the subjects were asked to relax with their eyes opened (resting condition, 'EO' eyes open). During this resting condition, subjects were instructed to fixate a point ~2 m in front of them in order to minimize disruptive effects of eye movements on the EEG. These averaged resting conditions served as baseline for our analysis. The sequence of blocks was chosen such that a maximum time interval was achieved between similar blocks in order to avoid short-term memorization of the items (Fig. 1c).

Behavioral Tests

Subjects were instructed to carefully perceive the meaning of the words and to let associations and imagery arise. Neither memorization nor immediate behavioral response to stimuli was requested. The reason for omitting behavioral response was that we wanted to determine correlates of semantic association which may occur anywhere in the time window after stimulus onset; frequency analysis is an adequate method to determine such responses since this method is not restricted to stimulus-locked responses but detects changes occurring anywhere in the time window of analysis. To do so, however, we had to keep this window free of other processes. In particular, behavioral responses have been shown to affect the spectral composition of the EEG several seconds *prior* to movement onset (Pfurtscheller and Aranibar, 1977; Stancak and Pfurtscheller, 1996). This excludes a design where subjects expect to perform a behavioral response.

Instead of demanding an immediate behavioral response, subjects'

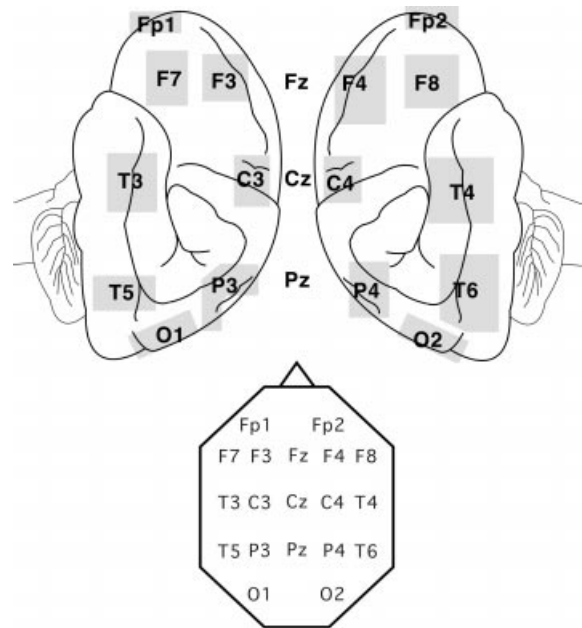


Figure 2. Electroencephalograms are recorded from 19 electrodes spread over the scalp (international 10/20 system). Top: electrode placement in relation to cortical structure; the shaded areas indicate the variance of electrode placement as determined in a MRI study (Homan *et al.*, 1987). Bottom: schematic head scheme with the 19 electrodes used throughout the paper.

active participation and depth of perception was monitored after the experiment. Five minutes following the last condition we carried out an episodic memory test, the remember-know (R/K) paradigm (Tulving, 1993). A series of the previously presented words was presented auditorily to each subject. For each item we investigated whether the subjects' memory was a 'remember' or 'know' memory, i.e. whether the item was remembered as a full past experience (episodic memory) or only as the fact of its occurrence (semantic memory). For this, the subject was asked to travel back in time and remember the situation when he/she saw or heard the word and to tell the experimenter what associations he was having, visual, olfactory, auditory or any other (Tulving, 1972), and further, whether he/she remembered the modality of its presentation, auditorily, visually or pictorially (source memory). The number of episodically remembered events, semantically remembered events and not remembered events were noted (Table 1); further, occurrences of episodic memories were subdivided according to the nature of associations, 'imagery' or 'other associations'. The R/K paradigm was carried out for both the single and the double presentations. Since subjects had been explicitly told prior to the experiment that they were not going to be tested on memory afterwards, the learning situation has to be considered incidental. The reliability of the obtained imagery scores was evaluated using EEG spectral parameters.

EEG Recording and Coherence Analysis

EEGs were recorded from 19 electrodes positioned on the scalp according to the 10/20 system (Homan *et al.*, 1987) (Fig. 2). The averaged signals from both ear lobes served as electrical reference. The digitization rate was 128 Hz, the data was filtered between 0.5 and 35 Hz. Eyeblinks and muscle artefacts were eliminated by visual inspection. Only subjects with muscle artefacts in less than three channels were included in the study, resulting in $n = 19$ subjects. The 2 s epochs of EEG during perception of items were Fourier-analyzed with a frequency resolution of 0.5 Hz. Averaged power spectra C_{xx} were computed for each electrode for each condition (average of all 40 items). Similarly, averaged cross-power spectra C_{xy} were calculated between pairs of electrodes. For data reduction only electrode-pairs that yielded sufficiently high coherence values were considered; these turned out to be the pairs of neighboring electrodes and the symmetrical interhemispheric electrode pairs (Fig.

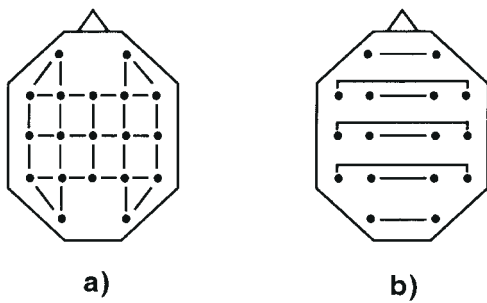


Figure 3. Lines between points denote electrode pairs where coherence was computed: (a) adjacent electrodes; (b) homologous electrodes of both hemispheres.

3a,b), which usually have coherence values >0.2 . Data reduction of the spectra was performed by averaging adjacent spectral lines to obtain average values for five frequency bands: theta (4–7.5 Hz), alpha (8–12.5 Hz), beta1 (13–18 Hz), beta2 (18.5–24 Hz), gamma (24.5–32 Hz). The final step was the computation of amplitude (square root of power) and squared coherence per frequency band. Squared coherence $K_{xy}^2(f)$ describes the linear relationship of two signals x and y . It is equal to the normalized average cross-power spectrum according to

$$K_{xy}^2(f) = \frac{|C_{xy}(f)|^2}{C_{xx}(f) C_{yy}(f)}$$

In this way we obtained amplitude values for 19 scalp locations and coherence values for 38 pairs of electrodes for all nine stimulus conditions. The calculation of coherence is based on averaging the real and imaginary parts of the cross-spectra independently in order to detect repeating phase relationships between the signals. Thus coherence is a statistical measure of the dominant synchronization between two signals for any stable phase lag between them. For a detailed description of the method, see Rappelsberger *et al.* (1986).

The question was whether amplitude or coherence parameters during the task differed significantly from those during the resting condition for any cortical site or pair of electrodes. As an example for a significant change, Figure 4 shows the coherence values for one electrode pair for all 19 subjects. Each subject's coherence value is based on an average of 40 perception-epochs, thus yielding coherence estimates of 80 degrees of freedom. In 17 of 19 subjects, the averaged coherence during perception was higher than during the resting condition. The significance of parameter-changes for the group of 19 subjects was evaluated using paired Wilcoxon tests. The obtained rank sums were converted to error probabilities, yielding an error probability of $P < 0.01$ in the example shown in Figure 4. Those electrode pairs where a change in coherence reached a significance level of $P < 0.1$ or better are marked with a square in the topographic probability maps. The size of the square reflects significance levels 0.01, 0.02, 0.05 and 0.1; filled squares represent an increase of coherence with respect to the resting condition, empty squares a decrease (e.g. Fig. 5a). Separate maps are computed for each frequency band. Analogously, changes in amplitude are depicted by a square on the electrode site. The problem of multiple comparisons cannot easily be overcome by an alpha correction due to the large number of electrode pairs in the coherence maps. The statistics should therefore be considered descriptive rather than confirmatory. A change in coherence was only considered relevant if (i) the error probability in the Wilcoxon test reached $P < 0.05$ or better, and (ii) the change appeared consistently in several subsets of data which were recorded during similar stimulus conditions. Increases of amplitude or coherence were interpreted as task-related enhancement of correlated cortical activity.

