Dissociable Neural Mechanisms for Encoding Predictable and Unpredictable Events

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Abstract

■ Attention is a necessary condition for the formation of new episodic memories, yet little is known about how dissociable attentional mechanisms for "top-down" and "bottom-up" orienting contribute to encoding. Here, subjects performed an intentional encoding task in which to-be-learned items were interspersed with irrelevant stimuli such that subjects could anticipate the appearance of some study items but not others. Subjects were more likely to later remember stimuli whose appearance was predictable at encoding. Electroencephalographic data were acquired during the study phase of the experiment to assess how synchronous neural activity related to later memory for predictable stimuli (to which attention could be oriented in a top-down fashion) and unpredictable stimuli (which rely to a greater extent on bottom-up attentional orienting). Over left frontal regions, gamma-band activity (25–55 Hz) early (∼150 msec) in the epoch was a robust predictor of later memory for predictable items, consistent with an emerging view that links high-frequency neural synchrony to top-down attention. By contrast, later (∼400 msec) theta-band activity (4–8 Hz) over the left and midline frontal cortex predicted subsequent memory for unpredictable items, suggesting a role in bottom-up attentional orienting. These results reveal for the first time the contribution of dissociable attentional mechanisms to successful encoding and contribute to a growing literature dedicated to understanding the role of neural synchrony in cognition. ■

INTRODUCTION

Considerable advances in our understanding of the neural correlates of episodic memory formation are owed to an experimental paradigm known as the "difference of memory" (DM) paradigm (Paller, Kutas, & Mayes, 1987; Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980). In combination with event-related neuroimaging techniques, the DM paradigm allows the back-sorting of study-phase neural activity on the basis of performance on a subsequent retrieval test. Items that were presented at study thus can be classified into those that were successfully encoded and those that were not, and patterns of brain activity associated with these two types of trial can then be compared. Using event-related functional magnetic resonance imaging (fMRI), the DM paradigm has been used both to confirm the involvement of medial temporal lobe structures identified by early lesion work (Scoville & Milner, 1957), and to define neocortical regions, notably those in the inferior frontal and parietal lobes, which contribute to successful encoding (Rugg, Otten, & Henson, 2002; Buckner, Logan, Donaldson, & Wheeler, 2000; Wagner et al., 1998). The DM paradigm has also been used with event-related potentials (ERPs) to reveal an unfolding sequence of encoding-related components locked to the onset of the stimulus: for example, an early negativity over left frontotemporal sites (Mangels, Picton, & Craik, 2001), a positive-going parietal component at 300–600 msec (Otten & Donchin, 2000; Paller et al., 1987), and a late sustained positivity at frontal electrodes (Fabiani, Karis, & Donchin, 1990). Similarly, successful encoding has been associated with increased electroencephalographic (EEG) synchrony in the theta (4–8 Hz) (Summerfield & Mangels, 2005a; Sederberg, Kahana, Howard, Donner, & Madsen, 2003; Klimesch, Doppelmayr, Russegger, & Pachinger, 1996) and gamma (>25 Hz) bands, particularly over anterior neocortical sites (Gruber, Tsivilis, Montaldi, & Muller, 2004; Sederberg et al., 2003) and within the medial temporal lobe (Fell, Klaver, Elfadil, et al., 2003; Fell, Klaver, Lehnertz, et al., 2001).

The DM paradigm capitalizes on moment-by-moment variability in the likelihood that our perceptual experiences will be laid down as new traces in long-term memory: that although some items will be successfully encoded, others will not. Crucial to our understanding of how new memories are formed, thus, is an understanding of the sources of variability in encoding success. Factors intrinsic to the events we experience are an important predictor of later memory. For example, stimuli that are novel or distinctive by virtue of their perceptual, conceptual, or emotional attributes enjoy a well-described advantage during learning (the Von

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Restorff effect) (Strange, Otten, Josephs, Rugg, & Dolan, 2002; Fabiani & Donchin, 1995; von Restorff, 1933). However, extrinsic factors, such as the depth of conceptual processing to which the study material is subjected (Craik & Lockhart, 1972) or the level of attentional resources available during encoding (Craik, Govoni, Naveh-Benjamin, & Anderson, 1996) also have a powerful modulatory role on both memory performance and neural activity that accompanies successful learning (Kensinger, Clarke, & Corkin, 2003; Mangels et al., 2001; Fletcher, Shallice, & Dolan, 1998).

