SHORT COMMUNICATION
Semantic memory retrieval: cortical couplings in object recognition in the N400 window

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Abstract

To characterize the regional changes in neuronal couplings and information transfer related to semantic aspects of object recognition in humans we used partial-directed EEG-coherence analysis (PDC). We examined the differences of processing recognizable and unrecognizable pictures as reflected by changes in cortical networks within the time-window of a determined event-related potential (ERP) component, namely the N400. Fourteen participants performed an image recognition task, while sequentially confronted with pictures of recognizable and unrecognizable objects. The time-window of N400 as indicative of object semantics was defined from the ERP. Differences of PDC in the beta-band between these tasks were represented topographically as patterns of electrical couplings, possibly indicating changing degrees of functional cooperation between brain areas. Successful memory retrieval of picture meaning appears to be supported by networks comprising left temporal and parietal regions and bilateral frontal brain areas.

Introduction

The processing of objects comprises at least three main subprocesses: (1) extraction of simple visual features from the retinal input; (2) integration of those simple features into a distinct visual shape; and (3) semantic memory retrieval in response to the established visual input. Support for this hierarchical account emerges from human lesion data (Sheridan & Humphreys, 1993), functional magnetic resonance imaging (fMRI) studies (Kanwisher *et al.*, 1997) and computational models (Riesenhuber & Poggio, 2002).

Confining our interest to the semantic aspects of object recognition, a distinct event-related potential (ERP) seems to be indicative of the timing of semantic processing. In fact, the so-called 'N400' component − a negative potential deflection peaking between 400 and 500 ms after stimulus onset − is sensitive to the semantic content (or meaning) of stimuli.

The N400 amplitude varies systematically with semantic processing demands, being reduced for meaningful and increased for meaningless stimuli. This sensitivity of the N400 to semantics is found not only for written or spoken words but also for line-drawings, photographs or faces − see Kutas & Federmeier (2000) for a review. At least two distinct semantic processes presumably appear within the N400 time-window. First, in the 'contextual integration' view reduced N400 amplitudes indicate the ease of integration of the eliciting item into the local context (e.g. a sentence context). Second, according to semantic relatedness studies and stimulus frequency/repetition effects, this

negativity is equally sensitive to the difficulty of semantic memory retrieval, reflecting 'long-term memory access' (Federmeier & Kutas, 1999; Kutas & Federmeier, 2000).

In search of neural structures showing this electrophysiological index of semantic processing, intracranial depth recordings in human patients identified mainly temporal brain areas as possible locations of neural generators of the scalp N400.

Additional areas identified outside the temporal lobes include the posterior fusiform gyrus, parietal and orbitofrontal cortex (Johnson & Hamm, 2000). The fact that several brain areas produce N400-like responses meets the general assumption that a distributed cortical network participates in the generation of the N400 and therefore in semantic processing (Kutas & Federmeier, 2000). For this reason it seems justified and necessary to apply measures that directly characterize extended dynamic networks. Standard ERP techniques and methods detecting oscillatory amplitude changes are restricted to changes of local voltage-fields and, consequently, do not provide information about dependencies between separate brain regions (Varela *et al.*, 2001).

The applied method, partial-directed coherence (PDC), is advantageous over other coupling measures (such as classical coherence or phase locking statistics) as it informs us whether and how two positions under study are functionally connected, rather than merely describing mutual synchronicity (Baccala & Sameshima, 2001). Common disturbing influences or sources (recorded at any third position) are not taken into account, so that due to this 'partial' coherence approach solely direct dependencies between two positions are characterized (Kaminski *et al.*, 1997; Sameshima & Baccala, 1999).

The attribute 'partial' in PDC refers to the fact that common sources are partitioned or separated and so they do not enter the determination of PDC values. The PDC values are 'directed' insofar as the obtained relationships are characterized by their direction of information transfer.

In the present study, we investigated PDCs in the N400 time-window of the EEG to characterize the interconnections of cortical networks during semantic processing of pictorial stimuli. We selected the beta-frequency band upon an *a priori* basis, resting on several studies focused on semantic and categorical processing that revealed the beta-frequency band to be predominantly reflective of more experience-dependent/cognitive-related processes and less on sensory-based ones (von Stein *et al.*, 1994, 1999; Schack & Krause, 1995; Krause *et al.*, 1998; Bhattacharya & Petsche, 2002).