Results

Different stimulations induced significant changes in EEG spectral parameters at different locations. At some electrode-sites only amplitude, i.e. the *local* degree of cooperativity was changed; at others a significant change occurred in coherence, the degree of cooperation *between* two electrodes. The induced pattern of

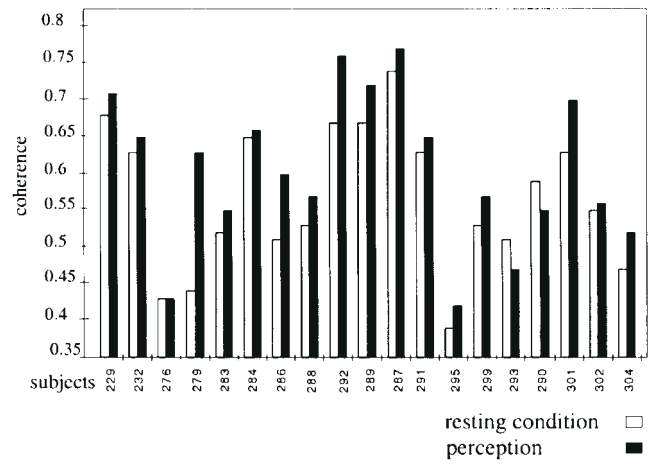


Figure 4. Coherence between the temporal electrode T5 and the parietal electrode P3 obtained in 19 subjects (frequency range 13–18 Hz). The average coherence during auditory perception of objects (black bars) is compared to the average coherence during the resting condition (white bars). The absolute value of coherence shows a remarkable intersubject variability depending on the individual resting state; perception of objects, however, induced an increase of coherence in 17 of 19 subjects. This increase of coherence yielded an error probability of $P < 0.01$ in a paired Wilcoxon test.

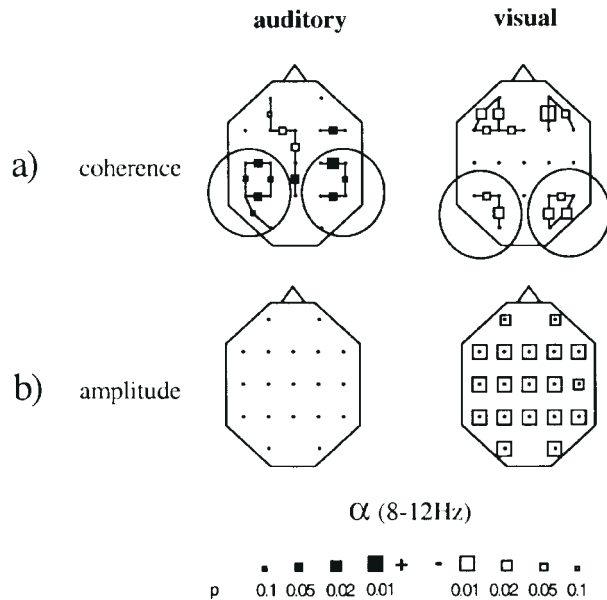


Figure 5. Changes of (a) coherence and (b) amplitude with respect to a resting condition in the alpha frequency range (8–12 Hz). Simplified head scheme viewed from above, nose in front; the points show the 19 recording sites on the scalp. Lines connecting two sites denote that during perception intervals coherence differed significantly from coherence during the resting condition. Filled squares symbolize an increase of coherence/amplitude, empty squares a decrease. The significance level of a change is coded by the size of the squares. (Wilcoxon test for independent samples, $n = 19$ subjects.) (a) Perception of words (*auditory*) elicits increases of coherence between temporal and parietal, temporal and central, and temporal and occipital electrodes in the alpha frequency range (8–12 Hz). Visual perception of words (*visual*) induces changes of coherence mostly posteriorly, between occipital and parietal, and occipital and temporal electrodes. Besides the localization, the direction of changes is also different: auditory perception leads to an increase of coherence whereas visual leads to a decrease. (b) Visual processing induces a significant decrease of alpha amplitude over most of the scalp.

changes depended on the task and on the frequency range examined. The lower frequencies turned out to be more modality dependent and showed more changes in amplitude.

