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Semantic priming increases left hemisphere theta power and inter-trial phase synchrony

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Abstract

Information is stored in distributed cortical networks, but it is unclear how distributed stores are synthesized into a unified percept. Activation of local circuits in the gamma range (30–80 Hz), and distributed stores in the low theta range (3–5 Hz) may underlie perceptual binding. Words have a crucial role in semantic memory. Within memory the activation of distributed semantic stores is facilitated by conceptually related previous items, termed semantic priming. We sought to detect event-related brain oscillations (EROs) sensitive to semantic activation and priming. Here we show that low theta evoked power and inter-trial phase locking (4–5 Hz) from 250–350 msec over left hemisphere language areas was greater to related than to unrelated words. Theta band event-related oscillations over left hemisphere language areas may provide a brain signature for semantic activation across distributed stores being facilitated by semantic priming.

Language processing depends on semantic memory, comprising representations of facts and knowledge about things. Semantic memory is distinct from episodic memory of personal events and from non-verbal procedural memory and implicit memory. Likewise, it is distinct from short-term working memory, where information is manipulated in a mental buffer. Within semantic memory the activation of stores is facilitated by conceptually related previous items, termed semantic priming (Schvaneveldt & Meyer 1973). During reading, word form analysis is thought to occur in the left temporal fusiform gyrus (Cohen et al 2000). Information flows to temporal and parietal language areas for further semantic memory processing. The first stage is lexical access, where entries are activated on a phonological level after grapheme-to-phoneme conversion, or directly via orthographic cues. Next, during lexical selection entries are chosen on a conceptual level, whereby words activate semantic stores, distributed preferentially across temporal and parietal cortex for nouns and frontal cortex for verbs (Damasio & Tranel 1993, Damasio et al 1996). Finally, semantic integration occurs, where chosen words/concepts are integrated with preceding context.

In terms of electrophysiology, the N400 event-related potential (ERP) is a sensitive index of language processing. The N400 typically spans 100 to 200 msec, and peaks about 400 msec. Some N400 activity may be sensitive to semantic activation processes. For example, less contextually plausible sentence endings within the same category as the most contextually appropriate ending may generate less N400 than more contextually appropriate endings among a separate category (Federmeier & Kutas 1999). As well, the N400 is sensitive to semantic network structure, with ambiguous network words showing larger N400 activity than unambiguous network words of the same contextual plausibility (Salisbury 2004,

2010). Still, the majority opinion is that most N400 activity serves as a neurophysiological sign of contextual integration (Kutas & Hillyard 1980, Holcomb 1993). Perhaps the most compelling evidence for N400 reflecting late stage contextual integration processes is that truly masked prime stimuli elicit RT priming but do not affect the N400 (Brown & Hagoort 1993), and N400 modulation correlates with masked prime detectability (Holcomb et al 2005). Earlier ERPs have been associated with phonological and lexical processes. For example, an early fusiform potential ~200 msec may be related to wordform analysis or orthography (Cohen et al 2000). Another potential between 200 and 300 msec, the phonological mismatch negativity, may reflect lexical entry analysis based on acoustic properties (Connolly & Phillips 1994, Diaz & Swaab 2007). Holcomb and Grainger (2006) suggest that P150 reflects word form activity, an N250 reflects the initial lexical analysis of letter order, a P325 represents lexical selection, and the N400 reflects form-meaning interface i.e., semantic entries. If N400 reflects contextual integration, then earlier electrophysiological signs of lexical access and selection have not been convincingly demonstrated, using either the ERP or event-related oscillation (ERO) methods.