In contrast to a previous study reporting alpha band coherence changes associated with object recognition (Mima *et al.*, 2001), we selected our time-window solely on the appearance of the significant meaning effect and contrasted both semantically distinct conditions directly to obtain differential coupling patterns.

The particular impetus for this investigation was to shed more light on the differential involvement of memory functions in response to semantically distinct visual objects.

Materials and methods

Subjects and stimulus material

Fourteen female volunteers, right-handed students (19–27 years old, mean 23.7 years), gave informed consent to participate in this study, for which they were paid afterwards. All participants were monolingual speakers of German, had normal or corrected to normal vision and no history of psychiatric disorders. The participants performed a picture recognition task. The stimuli were either grey-scale shaded images, selected from a version of Snodgrass and Vanderwart's object set (Rossion & Pourtois, 2001), representing objects of daily life such as apple, cup or chair (i.e. recognizable or meaningful objects, $n = 48$) or grey-scale shaded images of unrecognizable objects (i.e. meaningless objects, $n = 48$). The images of the unrecognizable objects were designed such that they physically matched the meaningful images in every possible way (e.g. complexity, part-structure, size) except for familiarity − see Kanwisher *et al.* (1997). That is, meaningless objects do not match any particular known object and therefore lack any specific reference.

Experimental procedure

Subjects sat in front of a 17″ LCD-screen at a distance of about 1.3 m and were confronted sequentially with the stimulus material (picture size: 5.2×7.4 cm). The temporal sequence of events within the trials was as follows. Preceding every item, a fixation cross appeared on the screen for 2.5–2.7 s (randomly selected). Within the fixation cross period, 1.5 s before the appearance of each item a warning tone was presented. The presentation of each item lasted for 2 s and was followed by a delay interval lasting for 1.65 s (± 150 ms). After this delay, a question mark appeared that prompted the subjects to judge using a response button box, whether the presented stimulus was meaningful or not. During the 1.5-s response interval subjects pressed the left button of the response box with the right index finger if they judged the stimulus as recognizable and the right button with the right middle finger if not. With the end of the response interval the fixation cross disappeared and the screen remained blank for 3 s until the next trial started. In general, this design complies with a delayed response paradigm.

EEG data acquisition and analysis

The EEG was recorded from 29 Ag–AgCl electrodes (Fig. 1) positioned on the scalp (10/20 system, unipolar leads, nose tip as reference, vertex as ground position, impedance <6 kΩ). The band pass of the amplifier was set between 0.3 and 50 Hz and included the 50 Hz notch-filter. The electrooculogram was recorded bipolarly from diagonally mounted electrodes at the right eye. EEG was recorded with 250 Hz sampling rate. The beginning of each stimulus presentation was marked by a trigger in the EEG file. Individual EEG recordings were scanned visually for artefacts. Only correctly answered trials, free of artefacts were included in the subsequent analysis. Because of excessive artefact contamination, data sets of two subjects were discarded from subsequent analysis. In total, about 65% of the trials per condition entered the subsequent data analysis.

ERP data analysis

The EEG signals were re-referenced offline to the averaged signals of both mastoid electrodes. ERP epochs were averaged separately for each condition from stimulus onset to 1000 ms post-stimulus onset using a 200-ms prestimulus baseline. Grand averages were smoothed with a 7 Hz low-pass filter for purpose of convenient illustration. For statistical analysis, electrodes were grouped into four regions of interest: left-anterior (AF3, F7, F3, FC1, FC5), right-anterior (AF4, F8, F4, FC2, FC6), left-posterior (CP5, CP1, P7, P3, PO3) and right-posterior (CP6, CP2, P8, P4, PO4).

According to visual inspection of ERP waveforms the time-window 400–550 ms was representative for the N400 effect and, subsequently, was evaluated in repeated-measures ANOVA. This analysis included Meaning with two levels (meaningful vs. meaningless), Hemisphere with two levels (left vs. right) and Region (anterior vs. posterior) as within-subject factors. Because of our focus, only the factor Meaning and its interactions are reported. Significant (i.e. $P < 0.05$) main effects and interactions were successively resolved by topographical factors. Significant interactions are reported only when *post-hoc* comparisons reached the level of significance.