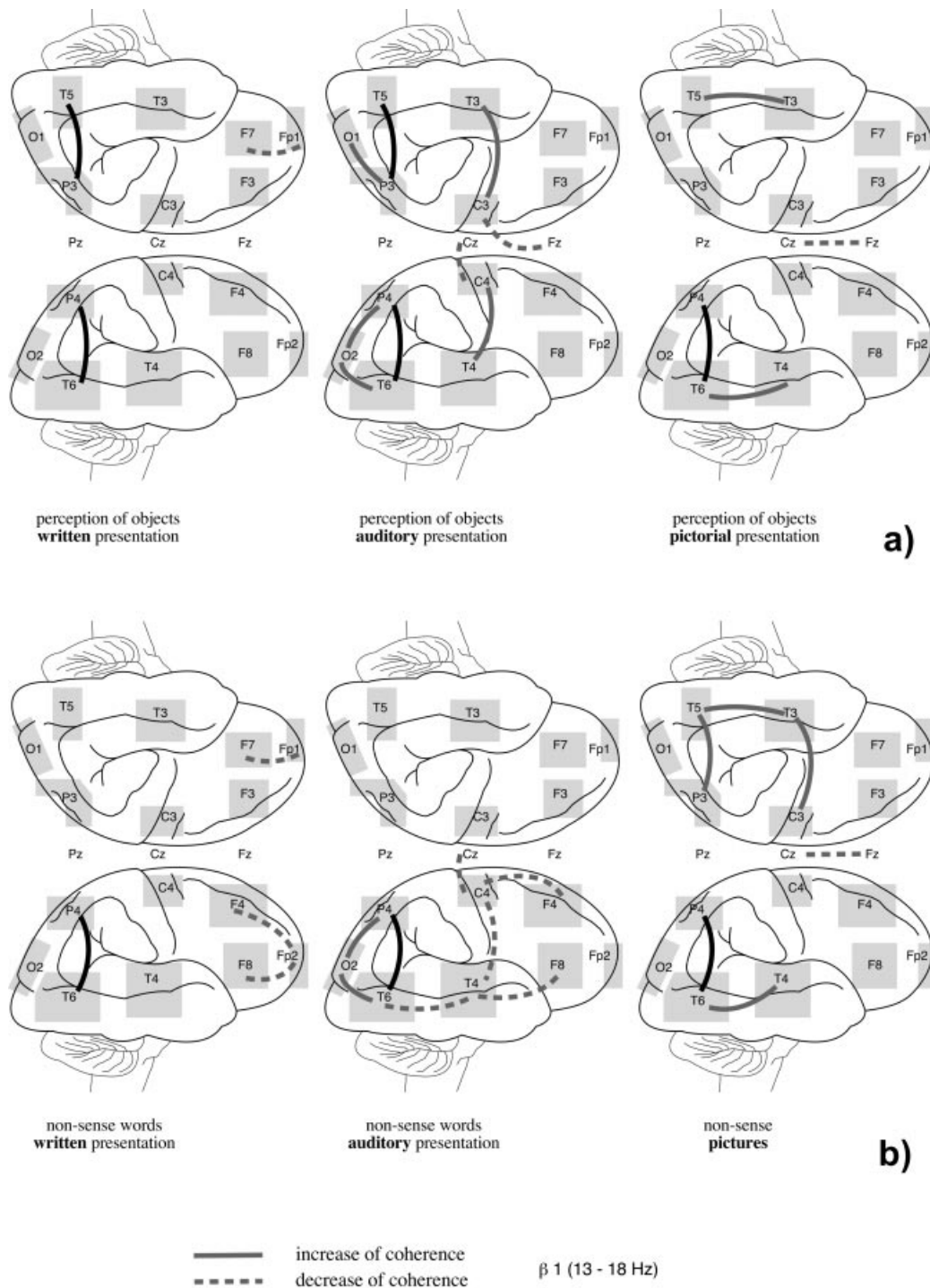
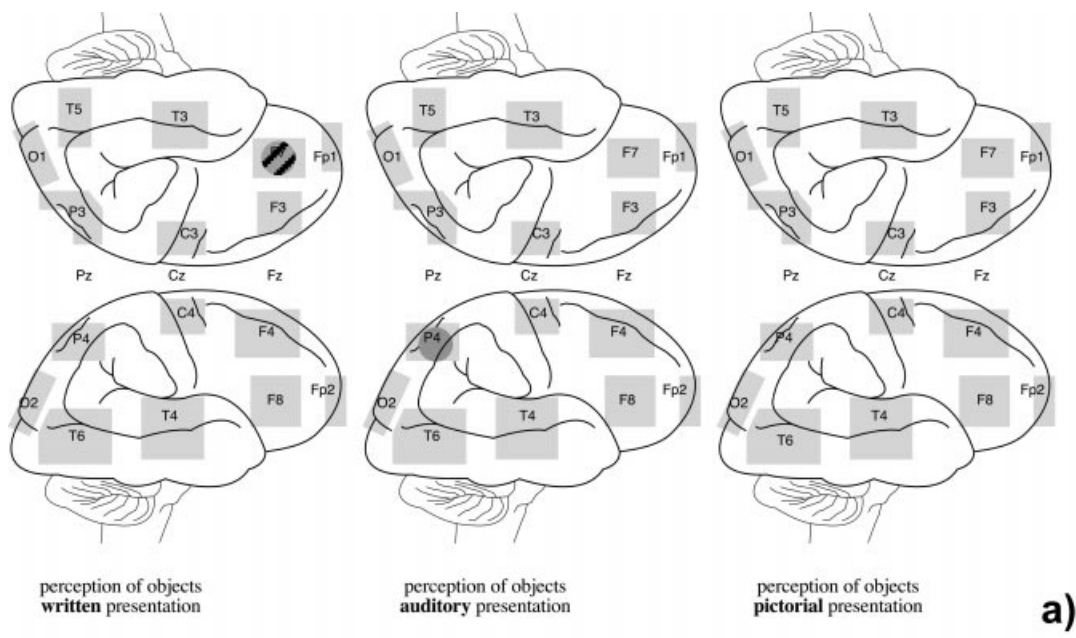


Figure 6. (a) Changes of coherence for all three conditions where objects were presented: written, auditorily and as pictures. For a better anatomical orientation, electrode positions are depicted in relation to cortical structure as determined by a magnetic resonance imaging study (Homan *et al.*, 1987). The shaded areas indicate the variance of electrode positions obtained with the 10/20 system with respect to the cortical surface. Note that the area does not reflect the area of electrical integration over cortical potentials measured by the electrode. Solid lines between cortical sites indicate a significant increase of coherence with respect to the resting condition, dashed lines indicate a decrease of coherence. Only changes in coherence that were significant with an error probability of $P < 0.05$ or better are depicted. Common to all three conditions dealing with objects is an increased coherence between electrodes above temporal and above parietal cortex (thick line) in the 13–18 Hz range, bilateral. (b) Same as (a) for the non-sense conditions. Common to the non-sense conditions is a similar increase in coherent activity, though mostly in the right hemisphere (thick line).

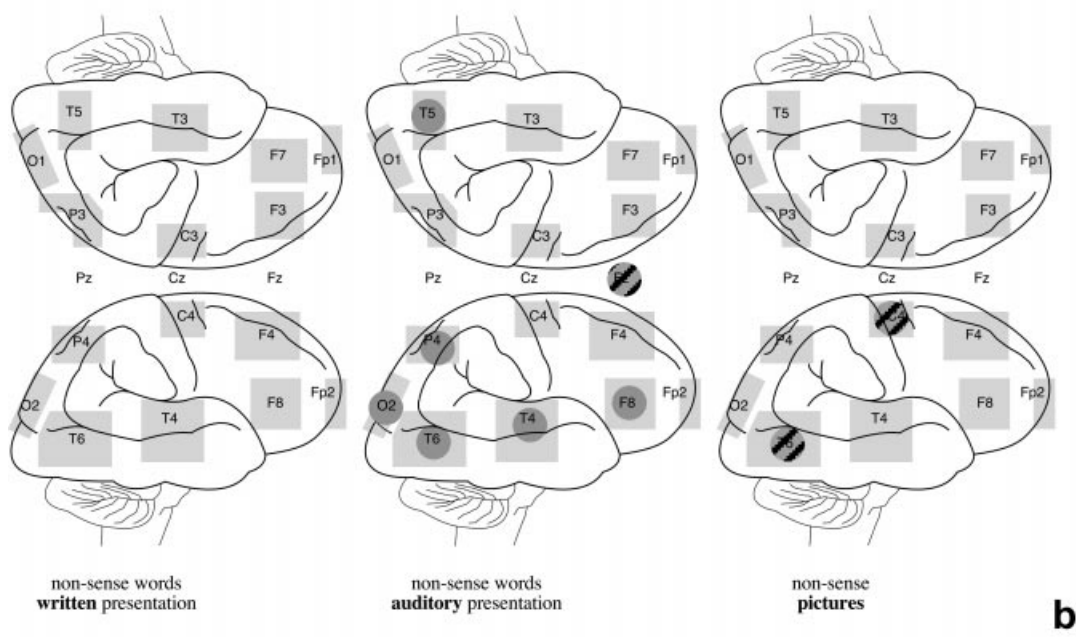
The changes correlated with semantics were more pronounced in the higher frequencies and in coherence.

Figure 5a demonstrates the changes in coherence as induced

by auditory (left) and visual (right) processing of objects. A major difference between the modalities is found in the coherence pattern in the low-frequency range (8–12 Hz, alpha).



a)



b)

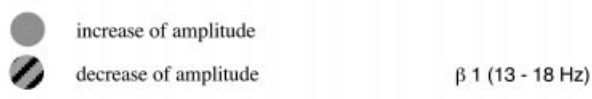


Figure 7. Changes in EEG amplitude for the same conditions as in Figure 6. Amplitudes change at several sites during the various conditions. No common pattern, however, is present.