In the cortex local cell assemblies are thought to form functional units through synchronous activation in the gamma range (Engel & Singer 2001). For example, in human depth recordings Mainy et al (2007) recorded increased gamma activity in several distinct cortical areas during working memory encoding, including medial temporal, temporo-parietal, and prefrontal areas. Oscillations may function as nested sets, where lower frequency activity binds higher frequency activity, which in turn binds smaller bits of information. Theta bursts occur during the up-phase of delta activity (Lakatos et al 2005), and gamma bursts occur during the up-phase of theta activity (Lisman & Buzsáki 2008). Thus local modules (gamma) can be functionally linked in temporal synchrony with distant modules via lower frequency regulation. In rats, task performance correlates with the degree of coupling between hippocampal theta and gamma during learning (Tort et al 2009). In humans, high delta/low theta (~3 Hz) appears to organize gamma during memory retrieval tasks (Burgess & Ali 2002). Bastiaansen et al (2005) showed that left hemisphere theta activity (4–7 Hz) in the EEG was increased following the presentation of words with extensive semantic memory stores (open class words) versus primarily syntactic words (e.g., the, or; closed class words), providing the first clue that theta might be related to distributed semantic activation. Thus, semantic activation and memory retrieval appear to elicit activity in the 3 to 7 Hz range which may serve to synchronize spatially distributed parallel processing modules. If so, we would expect that semantic priming, whereby semantic stores are somehow more quickly accessed when preceded by related information, should be reflected in greater trial to trial phase consistency in the theta range, particularly over areas related to noun storage in the left posterior language regions.

However, analysis of low frequency EROs are confounded by the stimulus-locked ERPs, which can be described as low frequency events, because the ERPs overlap to form a pseudo-oscillation that can be described in the frequency domain, but may not really reflect true underlying oscillatory activity. For example, the increased theta to open class words reported by Bastiaansen et al (2005) was maximal precisely where N400 is, and spanned several hundred msec. Thus, it was not clear if that activity truly reflected activation of semantic stores or rather reflected the N400 ERP itself. We predicted the existence of specific oscillatory activity within a restricted time window that underlies the actual lexical access and semantic activation. Wordform activity has been associated with ERPs at approximately 200 msec, and the N400, associated with contextual integration, a post-lexical access process, peaks at approximately 400 msec. Hence, if theta ERO activity is related to the actual activation of semantic stores, it should occur between about 250 and 350 msec, and be relatively circumscribed to left temporal and parietal language areas for nouns, where semantic stores are thought to reside (Damasio & Tranel 1993). We further

predicted that related words would show greater theta ERO activity than unrelated words, reflecting the spread of activation from the prime memory to the related word's semantic store as a function of the semantic priming effect.

Method

Subjects

Thirty-nine psychiatrically well controls (11F, mean age 31.2 (11.4 sd), all right-handed native English speakers) with good semantic memory performance (scaled WAIS-III Information 13.5 (2.4); Vocabulary 14.2 (2.8)) performed a lexical decision task while EEG was acquired.

Procedure

Subjects were presented two words, one at a time, on a computer screen approximately 1.1 meter away using Superlab Pro v.2 (Cedrus). A total of 200 pairs (Cue, Target) were presented. All Cue words were real words. Half of the targets were real words, the other half pronounceable nonword fillers. Half of the real Targets were related to the Cue, half were unrelated. The Cue was on screen for 1 second and the Target came on screen 250 ms after the termination of the Cue (1.25 sec SOA). Subjects indicated via a dominant hand Yes/No button press if the Target was a real word. The following word pair would not commence until a response was made. Related words were selected from a large corpus of stimuli (Nelson, McEvoy & Schreiber 1998). Nonword fillers were selected from several published sources (Besner & Swan 1982, Besner & Davelaar 1983, Besner, Coltheart, & Davelaar 1984, Bodner & Masson 1997, Borowsky & Besner 1993). Each Cue was used in an associated, an unrelated, and a nonword pair, and all Target words were used in associated and unrelated conditions. No Cue or Target was repeated for any subject, resulting in 4 versions of the task, counterbalanced between subjects. (The stimuli are available from Dr Salisbury.)