PDC analysis

PDC analysis was applied to non-averaged data within the N400 time-window (400–550 ms post-stimulus, as determined by the ERP analysis). In mathematical terms, the PDC characterizes the relationship between multivariate time series and can be derived from the parameters of a multi-variate autoregressive (MVAR) model (Baccala & Sameshima, 2001). The MVAR model is a mathematical modelling of the EEG time series, as described by Eq. (1).

$$Y_t = \sum_{k=1}^{p} A_k Y_{t-k} + X_t \qquad (1)$$

The vector Y_t contains the samples of all M channels at the time instance t. The matrices A_k indicate the MVAR parameters up to an order p, the off-diagonal elements represent the cross-terms between the channels. The multivariate process X_t is the so-called innovation process and is assumed to be a zero-mean white noise process with a variance-covariance matrix Σ. The name 'innovation process' reflects the fact that the observed process Y_t would be zero if X_t is zero and, accordingly, X_t can be considered as the driving force.

In this work, the Nuttall–Strand method was used to estimate the MVAR parameters, while the model order p was set to 15 in order to guarantee the resolution of any number of frequency components (10).
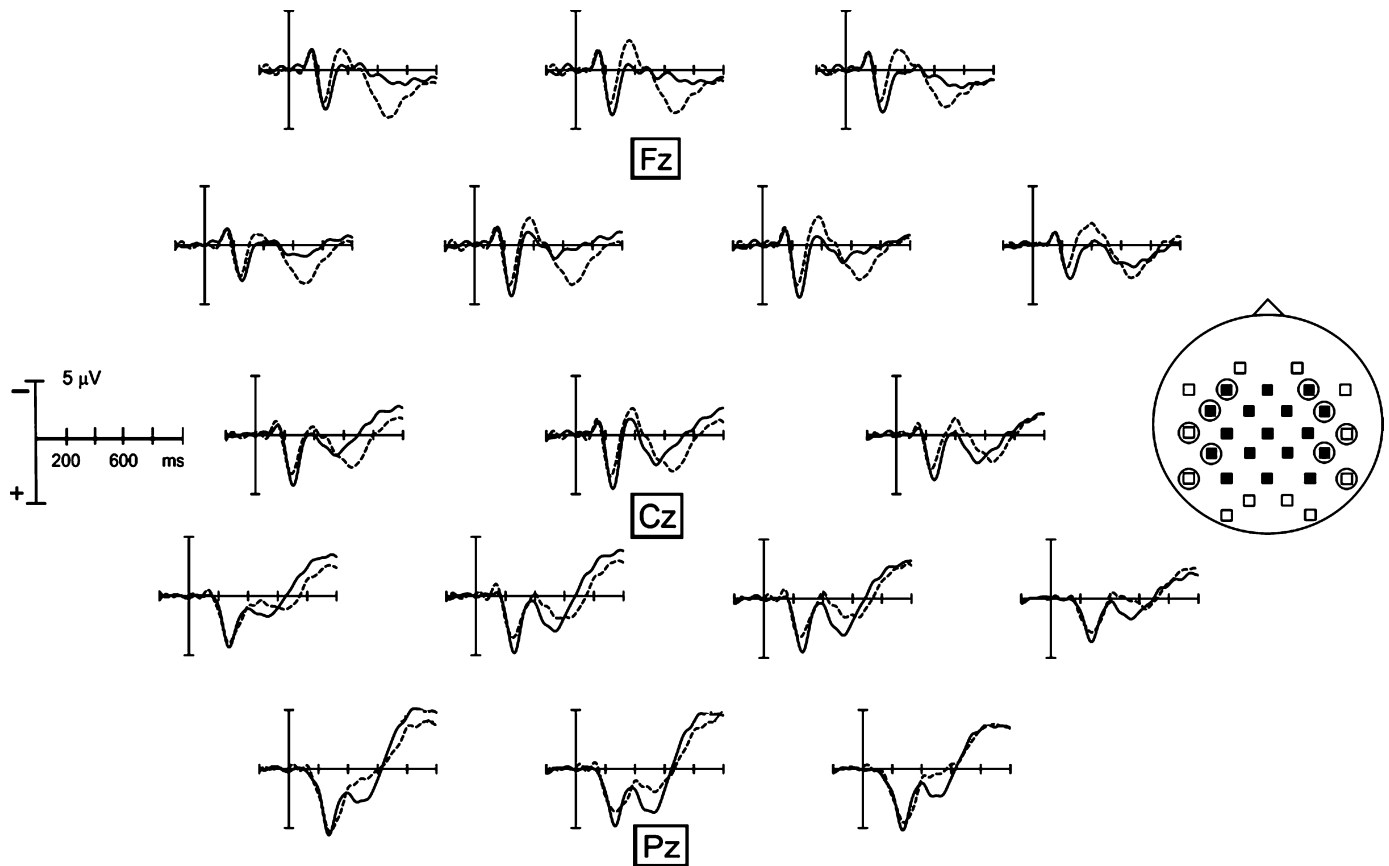
FIG. 1. ERP results for meaningful objects (continuous line) and meaningless objects (dashed line), each condition averaged separately over all subjects. The N400 effect appears in the time-window between 400 and 550 ms post-stimulus onset with a posterior distribution lateralized to the left hemisphere. The schematic illustration on the right indicates the 29-channel placement. All black-filled symbols represent those positions for which ERP results are plotted, while circles indicate the subgroup of 10 positions used for calculating PDC values.