In auditory processing there was an increased coherence between temporal, presumably auditory cortical electrodes and several other electrodes over occipito-temporo-parietal cortex, bilaterally (Fig. 5a, left). During visual processing, coherence changed more posteriorly, mostly between occipital and parietal electrodes, and between occipital and temporal electrodes (Fig. 5a, right). Although the observed change in coherence was mostly a *decrease*, this does not mean that the underlying

cortical areas were inactivated. Since EEG signals are measured at distant sites, a decrease in coherence between them may well stem from a functional compartmentalization of the active cortical area. Our investigations of primary processes, however, are described elsewhere (von Stein, 1994; von Stein *et al.*, 1994a) and will not be discussed further in this paper. The aim of this work is to describe an EEG correlate of concept integration and supramodal object representation.

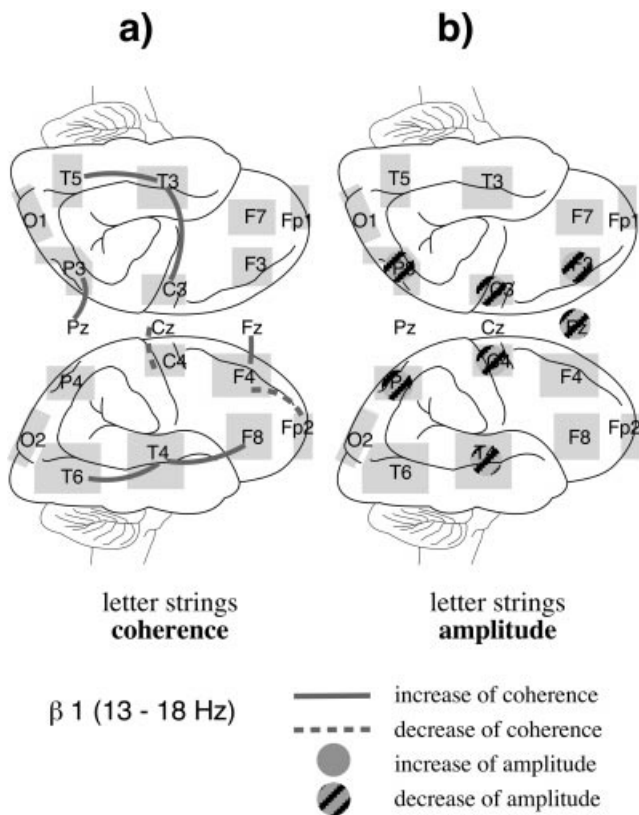


Figure 8. (a) Changes in coherence during presentation of letter strings with respect to the resting condition. Compare with the changes during visually and auditorily presented non-sense words (Fig. 6b): all three word-like stimuli are similar in that they lack meaning while maintaining the physical structure of a word; the difference is that both non-sense words are pronounceable, whereas the letter strings have no auditory correlate. Only in the case of pronounceable non-sense words the same temporo-parietal synchronization as during object perception was found. (b) Changes in amplitude.

Changes of Coherence During Perception of Objects

What are the areas involved in all three ways to perceive the objects? There was one pattern that was present in all cases of object perception, whether shown as pictures, written as words or named auditorily: an increase of coherence between temporal and parietal recording sites, in the beta1 (13–18 Hz) frequency range. Figure 6a shows the changes of coherence in this frequency range for all three modes of perception. Solid lines connect pairs of electrode sites where coherence increased significantly. Among the multiple connections, only coherence between temporal (T6/T5) and parietal (P4/P3) electrodes was significantly enhanced in all three conditions (Fig. 6a, thick line). The increase was significant with $P < 0.01$ for the auditory presentation and $P < 0.05$ for the visual verbal and pictorial presentation, in a group of 19 subjects (see also Fig. 4). The change in coherence was bilateral, except during pictorial presentation. The temporo-parietal increase of coherence was the only pattern of activity that was common to the three semantic conditions. In all three cases, temporo-parietal coherence appeared in one and the same frequency range, the beta1 range (13–18 Hz). Patterns of induced coherence in the alpha frequency range did not show any overlap across modalities but were specific for the modality (see Fig. 5a), patterns in the gamma range did not show any relation at all with either semantics or modality (see below, Fig. 11a). During other conditions, such as presentation of abstract words, a continuous text or during letter strings (see

below), coherence at temporo-parietal electrodes did not change. Therefore, we conclude that the enhancement of coherence between temporal and parietal electrodes seems specific for modality-independent processing of objects and might reflect a higher-order semantic aspect of processing.

Comparing the changes of coherence with changes in amplitude during perception of objects (Fig. 7a) shows that for amplitudes there was no overlap among conditions. This was true also for the alpha frequency (see Fig. 5b) and for the gamma frequency (Fig. 11b). Thus it appears that modality-independent processing is not accompanied by changes in spectral power but only consists in an increase of coherence.

Changes in amplitude also help to answer the question whether the enhancement of coherence is due to volume conduction in the extracellular fluid or to functional interaction. If the increase in coherence between temporal and parietal electrodes were due to volume-conducted signals, we would expect an increased amplitude at the respective sites (see Discussion). In four out of six conditions with enhanced coherence, however, the amplitude did not increase at all at temporal or parietal sites (sense visual, sense pictorial, non-sense visual, non-sense pictorial; Fig. 7). At one electrode there was even a decrease in amplitude (non-sense pictorial). Only in two cases was the increase in coherence also accompanied by an increase in amplitude above one of the two sites (sense auditory, non-sense auditory). In view of these results, volume conduction seems an unlikely cause for the observed increase in coherence.

EEG Changes During Non-sense Items

Comparing this finding with the coherence-changes in *non-sense words* gives further interesting results (Fig. 6b). First, the pattern of coherence for each non-sense condition (*written, auditory, pictorial*) is rather similar to its corresponding 'sense' condition in Figure 6a. (To judge how dissimilar coherence patterns can be, see, for example, the changes of coherence in the gamma range, Fig. 11). In addition, the common pattern of coherence across conditions also remains the same: during both visually and auditorily presented non-sense words, the same temporo-parietal electrodes as in Figure 6a showed increased coherence, and in the same frequency range (beta1). In this case, however, the coherence-increase was unilateral, more on the right hemisphere, except for the pictorial presentation where it was bilateral. What is the correlate of this right temporo-parietal cross-modal pattern? Comparing the coherence-changes for the pronounceable visual and auditory non-sense words with their non-pronounceable control condition (letter strings) in Figure 8a suggests a possible solution. During letter strings there was no increase in temporo-parietal coherence. Therefore the increase in right temporo-parietal coherence during non-sense words may be constrained by the pronounceability of a string of letters. Such a supramodal process, which relies on the fact that words are transferable from one modality to the other, might be termed supramodal Gestalt representation.

Changes in amplitude for the non-sense stimuli are shown in Figure 7b. As for coherence, the pattern of amplitude-changes for each non-sense condition (*written, auditory, pictorial*) shows similarities with its corresponding 'sense' condition in Figure 7a. Again, however, no overlapping pattern across modalities was observed in amplitude. Thus, similar as during the meaningful conditions, the increase in temporo-parietal coherence during the non-sense condition is not accompanied by an increase in spectral power.