EEG Recording & Analysis

EEG activity was recorded from 60 scalp sites and the nose tip using a pre-configured 64-channel cap (custom designed Electro-Cap International sintered Ag-AgCl caps). Activity was amplified and recorded continuously with embedded digital stimulus triggers using SynAmps and Scan Acquire (Neuroscan/Compumedics USA). During recording the right mastoid served as the reference, with the exception of two bipolar electro-oculogram channels. Two electrodes located medially to the right eye, one above and one below, were used to monitor vertical eye movements and blinks. Electrodes placed at the outer canthi of the eyes were used to monitor horizontal eye movements. The forehead served as ground. All electrode impedances were below 5 kOhms. The EEG amplifier bandpass was 0.10 (6 dB/octave roll-off) to 100 Hz (24 dB/octave rolloff). EEG was digitized at 500 Hz.

Initial off-line processing was performed with BrainVision Analyzer (Brain Products GMBH). For ERP averaging, raw EEG data were lowpass filtered to 8.5 Hz to remove high frequency activity, muscle and ambient electrical noise, and eye blink and movement correction algorithms (Gratton, Coles, & Donchin 1983) were used to remove HEOG and VEOG artifact. Bad channels were replaced with the linear average of 6 to 8 surrounding sites if possible. Recordings were rereferenced to averaged mastoids. The EEG was segmented based on Target word delivery into epochs of 1100 ms duration, including a 100 ms pre-stimulus baseline. Epochs were baseline corrected by subtraction of the average pre-stimulus voltage at each site. Subsequently, epochs that contained voltage exceeding ± 100 μ V at F7, F8, FP1, or FP2 were rejected. Averages were constructed for related and

unrelated Targets. Only correct target trials were included in the analyses (correct response between 200 and 3000 msec of Target onset).

For ERO analyses, individual unfiltered trials from -300 to 800 msec were exported to Matlab for wavelet-derived frequency-in-time measures. Wavelet analysis of each individual trial and the average of individual trials (the averaged ERP waveform) provided the basis for intertrial phase locking and evoked power respectively (Software provided by C.Torrence and G. Compo; <http://atoc.colorado.edu/research/wavelets>). A complex Morlet wavelet with Morlet's constant of 6 and a fixed cycle length of 6 was used over the 2–20 Hz range with 16 frequency bins (a separate analysis for gamma activity from 20 – 80 Hz revealed no effects). Baseline correction for each frequency bin used –250 to –100 msec pre-stimulus interval. Evoked power was derived from the squared amplitude coefficient of the wavelet transform of the ERP. Phase locking was calculated based on the trial-to-trial phase angle at each specific site and time point within specific frequency bands. Essentially, this measure indicates the temporal stability of EROs from trial to trial. This differs from standard inter-electrode coherence (correlation of phase angle between sites). Unlike coherence, PLF measures stimulus-locked influence on phase from trial to trial at a specific site (Tallon-Beaudry et al 1996, Barrie et al 1983), and indicates the degree of phase similarity of specific frequencies over time as a function of the stimulus, rather than the synchrony between sites (i.e., coherence). Whereas coherence is thought to reflect synchronous communication between separate cortical modules, and is perhaps susceptible to volume conduction artifact, PLF indicates the degree to which the phase of a specific frequency is consistently influenced by the stimulus. Conceptually, phase locking is analogous to anisotropy in diffusion tensor imaging. Each timepoint for a specific frequency has an associated phase angle. At point 0-t before the stimulus, there are many different phase angles from trial to trial. Because phase angle describes a circle (360°), this condition can be said to have high circular variance, akin to an isotropic distribution; because phase across trials is random, the phase angle distributions describes a circle. However, at point 0+t, if the phase of the oscillation is influenced by the stimulus, phase angles should be more consistent across trials and there will be less circular variance, akin to an anisotropic distribution. A phase locking factor (PLF) was calculated as 1 minus the circular variance for each time-frequency point. Evoked power was analyzed from bilateral FrontoCentral and Central sites where it was maximal (FC1/2, 3/4, 5/6; and C1/2, 3/4, 5/6). Phase was analyzed from bilateral FrontoCentral, Central, and CentroParietal sites where it was maximal (FC1/2, 3/4, 5/6; C1/2, 3/4, 5/6; and CP1/2, 3/4, 5/6).

Results

Subjects made significantly faster lexical decisions about related words (784.6 msec (195.8 sd)) than about unrelated words (810.3 msec (196.7 sd), $t_{38}=3.68$, $p=.001$), evidence of semantic priming.