The MVAR parameters are transformed into the frequency domain, which yields an M × M matrix $\bar{A}(f)$ for each frequency f. Then, the PDC can be obtained according to Eq. (2):

$$PDC_{mn}(f) = \frac{\bar{A}_{mn}(f)}{\sqrt{\bar{A}_{Cn}^{H}(f)\bar{A}_{Cn}(f)}} \qquad (2)$$

where $\bar{A}_{mn}(f)$ is the m,n-th element and $\bar{A}_{Cn}(f)$ is the n-th column of $\bar{A}(f)$. These PDC values provide information about the information flow for each electrode pair and each frequency (spectral frequency resolution: 1 Hz). The implementation of all computational steps is available online from the open source project BIOSIG under *http:// biosig.sf.net* (Schlögl, 2003).

To determine which changes were consistent across subjects, we calculated the difference of the PDC values between the meaningful and meaningless condition for each subject. The computation of PDC values was performed separately for each spectral line. Following this, a statistical test (*t*-test) was performed to determine whether the PDC differences of all subjects were significantly (i.e. $P < 0.05$) larger (or smaller) than zero. This indicates whether a change in PDC was consistent across subjects. Subsequently, statistical results of adjacent spectral lines were summarized for the sake of data reduction. In this way parameters for the beta-frequency band (13–30 Hz) were obtained. The beta band has been chosen on an *a priori* basis (see Introduction). Statistically significant increases and decreases of PDC values for the 13–30 Hz frequency band are shown in Fig. 2.

Results

ERPs

Whereas on the behavioural level the error rates remained very low (less than 2%), lacking any significant difference between conditions, the ERP results revealed a meaning effect. The ERP waveforms (see Fig. 1) indicate more negative-going potentials to meaningless as compared with meaningful objects in a time-window between about 400 and 550 ms after stimulus onset. This time-window and polarity are consistent with the N400 effect as described in the literature. The statistical analysis of variance in this time-window revealed a reliable three-way interaction Hemisphere × Region × Meaning ($F_{1,11} = 4.16$, $P < 0.05$). This three-way interaction was followed up by investigating the two-way interaction Region × Meaning separately for each hemisphere. While the investigation of the left hemisphere revealed a significant Region–Meaning interaction ($F_{1,11} = 6.60$, $P < 0.026$), this interaction failed to reach significance at the right hemisphere ($F_{1,11} = 3.44$, n.s.). Looking at the main effect Meaning at left anterior and posterior sites a significant effect appeared only at the left posterior position (posterior: $F_{1,11} = 6.19$, $P < 0.03$; anterior: $F_{1,11} = 0.13$, n.s.). In short, these results indicate that the Meaning effect as reflected by the N400 has a posterior distribution lateralized to the left hemisphere.