Summing up, processing of meaningful words is reflected in

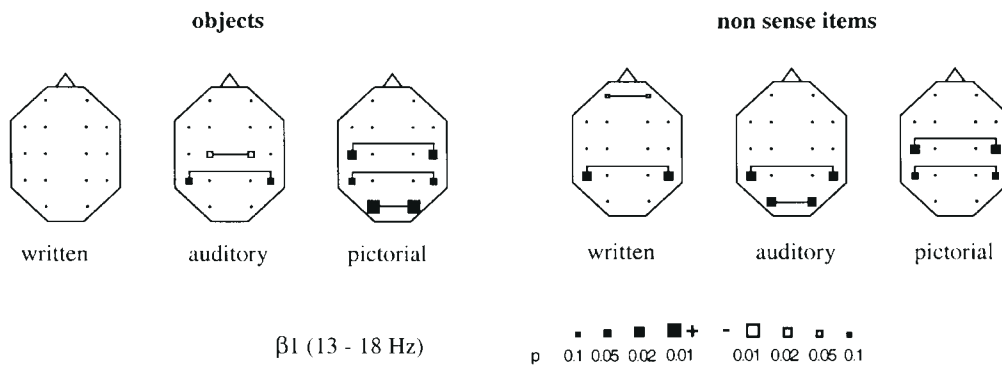


Figure 9. Interhemispheric changes in coherence with respect to the resting condition. Coherence increases between left and right temporal electrodes in nearly all conditions dealing with entities.

bilateral increase in temporo-parietal coherence; when the semantic content is missing, the activation tends to be restrained to the right side.

Interhemispheric Coupling

This result suggests a lateralization in the cross-modal processing of meaningful words – semantic representation on the left, word-Gestalt representation on the right. It is interesting to know how both parts relate to each other. Important evidence may already be gained from frequency analysis: besides knowing that both are activated during processing, we also know that they are activated in the same frequency range. Therefore we might expect a cooperative behavior between the two. Figure 9 supports this consideration. The interhemispheric coherence between left and right temporal electrodes is increased in nearly all these conditions, in the same frequency range (13–18 Hz). Remember that changes of coherence may occur in five different frequency ranges. It is therefore significant that the same frequency band is affected in all these cases. This is evidence that a coupling or information transfer between both cortical processes can indeed be observed.

Pictorial Presentations

Pictorial presentation of objects (Fig. 6a) induced increasing coherence at the same electrodes and in the same frequency range, but *only* at right temporo-parietal electrodes. Since pictures contain semantic information, this result does not support our current interpretation. During perception of pictures, however, coherence is increased between the two electrodes at temporal cortex: T3 and T5 (on the left hemisphere), and T4 and T6 on the right (Fig. 6a). Also, coherence between the two hemispheres is increased at multiple temporal sites (Fig. 9). Thus, instead of a bilateral *temporo-parietal* activation as in the other semantic conditions, we found a bilateral involvement of *temporal* electrodes during processing of pictures. A strong involvement of temporal cortex in the processing of pictures is in line with the role of temporal cortex in visual processing.

Sense Minus Non-sense

Finally, we examined correlates of semantic processing by computing the difference between meaningful words and non-sense words. We have computed this difference separately for auditory words and for written words (Fig. 10a,b). A significant difference between words with meaning with respect to words without meaning was revealed at left temporal electrodes in the

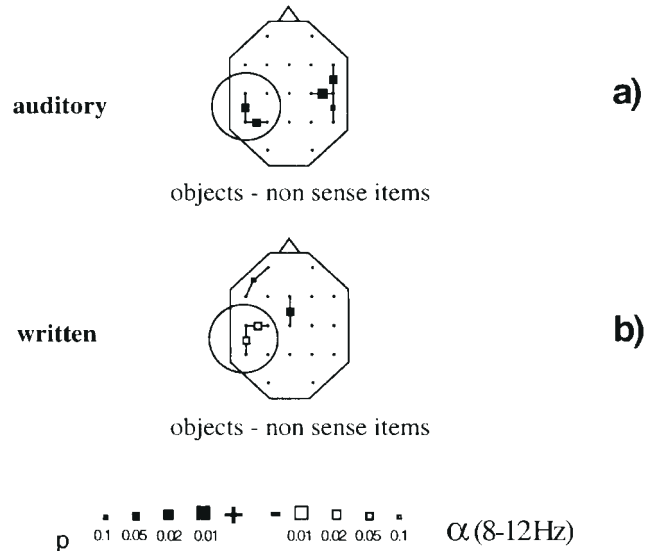


Figure 10. Significant differences in coherence during presentation of words denoting objects compared to non-sense words (direct comparison of coherence values in a paired Wilcoxon test). (a) Auditory presentation. Semantic processing is reflected in a left temporal increase of coherence. (b) Written presentation. Semantic processing is reflected in a change in coherence at the same cortical site.

low-frequency range (Fig. 10a): coherence in the 8–12 Hz (alpha) range increased between anterior and posterior left temporal electrodes during auditory processing of meaningful words ($P < 0.05$). The same comparison was made independently for the visual condition (Fig. 10b). Coherence changed at the same site between anterior and posterior temporal electrodes in the alpha range. Thus, for both modalities the comparison with the non-semantic control condition points to the same area – i.e. left temporal cortex – as being responsible for semantic processing. Therefore, as in the previous finding, also this approach indicates that left temporal cortex was engaged in processing of meaning; the frequency range, however, was alpha (8–12 Hz) in this case.

Changes in Gamma

As an example for spectral changes in higher-frequency ranges, Figure 11 shows the changes of coherence and amplitude in the gamma frequency range (24–32 Hz). Coherence changes at several sites in most of the conditions. The pattern of changes, however, cannot be attributed to one of the two aspects of

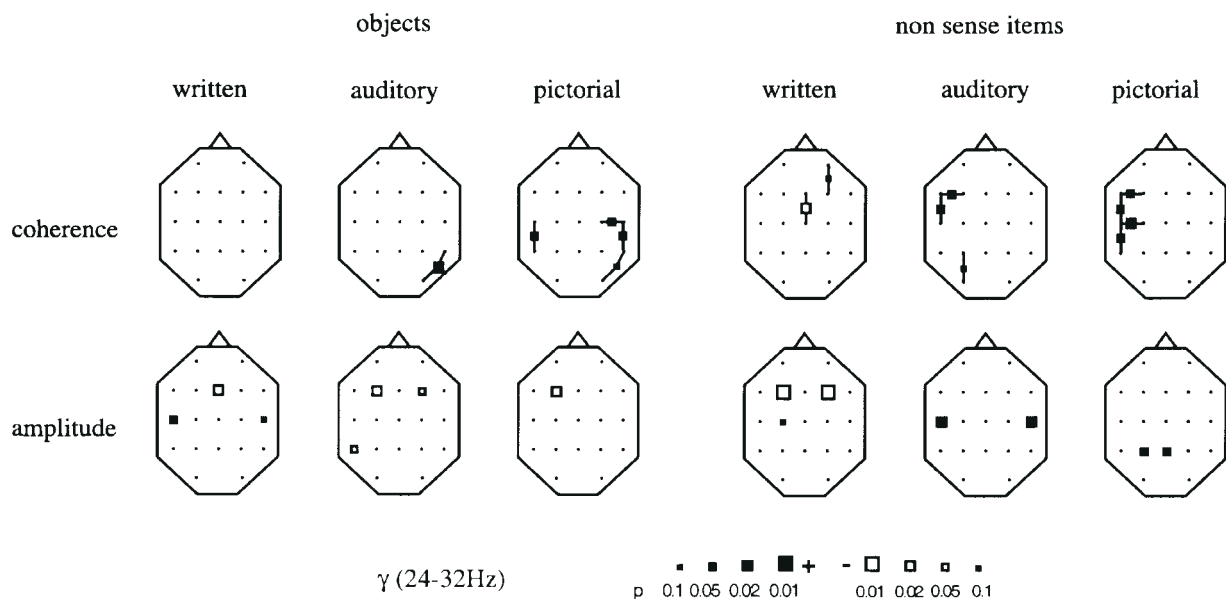


Figure 11. Changes in the *gamma* range of coherence (upper row) and amplitude (lower row) during presentation of objects and non-sense items. Both coherence and amplitude change at several sites with respect to the resting condition; the pattern of changes, however, cannot be attributed to one of the two aspects of processing addressed with this study, semantics or modality.

processing addressed with this study, semantics or modality. Reasons that no sensory-specific gamma changes were observed might be, on the one hand, that the gamma range investigated here was chosen as rather low to avoid contamination with muscle artefacts. On the other hand, sensory-specific changes in gamma might occur on a shorter timescale; the window of our analysis, however, was chosen to be rather long (2 s) to detect late, longer-lasting semantical components of processing.