The relationship between attention and encoding is of particular interest to researchers studying the neurobiology of memory, as it has been shown that unattended items typically cannot be later recalled or consciously recollected (Craik et al., 1996; Gardiner & Parkin, 1990). Given that attention is a necessary condition for episodic encoding, it is likely that a subset of the brain activity found to predict later memory in the DM paradigm reflects the orienting of attention to the study material, independent of other neural phenomena that may vary with stimulus distinctiveness, level of conceptual processing, or the formation of the declarative memory trace itself. Accordingly, some previous DM studies have divided attention during the study phase in an attempt to identify neural correlates of successful encoding that exhibit a parallel sensitivity to reduction in attentional load (Kensinger et al., 2003; Mangels et al., 2001; Anderson et al., 2000; Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000). One result that has consistently emerged from these studies is that activity in the left inferior prefrontal cortex, which is perhaps the neocortical zone most consistently implicated in successful encoding under full attention conditions, does not predict later memory when an attention-demanding secondary task is imposed at study. One corollary of this finding is that reductions in attentional resources impair later memory at least in part because under divided attention, left inferior frontal regions are no longer able to contribute to encoding. Drawing upon these data, as well as upon evidence that left frontal cortical sites observed to be active in DM studies overlap with those thought to subserve semantic retrieval (Thompson-Schill, 2003) and phonological rehearsal (Davachi, Maril, & Wagner, 2001), it has been proposed that dividing attention impairs memory because it precludes elaborative conceptual processing (such as thinking about the meaning of an item or rehearsing it in working memory) that rely on these left anterior structures (Naveh-Benjamin, Guez, & Marom, 2003; Naveh-Benjamin, Craik, Gavrilescu, & Anderson, 2000; Craik et al., 1996; Craik & Lockhart, 1972). This theory is consistent with the view that the (attention dependent) function of the left prefrontal cortex in successful encoding is to rehearse, associate, or otherwise conceptually elaborate information in the service of optimal encoding (Fletcher, Shallice, & Dolan, 2000).

Dividing attention at study offers insight into how encoding success varies under different levels of global processing resources but is less well suited to exploring how dissociable attentional networks for orienting and selection are involved in memory formation. Contemporary theories describe attention as a modular system (Corbetta & Shulman, 2002; Mesulam, 1998; Posner & Petersen, 1990), with dissociable mechanisms for ''top-down'' (or ''endogenous'') and ''bottom-up'' (or ''exogenous'') orienting. Top-down attention involves the selection of a relevant feature, representation, or location from an expected or predictable stimulus, whereas bottom-up orienting occurs to stimuli that capture attention by ''popping out'' unexpectedly from an undifferentiated context. It makes intuitive sense that these attentional mechanisms may make different contributions to encoding. For example, during serial list learning, where items follow each other in predictable succession, attention can be reliably oriented in a top-down fashion to each study item. However, when an item occurs unexpectedly, the degree to which attention can be disengaged from the current task and reoriented to the novel stimulus in a controlled fashion is likely to be a good predictor of learning.

The object of this study was to compare how bottom-up and top-down attentional mechanisms contribute to successful encoding. In order to do this, we employed a novel variant of the DM paradigm that was nevertheless reminiscent of early manipulations of item presentation rate during learning (Glanzer & Cunitz, 1966). In this paradigm, we varied the time available prior to stimulus presentation independently of the time subsequent to stimulus presentation. In the encoding phase of the experiment, subjects viewed a visual event every 2000 msec, but only one third of these events were study items (which they were instructed to encode); the remaining items were fixation crosses. A sequence of events was constructed such that an equal number of the possible permutations of zero, one, or two fixation cross-stimuli preceding and following the stimulus was presented in each block. On average, thus, every second visual event was a study item, but crucially, subjects' expectations varied in an ''aging interval'' fashion following the preceding study item. Because there were never more than two crosshairs between items, study items that were preceded by two crosshairs were *predictable* because subjects could be 100% certain that a to-be-encoded stimulus would be presented. By contrast, immediately following each study item, there was only a 33% chance that another study item would be presented, so these items were *unpredictable*. We reasoned on the predictable trials, subjects would be able to orient their attention (in a top-down fashion) towards the current stimulus, leading to improvement in memory performance. By contrast, on those trials that were unpredictable, we hypothesized that neural correlates of bottom-up attentional

orienting would turn out to be robust predictors of subsequent memory.

In order to explore neural correlates of top-down and bottom-up attention that predicted subsequent memory during encoding, scalp EEG activity was recorded during the study phase of the experiment. We used signal processing techniques that involve decomposing the EEG signal into its spectral components in order to explore how synchronous neural activity (4–55 Hz) varied with expectation and learning. In particular, we were interested in how rhythmic EEG activity at 4–8 Hz (theta-band activity [TBA]) and at 25–55 Hz (gamma-band activity [GBA]) varied with manipulations of attention and encoding. TBA over the dorsomedial frontal cortex ("frontal midline theta" or "FM theta") is a correlate of successful encoding (Summerfield & Mangels, 2005a; Weiss & Rappelsberger, 2000; Klimesch et al., 1996) and working memory processes (Rizzuto et al., 2003; Raghavachari et al., 2001; Gevins & Smith, 2000; Sarnthein, Petsche, Rappelsberger, Shaw, & von Stein, 1998). Recently, reset of the phase of TBA by bottom-up stimulation has been linked to the activation of attentional control processes (Makeig, Delorme, et al., 2004) giving rise to a family of ERP components known to underlie attentional orienting and encoding (such as the P2 and P300). We thus conjectured that TBA might contribute to encoding as it reflects the bottom-up activation of attentional control mechanisms triggered by novel or unpredictable stimulation (such as where one study item followed unexpectedly on from another study item).