Note that the apparent N300 effect within the time-window between 300 and 400 ms and its fronto-central distribution (anterior: $F_{1,11} = 57.79$, $P < 0.0001$; posterior: $F_{1,11} = 2.91$, n.s.) is not the focus of our current concern of affair.
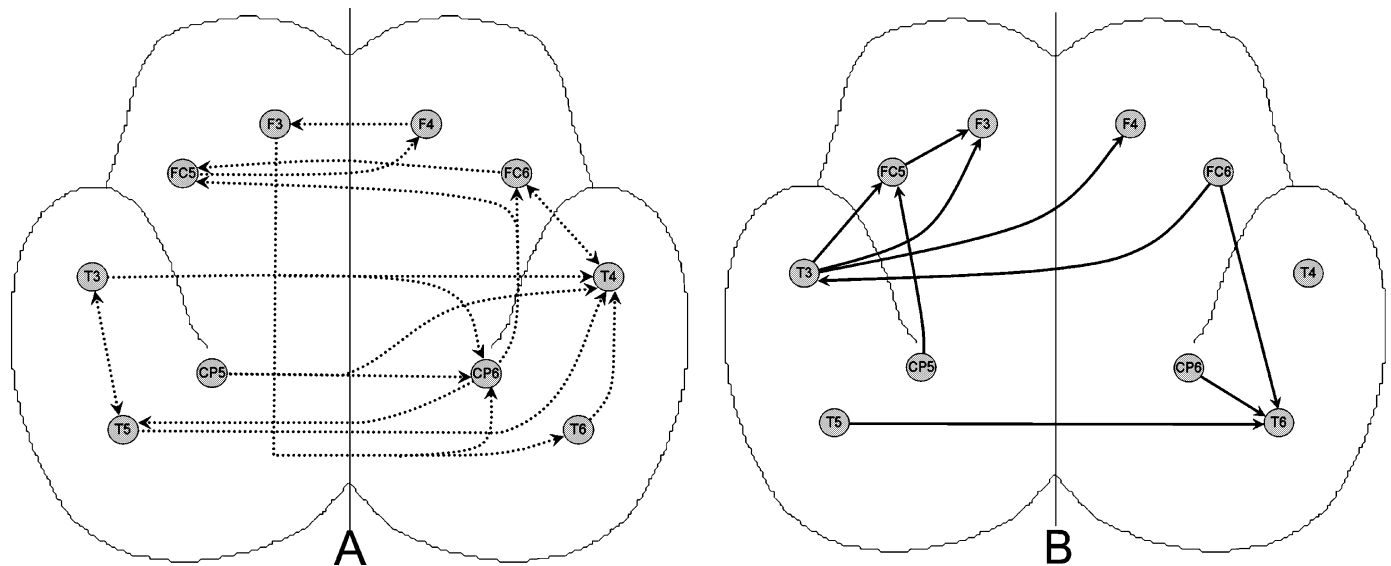
FIG. 2. (A) Significant coherence increases for meaningless (as compared with meaningful) pictures within the time-window of the N400 (meaningless > meaningful). (B) Coherence increases for recognizable objects compared with unrecognizable objects (meaningful > meaningless). Arrows indicate the direction of information transfer. For all: significance level $P < 0.05$.

PDC

The calculation of coherence changes and information transfer between the selected sites revealed quantitative and topographical differences between meaningful and meaningless objects for the investigated beta-frequency band (13–30 Hz) within the N400 time-window.

The number of coherence increases for the meaningless condition surpasses that for the meaningful condition. In particular, during processing of unrecognizable objects (relative to meaningful objects) the network of coherence increases converges towards temporal (T4) and parietal (CP6) positions of the right hemisphere (Fig. 2A). While the temporal position almost exclusively receives stronger information input (Fig. 2A), the parietal site is equally engaged in input and output connections. Accordingly, a greater number of interhemispheric coherence increases during processing of unrecognizable objects are observed, whereas temporal and parietal electrodes of the right hemisphere serve as prominent converging sites.

On the other hand, larger PDC appeared in intra- than interhemispheric couplings during the processing of meaningful with respect to meaningless objects (Fig. 2B). The most prominent source of higher information output turned out to be the left temporal position T3, significantly linked to frontal positions of both hemispheres. For this case, the intrahemispheric network is particularly dense at the left hemisphere involving temporal, parietal and bilateral frontal positions.

Considering both conditions together, anterior temporal positions contribute most frequently to coherence changes, whereas the actual networks of increases and decreases involve different connections for each temporal site. Whereas left temporally main emphasis is put on increases for meaningful object processing, the homologue right temporal position provides this centre for meaningless object processing.

Discussion

Unrecognizable or meaningless objects, i.e. stimuli lacking any specific significance for the individual, elicited an increased negative-going ERP wave between 400 and 550 ms. This N400 effect may reflect the unease of processing meaningless stimuli, necessitating more processing resources (Federmeier & Kutas, 1999; Kutas & Federmeier, 2000). The time-window and scalp topography of our N400 effect are consistent with earlier reports of N400 to pictures (Barrett & Rugg, 1990; Hamm *et al.*, 2002; Schendan & Kutas, 2003). The differences in cortical coupling changes observed in the N400 time-range point in the same direction as the N400 ERP effect, insofar as the number of coherence increases for meaningless objects surpasses that for meaningful objects. This observation reinforces a recent study of auditory word comprehension applying the same coherence measure to the N400 time-window (Supp *et al.*, 2004).