Behavioral Data

The behavioral data collected to judge memory and active imagery during the experiment show that subjects were actively participating and semantically perceiving the stimuli. Results of the R/K episodic memory paradigm are shown in Table 1. On average (Table 1b) 50% of the items were retrieved episodically ('remembered', R), 15% were retrieved semantically ('known', K) and 35% were not retrieved at all ('none'), for single presentations (Table 1b). These numbers are in good agreement with other studies (i.e. Düzel *et al.*, 1997). Further, between the different modalities, visually presented words led to the best episodic memory performance (59%), followed by auditory words (50%) and, finally, by pictures (41%); for semantic memory a slight tendency for the opposite was found (visual, 11%; auditory, 14%; pictorial, 20%). Thus on average, and most strongly for the episodically remembered events, an interaction was observed between sequence of presentation and modality of presentation: visual words, which are the first items presented during the experiment, scored highest, while pictures scored lowest. While this could be accounted for by a verbal overshadowing effect (Schooler and Engstler-Schooler, 1990), another interpretation is that pictorial material, although usually better retrieved than verbal material, leaves less space for own active associations and is thus weaker encoded episodically. This is in line with findings of better memory performance for words embedded in a highly imaginable content than for words alone (Vogel *et al.*, 1987). With double presentation the average number of both remembered and known items increased and

the number of forgotten items dropped (from 35 to 12%), as expected. Interestingly, the increase was far higher for 'knowing' (from 15 to 30%) than for 'remembering' (from 50 to 55%), which is in agreement with the general notion of episodic memory (i.e. Tulving, 1972, 1993). In conclusion, the results of the R/K paradigm reproduce previous findings about memory performance and demonstrate that subjects were actively perceiving the items presented during the experiment, showing both episodic and semantic encoding. Further, the total number of recollected words (both episodically and semantically) was 65%. This is evidence that the presented words had been deeply rather than shallowly encoded (Craik and Lockhard, 1972), i.e. subjects had paid attention to the words' meaning rather than to their sound or graphemic properties.

The reliability of the R/K test and the corresponding imagery scores (e.g. Table 1a) was confirmed by the fact that separate analysis of the EEG of subjects with mental imagery and without mental imagery revealed significant differences. In particular, EEG amplitude above the occipital cortex was significantly higher in subjects who had visualized the items compared to subjects who had not; additionally, this difference turned out to be reproducible across modalities (von Stein *et al.*, 1995b).

Discussion

We have determined EEG amplitude and coherence between signals from 19 electrodes loosely spread over the whole scalp (10/20 system). The question was whether any significant change in amplitude or coherence was induced when subjects were presented with stimuli as compared to a resting condition. The stimuli were objects encountered in daily life, presented in three different modes: auditory and visual words, and pictures. We were interested in common electrophysiological patterns that were present during semantic activation independent of modality. We found a significant increase of coherent activity between several pairs of electrodes during perception with respect to the resting condition. Among the different electrode-pairs that were activated coherently, only one

pair was consistently engaged during all three modes of stimulus presentation: the electrode-pair temporal-parietal (T5–P3, T6–P4 respectively). The frequency range of this coherent activity was 13–18 Hz. In other frequency ranges we did not find common patterns of enhanced coherence. No changes in EEG amplitude were common to all three modes of presentation. Thus, as a common electrophysiological pattern for modality-independent processing of objects, we found an increased coherence between signals over temporal and over parietal cortex.

These findings suggest that supramodal processing might be correlated with an enhanced coherence of 13–18 Hz activity between temporal and parietal electrodes. In a recent investigation in our laboratory, a similar study was performed with the aim of differentiating between coherence maps related to concrete and to abstract concepts (Weiss and Rappelsberger, 1996; S. Weiss *et al.*, in preparation). Words evoking different types of concepts were presented to 15 subjects either auditorily or visually. Apart from interesting differences between concrete and abstract concepts, coherence increased between T5 and P3, and T6 and P4 in the 13–18 Hz range, during both auditory and visual presentation of words designating concrete objects. Thus, for the same stimulus conditions, coherence increased between exactly the same electrodes and in the same frequency range as in the present study. Thus the study reproduced with high similarity the results of the present study. With this support we may conclude that modality-independent processing of objects is indeed accompanied by an increased coherence between temporal and parietal electrodes.

Relationship Between Scalp EEG and Cortical Processing

How is this EEG result related to cortical processing? The EEG measured at a site on the scalp consists of the summed electrical field potentials from cortical neurons in a certain volume of tissue under the electrode. Cortical field potentials are generated by postsynaptic dendritic currents. They contribute to the scalp potential only if the dendrites are arranged perpendicularly to the scalp; effective contributions come mostly from the synchronized components of cortical activity (Cooper *et al.*, 1965; Elul, 1972; Nunez, 1995). A dipolar field is produced by synchronous input, which can be singled out by averaging methods (evoked potential). It is a far-reaching field that influences the potential landscape over large parts of the scalp. In addition, there is a continuous change in cooperativity within the cortical network even without external stimulation (intrinsic potentials) (Lopes da Silva, 1991; Bullock, 1995). This changing pattern of synchronization and desynchronization within different neuronal groups of the network generates the macroscopic potentials of the ongoing EEG (Elul, 1972). Since intrinsic potentials stem from the network interactions they generate low-amplitude fields which are effective only in close proximity, thus they influence the potentials mostly at individual scalp electrodes. Changes in the degree of synchronization of this intrinsic activity are reflected in changes in EEG amplitude at the scalp. Our study of EEG spectral parameters aimed at detecting stimulus-induced changes of this intrinsic activity.

While EEG amplitude predominantly reflects the amount of underlying synchronized activity, the degree of interaction between two signals can be measured by *coherence*. Coherence is a statistical measure: the value of coherence depends on the amount of repeated correlations between events in the frequency domain. The phase relationship between the two signals is irrelevant; however, it must be stable. Since the signal at each electrode site reflects the network activity under the

electrode, coherence should measure interactions between two neuronal populations; while cortico-cortical correlations occupy only a minute part of the power of the EEG signal at each site, the statistical nature of coherence helps to unravel them from the noise if they repeat consistently.