Related words and unrelated words differed in the N400 elicited (Figure 1A), with a prominent differential N400-effect (Figure 1B). N400 activity over 375–475 msec (grand average peak ± 50 msec) was significantly more negative for unrelated words than for related words along the traditional midline (Fz, Cz, Pz; $F_{1,38}=11.17$, $p=.002$) and more extensively over both hemispheres (left and right FC, C, and CP chains, sites 1 to 6; $F_{1,38}=5.76$, $p=.02$).

Real words (both related and unrelated) diverged from pseudowords in the interval preceding N400 (Figure 2, inset), consistent with our prediction for lexical access and selection processes prior to the contextual integration reflected in N400. Frequency-in-time analyses from 250–350 msec of high delta (3 Hz) and low theta (4.5 Hz) power showed

significant differences for related and unrelated words ($F_{1,38} = 16.17$, $p < .001$, Figure 2), with greater theta power to related than to unrelated words ($F_{1,38} = 3.99$, $p = .05$) and greater delta power to unrelated than to related words ($F_{1,38} = 8.23$, $p = .007$). Both theta and delta power were slightly larger over the left (hemisphere: $F_{1,38} = 9.53$, $p < .001$), but generally larger over central scalp areas ($F_{1,38} = 9.70$, $p < .001$).

Of particular interest was an increase in trial to trial phase synchrony (PLF, phase locking factor) over the left hemisphere ($F_{1,38} = 17.84$, $p < .001$, Figure 3). The maximally synchronous frequency was different for related and unrelated words (relatedness $\times$ band: $F_{1,38} = 15.78$, $p < .001$). Theta phase locking was markedly greater over left hemisphere language areas for related words ($F_{1,38} = 8.78$, $p = .005$; hemisphere: $F_{1,38} = 8.58$, $p < .006$). Unrelated words had greater phase synchrony in the delta band than related words ($F_{1,38} = 4.66$, $p = .037$), that was greater over left hemisphere language areas ($F_{1,38} = 15.28$, $p < .001$).

Discussion

Related words showed increased theta band power and trial-to-trial phase locking during a time interval in which lexical access and selection presumably occurs, by contrast with greater delta band power and phase locking for unrelated words. To the extent that priming acts to make related information more readily available, i.e., stores are pre-activated by preceding context, we hypothesize that access to the memories can rely more on solely cortical processes, reflected in a higher “binding” frequency in the low theta band. The speeded lexical access and selection is reflected in greater trial to trial temporal stability, as semantic priming acts to reduce the latency of semantic activation, in turn reflected in greater PLF values. Unrelated words, by contrast, need involvement of medial temporal lobe components that coordinate distributed cortical engram activation, including rhinal and parahippocampal cortices, and thus longer range communication. Additionally, unrelated words show weaker trial-to-trial temporal stability due to greater variability in the time needed to activate unrelated (random) memory stores. Due to involvement of subcortical structures and greater temporal variability unrelated words show a binding frequency in the high delta band.

Although we have described activity in the delta and theta bands that precedes the major N400 ERP component, it is possible that we are really describing the ERPs themselves in another way, and the oscillations reported here do not reflect fundamental oscillatory activity. We think this is unlikely to be the case. First, there is little ERP difference between related and unrelated words in the period we are examining. The N400 effect follows this activity (see Figure 1). Second, theta activity is largely gone during the N400 and P600 intervals, localized temporally to the early period. Figure 4 shows that the burst of theta activity for related words is localized in time to the 250–350 msec interval, preceding the semantic integration indexed by N400. The delta activity characteristic of unrelated target words extends into the N400 interval, but not the P600 window. This is consistent with longer latency of activation of unrelated word networks. One must be cautious in interpretation of the delta activity, as it may contain substantial contributions for the ERPs. Still, the theta activity and increased PLF appears to occur prior to substantial ERP activity of N400 and P600. If the theta activity seen in the earlier period was due to the N400 or P600, then it should be apparent in the N400 or P600 intervals. Finally, ERPs should arise largely instantaneously across the scalp. Because PLF increases showed a specific topography, largest over left hemisphere language areas, it seems unlikely the PLF reflects only reduced ERP latency jitter; one would expect that would be broadly reflected across the scalp. In some sense, even if the theta activity was related to earlier ERP activity, the PLF effects would still be an informative new insight into semantic processing. Future work

should help disentangle ERP and ERO activity by manipulating factors known to affect semantic integration times and N400 latency. If long-range theta activity is truly related to the early semantic processes of lexical access and selection, they should be little affected by such manipulations.