For the general functional significance of the obtained PDC changes it has to be noted that the topographical patterns of the relationships between electrode pairs presumably rest upon synchronization of underlying neuronal populations. Therefore, differential coupling patterns in the form of coherence increases or decreases may reflect relatively increased or decreased functional cooperations between the respective brain areas. Coming to the specific topography of the positions most frequently involved in the reported coherence changes, they show to be in line with neuroimaging (Vandenberghe *et al.*, 1996; Mummery *et al.*, 1999) and source localization studies – see references in Johnson & Hamm (2000) – using N400 paradigms. These studies suggest distributed cortical networks encompassing temporal, parietal and frontal brain regions as crucial parts of a cortical network for semantics. In detail, the finding of a crucial role of the left anterior temporal position (including its frontal network of coupling increases) fits well to findings from functional imaging and clinical neuropsychological work indicating the left anterior temporal cortex to play an important role in retrieving object-related semantic information (Mummery *et al.*, 1999). Furthermore, the prominent right temporal position for unrecognizable object processing is in line with brain activation studies (Grill-Spector, 2003; Rossion *et al.*, 2003), demonstrating larger activations for unfamiliar than familiar stimuli within the right temporal lobe. Thus, unfamiliarity of objects seems to be one factor leading to differential activation patterns between the left and right hemispheres with a

particular focus in temporal areas. On the whole, the topography of the positions mostly engaged in our coherence changes corresponds well to brain regions associated with semantic processing pinpointed by functional imaging results.

Besides topographic aspects, the present results may even supplement neuroimaging findings by elucidating the functional dynamics underlying semantic processing. To illustrate this, taking all present coupling results together, bilateral anterior temporal positions are most prominently engaged in the coherence changes. This topographic finding is in line with reports of bilateral temporal source estimates of N400 effects to pictures (Hamm *et al.*, 2002). Of particular interest, however, the actual networks of coherence increases, involving anterior temporal regions, vary in dependence of semantic content. Whereas in processing meaningful objects the left anterior temporal position transmits more information to frontal positions, the right anterior temporal region is a major recipient of stronger temporal, parietal and frontal projections during meaningless object processing. These differences in the functional-dynamic network suggest distinct functional roles for left and right anterior temporal regions during processing of object semantics. More specifically, in the case of meaningful objects, left temporo-parietal areas feed increased information input to bilateral frontal sites, most likely related to semantic processing. This enhanced information transfer to frontal sides seems plausible in the course of task processing demands.

Next, based on the lower number of PDC increases obtained for meaningful objects, we suggest that these sparser connectivity increases, mostly present as intrahemispheric couplings, may reflect lower extent of effort in semantic retrieval. In contrary, given the greater number of higher PDC values for meaningless objects, this pattern may indicate difficulty of retrieving information from semantic memory (Supp *et al.*, 2004).

Given this denser network of coherence mostly expressed as interhemispheric couplings, unsuccessful meaning activation may lead to enhanced recruitment of more distributed left and right areas, particularly converging towards the right temporal position. We assume that these regional changes in neuronal couplings and information transfer are due to recruiting more neural resources in the extensive but unsuccessful search within the object-related memory. Last, the pattern of the left-sided temporo-parietal-frontal couplings of PDC increases for meaningful objects may emerge on the basis of implicit picture naming necessitating the recruitment of language-related networks.

In conclusion, viewing meaningful, recognizable pictorial objects results in differential coupling increases (within the beta-frequency) that involve the left anterior temporal and parietal position, forming a functional network with frontal positions during the N400 time-window. This left temporo-parietal network provides enhanced information input to bilateral frontal positions, which may reflect cortical coupling patterns underlying successful semantic memory retrieval in response to meaningful pictorial objects. This proposal is in line with the general conjecture to regard the N400 time-window as interval for semantic processing. Finally, the greater number of coherence increases for meaningless object processing suggests enhanced recruitment of more distributed left and right areas during unsuccessful memory search.

Acknowledgements

Abbreviations

ERP, event-related potential; MVAR, multivariate autoregressive model; PDC, partial-directed coherence.

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