In the light of these considerations our finding of increased coherence between temporal and parietal electrodes provides evidence that supramodal semantic processing induces an increased interaction between neuronal populations of temporal and of parietal cortex. How precise is this localization? The spatial resolution of EEG has been estimated to be ~5 cm (Nunez, 1995; Srinivasan *et al.*, 1998). Thus the signal at one electrode stems from an area of ~10 cm² of cortical tissue. Since this is about the size of a cortical area this means that the signals measured at the two electrodes in question stem from gross anatomical areas like temporal cortex (T5) and parietal cortex (P3). It is important to note that besides indicating the degree of cortico-cortical interactions, an increase in coherence might stem from two other situations. The second possibility is that the two sites receive common input from a third area (e.g. the thalamus), a situation which cannot be differentiated from true cortico-cortical interactions by scalp recordings alone. We are, however, only interested whether a common dynamics occurs at two sites at all. A third, more trivial possibility is that inter-electrode coherence is just due to activity volume-conducted to the two electrodes. Given the spatial resolution of 5 cm, volume conduction along the 7 cm interelectrode distance should be a minor contribution. Nevertheless, to distinguish between volume-conducted coherence and physiological coherence, it is helpful to consider additionally the behavior of EEG *amplitude* in the respective electrodes: a volume-conducted signal will lead to an increased amplitude at both electrode sites. Since in our case no common increase in amplitude was seen and in some cases amplitudes even decreased, volume conduction is less likely and our results can be interpreted as true physiological coupling between the two cortical sites. It must, further, be mentioned that while under certain conditions EEG results allow us to draw conclusions about increases or decreases of correlated activity in the cortical network, we cannot exclude the possibility that single neurons also react specifically in the investigated process. In conclusion, the result of this study was that supramodal processing was accompanied by an enhanced coherence between signals at T5/T6 and P3/P4, which is in agreement with an increase of coherent activity between neuronal populations of temporal cortex and parietal cortex in a frequency range of 13–18 Hz.

Synchronized Activity as Basis for Binding of Objects

A growing body of evidence shows that correlated activity between similar neurons plays a role in cortical processing. The first findings (Eckhorn *et al.*, 1988; Gray *et al.*, 1989) in cat area 17 have shown that, for example, neurons of similar preferred orientations tend to correlate their firing when activated with a coherently moving stimulus. Since then the functional significance of synchronization has been shown in a number of studies, making it a possible mechanism for binding of features in the visual domain (e.g. Eckhorn, 1994; König and Engel, 1995). Synchronization has been found locally, but also between neurons from different visual areas (Eckhorn *et al.*, 1988; Frien *et al.*, 1994; Bressler, 1996) and across the two visual hemispheres (Engel *et al.*, 1991), and recently the relevance of coherent activity has also been found in other cortical areas such as the motor cortex (Murthy and Fetz, 1992) and the auditory cortex

(deCharms and Merzenich, 1996). Few studies, however, have shown correlations between neurons from different modality-specific areas. If coherent activity between the different feature representations of an object is a possible mechanism to guarantee their binding into a unified percept (for review, see König and Engel, 1995), then coherent activity should also be observed between neuronal populations from areas serving different submodalities or modalities. Such coherent activity between different modality-specific areas during object perception, however, has not yet been shown. The few reports on such inter-areal correlations have been found during sensory-motor integration (Roelfsema *et al.*, 1997). Although our results clearly take place on a crude spatial scale compared to intracortical recordings, they nevertheless are first evidence that object perception indeed seems to induce coherent activity between functionally different cortical areas. Coherent activity between temporal and parietal cortex during supramodal concept processing may demonstrate the existence of widely distributed neuronal ensembles representing multimodal entities.

The Role of Temporal and Parietal Cortex in Semantic Processing

The localizatory aspect of our main result, that EEG coherence increases over parieto-temporal cortex, agrees well with the assignment of symbolic representation to this area described in the early literature. The area of posterior parietal cortex, especially left angular gyrus, is known as a supramodal, integrating area (e.g. Luria, 1973). Lesions in that region lead to failure in cross-modal matching. Patients who are able to identify an object among others in one modality are not able to recognize it in another modality (Butters and Brody, 1968). Thus, it seems that this area is necessary to integrate different modalities to form a concept. Patients with parietal agnosias suffer from the same deficit in forming higher integrative concepts (Kolb and Whishaw, 1985, p. 384). More recent clinical studies have confirmed the importance of left parietal cortex in semantic processing. Semantic processing on the single word level breaks down with parietal lesions (Hart and Gordon, 1990). Pretrial DC potentials at parietal sites are predictors for semantic facilitation (Stamm *et al.*, 1987). Temporal cortex, on the other hand, is part of the ventral stream of visual processing and a higher-order visual association cortex. It plays a crucial role in processing of complex visual form and particularly in object recognition (e.g. Desimone *et al.*, 1984). The posterior part of temporal cortex is thought to be more involved in visual perception, whereas anterior temporal cortex is more related to complex visual memories (Iwai and Mishkin, 1968). Temporal cortex has also been shown to be involved in visual imagery (e.g. Roland and Gulyas, 1994). An increase of correlated activity between both structures – temporal cortex and parietal cortex – during perception of objects as suggested by our results might therefore indicate an interaction between visual representations (temporal cortex) and higher-order representations (parietal cortex) for multimodal semantic integration in humans. Regarding connections between temporal and parietal cortex, recent findings in macaque monkeys have shown that area TEO, in rough correspondence with the area covered by our electrode T5, has extensive connections to parietal cortex (Webster *et al.*, 1994). Anatomical studies (Mesulam, 1990) have demonstrated that parietal cortex is a highly connected, supramodal center in the cortex, connected with different sensory cortices, association cortices, subcortical structures, etc. The high degree of

connectivity provided by this cortical area supports the proposed function of multimodal semantic integration. The interactions between temporal and parietal cortex are also interesting with respect to the integration of information carried by the dorsal and the ventral stream. It has often been proposed that the two have to be integrated at various levels (DeYoe and van Essen, 1988). We here provide evidence that interactions between temporal and parietal cortex might indeed exist during higher-level semantic processing of objects.

Interestingly, we did not find evidence for *local* activations showing overlap across conditions, i.e. we did not find overlap in amplitude-changes. This result would explain seemingly contradictory results regarding visuo-auditory integration that were found by Posner (see Posner *et al.*, 1988; Peterson *et al.*, 1988). In these positron emission tomographic studies, aimed at similar supramodal processes as our study, *no* overlapping pattern of activity for auditory and visual processing of words was found. This difference is interesting, shedding some light on the different aspects of cortical processing gathered with different methods. We, too, did not find overlapping changes in amplitude; overlapping activity appeared only in the *interactions* between two sites, i.e. in coherence. An increase in coherence without an increase in amplitude might be interpreted as increased phase-locking between the neuronal activity of two cortical sites without an increase in the number of active neurons. Thus, what was commonly induced during auditory processing and visual processing of words seems not to be a global activation of one specific area but rather a phase-locking between neurons of different cortical areas, i.e. members of a distributed ensemble.