Previous work has tried to find gamma band activity related to semantic memory for words. Pulvermuller and colleagues (1996) reported a relative decrease of beta and low gamma activity (14–33 Hz) using MEG to spoken non-words versus words in the left hemisphere from 300 – 600 msec, likely overlapping N400 processes. Eulitz et al (1996) reported an increase in higher frequency gamma to words versus nonwords (~60–65 Hz) specific to the left hemisphere at around 240 msec. Others have been unable to detect differential gamma to words versus nonwords, nor were we able to detect any gamma burst to real words, or any gamma modulation by relatedness. It simply remains unclear what happens in lower and higher gamma bands during word processing. Although alpha activity has been linked to learning and semantic memory (Klimesch et al 2008), we were unable to detect any effect or relatedness on alpha PLF or evoked power in the 150 – 300 msec range. From 250–400 msec, we saw no differential effect of relatedness on alpha power, and no specific differential effect on PLF in the hemispheres. We did see relatively greater alpha PLF over frontocentral sites for related words than unrelated words (0.029 vs 0.014, respectively), suggesting that there may be greater anterior alpha trial-to-trial phase coherence for related words, but the magnitude of phase locking was nearly 10 times smaller than for theta and delta, which were left lateralized. Thus it seems unlikely that alpha activity underlies priming on this specific task. In addition, Klimesch et al (2008) suggest that theta oscillations are specifically related to retrieval of episodic memories. Here, however, we detected theta bursts ostensibly related to semantic retrieval. Future work needs to confirm whether our theta findings reflect specific frequency band associates of semantic activation and priming, by contrast with activity in other bands (i.e., alpha, beta, gamma).

In summary, we showed increased theta band activity to related words on a semantic priming task, by contrast with greater delta activity to unrelated words, in a time interval where the semantic activation should occur. Of particular interest was an increase of theta band trial-to-trial phase locking, which we suggest reflects quicker and more efficient access to and activation of semantic stores. Activity in the theta band may be associated with a fundamental quality of semantic memory, namely semantic priming, a cornerstone of theories of human memory function. This novel finding may provide a new avenue for studies of semantic activation, and provides a new, earlier measure of semantic activation than previously described.

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Figure 1.

Panel A. Event-related potential to related (black) and unrelated (blue) words. Panel B. N400 effect difference waveforms for semantically unrelated words. Note the later time course of N400 differential effects, linked to difficulty in semantic integration. FC = frontocentral, C = Central, CP = Centroparietal, odd numbers = left hemisphere sites, even numbers = right hemisphere sites.

Figure 2.

Power for theta and delta bands during the 250 – 350 msec time interval preceding N400. Inset: Note that related (black) and unrelated (blue) words diverge from nonword fillers (red) during this early interval, but not from one another. Related words are associated with greater power in the theta band whereas unrelated words are associated with greater power in the delta band. Shaded bar in the voltage-in-time waveforms indicate time interval for topographic maps.

Figure 3. Phase for theta and delta bands during the 250–350 msec interval. Note that related words are associated with increased trial-to-trial theta phase synchrony, whereas unrelated words show moderate phase increases in the delta band. Shaded bar in the voltage-in-time waveforms indicate time intervals for topographic map.

Figure 4. Theta and delta power over the early, middle (N400) and late (P600) time intervals. Note that the theta burst is localized in time to the early, pre-semantic integration interval, and localized to the posterior left hemisphere. Shaded bars in the voltage-in-time waveforms indicate time intervals for topographic maps.