Besides an overlapping activation for presentations denoting objects, we found a second overlapping activation for all presentations dealing with entities that are transferable between modalities: pronounceable non-sense words, visual and auditory, induced a similar increase of coherence between temporal and parietal electrodes but unilateral at the *right* hemisphere. This suggests that only left temporo-parietal synchronization is specific for processing of semantics. This finding is in agreement with a considerable amount of literature describing a left hemispheric dominance for processing of language and semantics (for a review on hemispheric specialization, see e.g. Kimura, 1973). Right temporo-parietal coherence in our data appears less specifically whenever supramodal integration takes place. The only constraint seems that the items exist in more modalities and can be transferred between them; non-pronounceable non-sense words (letter strings) did not produce this activity. This activation might be tentatively interpreted as a phonological-graphological integrative process which could be called *multimodal Gestalt* representation. If we interpret right temporo-parietal activation in this sense, this may also explain why pictures of objects, with their pronounced Gestalt aspect, predominantly activated right temporo-parietal cortex. Also, from clinical experience, agnosias for pictures are more related to lesions in right parietal cortex. The site of our activation – right temporo-parietal – fits well with the known role of right parietal cortex in processing spatiotemporal patterns. Perceptual integration of geometric patterns is disrupted in patients with right parietal lesions (Warrington and Taylor, 1973). Prosodic information as well as musical thinking and processing of other non-verbal entities have also been related to the right hemisphere (Kimura, 1973). A right hemisphere lateralization has been found in discrimination of non-verbal environmental sounds as opposed to semantically related sound sources

(Schnider *et al.*, 1994). Sensory feature integration as proposed by our results is therefore a probable task for right parietal cortex. The discussion of hemispheric lateralization of coherence patterns, however, has to be viewed with due caution since we did not test our results in this respect. Our main statement thus is that multimodal processing is accompanied by an enhanced coherence between signals from temporal cortex and parietal cortex.

Multimodal Binding or Attentional Mechanisms?

Because of its high connectivity, posterior parietal cortex is considered as part of the attentional system (Posner *et al.*, 1988; Mesulam, 1990). An interesting alternative idea to the binding proposal is to interpret the activity of this area during processing of objects as a process of *selective attention*. It might be the searchlight of attention (Treisman, 1988) binding together the different aspects of an object. Posterior parietal cortex might be where the searchlight is located, and its light might be a synchronization of 13–18 Hz. Indeed, parietal lobe, especially *right* parietal lobe, has been found to play a fundamental role in attention as evident in the neglect syndrome (e.g. Heilman and Watson, 1977). Further, attention-related 10–20 Hz oscillations have been found in cats (Chatila *et al.*, 1992). Therefore, the observed increase of coherent activity in the 13–18 Hz range between parietal and temporal electrodes might be interpreted as a parietally driven attentional process subserving binding into semantical entities. This interpretation would not contradict the previous solution of binding by synchrony (von der Malsburg and Schneider, 1986; Singer 1993), where oscillatory activity is thought to guarantee the coupling of widespread cortical ensembles and thus ‘bind together’ the distributed representations belonging to an entity. An interesting patient described by Friedman-Hill *et al.* (1995) has problems attributing color and shape to one object. While correctly describing all single features present on a screen, he miscombines them among the objects. This means he has problems integrating or ‘binding’ different features into one entity. The site of his lesion is parietal cortex, as in our experiment. Thus the result of our experiment seems to combine both types of concepts. It indicates that parietal cortex plays a role in binding features into entities, and, additionally, that synchronous activity in the 13–18 Hz range plays a role in this process. Further, there is evidence that what is referred to as attention might be activation of backward connections from higher cortical areas possibly due to internally emerging synchronization (Cauller, 1996). Our results favor this idea. Top-down (semantically) driven synchronization might bind the different modality inputs into one semantical entity. The interplay between dynamics in different frequencies such as alpha, beta1 and – probably in a shorter time window – gamma might play a crucial role in this process.

Synchronization in the Beta1 Range (13–18 Hz)

A last question remains: why was the synchronization frequency the beta 1 (13–18 Hz) and not the gamma (20–100 Hz) range as in visual cortex?

In the ‘binding by synchrony’ discussion the focus is mainly on gamma oscillations. The reason this specific frequency stands out may lie in the spatial averaging obtained by the type of electrode used to record it. Electrodes perceiving signals from larger populations might perceive different ensembles with different frequencies. According to our EEG results, several further, lower-frequency ranges play roles in cortical processing (Petsche *et al.*, 1992, Rappelsberger and Petsche, 1988; von

Stein *et al.*, 1994b). Reports exist on specific activity in the delta range (0.5–4 Hz: Kaplan, 1995), theta range (4–8 Hz: Machleidt *et al.*, 1989; Sarnthein *et al.*, 1998), and several frequencies in the beta range (Rappelsberger *et al.*, 1991; Petsche *et al.*, 1993; von Stein *et al.*, 1993; von Steine and Petsche, 1995b). Also alpha (8–12 Hz) activity has been shown to be specific for cognitive processes, which contradicts the assignment of alpha as a mere resting rhythm (von Stein *et al.*, 1994a; von Stein and Petsche, 1995b; Petsche *et al.*, 1997). Among the different frequency ranges, the beta1 range (13–18 Hz) in particular has repeatedly been found during higher-level cortical processing. For example, Rappelsberger and Petsche (1988) found an increase of beta1-coherence during a spatial imagination task; Weiss and Rappelsberger (1996) found beta1 frequencies to be the most responsible for basic semantic processing. Flexer *et al.* (1995) used artificial networks to classify EEG maps and found the best results for classifying different spatial tasks in the beta1 range. Stimulus-induced oscillations in the 13–18 Hz range have also been reported in intracortical recordings in cat visual cortex (Bringuier 1992).

The reason for different frequency ranges in cortico-cortical synchronization might be different dynamics of interaction. Several parameters influence the dynamics of activation-spreading in a cortical network, among them the matrix of connectivity, the length of connections, intracellular parameters such as refractory period, EPSP kinetics, asynchronous gain, etc., and more. Since the *matrix of connectivity* depends on learning, similar stored representations might have similar connectivity matrices and therefore similar synchronization patterns such as the frequency of synchronization. The length of connections, i.e. the *size of included networks*, may be similar for similar kinds of representations; representations involving networks with the same spatial extension, e.g. networks of the same sensory region, may lead to similar frequencies, etc. The most likely explanation why our observed frequency lies in a lower range than visual cortex synchronization is the latter one, namely the size of the representing ensembles. It has been shown theoretically as well as empirically (Eckhorn, 1994) that larger ensembles produce lower synchronization frequencies than smaller ensembles. Semantic ensembles, which are multimodal, should be more widely extended than the ensembles between columns in visual cortex. Therefore we propose that the low frequency range of our synchronization is a manifestation of cooperative activity in a large neuronal ensemble representing heteromodal entities.

Conclusions

We found coherent activity between temporal and parietal EEG electrodes during perception of objects, independent of whether the objects were presented as written words, as spoken words or as pictures. The frequency range was 13–18 Hz; no common activity was found in other frequency ranges or in amplitude. Since the findings were obtained using EEG scalp signals, this is evidence that populations of neurons in temporal cortex interact with populations of neurons in parietal cortex during supramodal processing of objects. This temporo-parietal synchronization tended to be lateralized to the left hemisphere for semantic integration, to the right hemisphere for non-semantic integration; at both hemispheres synchronization occurred with the same frequency (13–18 Hz), and furthermore the hemispheres were coupled with this same frequency (interhemispheric coherence). Our findings are evidence for widely distributed neuronal cell ensembles for semantic and

Gestalt processing, within and between the hemispheres, that are coherently active in the 13–18 Hz range. They might, further, indicate that binding of larger distributed, multimodal neuronal ensembles is mediated by coherent activity among neurons as proposed for the visual system, but in lower frequency ranges.

Notes

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