Recent reports have indicated that >25 Hz activity (GBA) may also predict later memory (Gruber, Tsivilis, et al., 2004; Sederberg et al., 2003). This finding coincided with the emergence of a prominent theory linking high-frequency oscillatory activity in the early stages of the poststimulus period (∼150 msec) to top-down attentional processes (Herrmann, Munk, & Engel, 2004; Debener, Herrmann, Kranczioch, Gembris, & Engel, 2003; Engel, Fries, & Singer, 2001) or expectation (Miltner, Braun, Arnold, Witte, & Taub, 1999). Thus, one possibility is that the involvement of neocortical GBA in successful encoding reflects top-down attentional processes that facilitate orienting of attention to an expected or predictable study item rather than declarative memory trace formation per se. We thus hypothesized that GBA would predict later memory for predictable trials, which were preceded by a sufficiently long prestimulus period for attention to be oriented to them in a predictive fashion.

In a previous study from our laboratory with a similar design, subjects learned word–color associations with a fixed interval between study items (Summerfield & Mangels, 2005a). In this study, theta-band synchrony proved to be a particularly reliable predictor of the encoding of the association between the word and the color rather than of later recognition memory for the

word alone. Drawing upon this finding, in the present study we chose to define later memory for the word–color association as criterial for successful episodic encoding. This decision also reflected the consideration that contributors to the variance in encoding success that are tapped by the DM paradigm, such as attention, do not impact encoding monolithically. For example, the impairment to later memory under divided attention is more manifest when the criterion for later retrieval is vivid recollective details of the learning episode, compared to where subjects are merely required to recognize an item as old or new on the basis of a sense of semantic "gist" or familiarity (Gardiner & Parkin, 1990). Although it is thought that the mechanisms by which new associations are encoded overlap with those leading to later conscious recollection (Hockley & Consoli, 1999), it remains controversial whether divided attention has greater effect on associative encoding than on item-only encoding (Castel & Craik, 2003; Naveh-Benjamin, Guez, et al., 2003). Our study was not intended to speak specifically to this debate, but rather to use word–color encoding as a model for how a new episodic memory trace, consisting of composite sensory and semantic information, is formed under varying conditions of bottom-up and top-down attention.

METHODS

Subjects

Nineteen paid volunteers (12 women) were recruited via posters placed in Columbia University's psychology department. Subjects were neurologically normal right-handers aged between 18 and 35 years. All subjects gave informed consent to participate in the study, which was approved by Columbia University Institutional Review Board.

Procedure

Four study-test blocks were presented. In each study phase, subjects viewed lists of 45 medium-frequency (length 3–11 letters) nouns in one of four font colors: red, yellow, green or blue. Words remained on the screen for 1000 msec and were followed by a blank screen for 1000 msec. Interposed between each word were zero, one, or two successively and centrally presented crosshair stimuli. Crosshairs also remained on the screen for 1000 msec and were followed by a blank screen for 1000 msec. Stimulus sequences were carefully generated such that in each block (of 45 items) each of the nine possible permutations of crosshairs before and after the study item was presented an equal number of times (permitting, across the four blocks, 20 trials per level of *pre* and *post*; for EEG analyses, 60 trials per level of *pre* collapsed across *post*). Filler words were presented at the beginning and end of each block. Memory

performance for these filler words was not examined. Subjects were instructed to ignore the crosshairs and to remember as many of the 45 word–color associations as possible. Although no training was given, subjects were verbally instructed that no more than two crosshairs would be presented between words.

Following a brief distracter task (counting backwards by threes from a random three-digit number for 20 sec), subjects undertook the test/retrieval phase, in which they were presented with 90 probe words in white font, half of which were old (i.e., had been shown in the immediately prior encoding phase) and half of which were new (distracters). Two thousand milliseconds after presentation of the word, subjects were prompted to make a keypress to indicate whether the probe was old or new, and to assess their confidence in this judgment by responding in one of four categories: ''sure old,'' ''think old,'' ''think new,'' or ''sure new.'' Immediately following this response, a second prompt appeared, asking subjects to indicate in which of the four font colors the word had been presented. Again, for each option, subjects could indicate that they were ''sure'' or that they ''guessed'' that this was correct, giving a total of eight response options (''sure red,'' ''guess red,'' ''sure blue,'' etc.). Following this response, a blank screen was presented for 1000 msec, and then the next memory probe.

EEG Recording and Artifact Rejection

EEG activity was recorded during the encoding and retrieval phases of the experiment, although in this report only data from the encoding phase are discussed. EEG was acquired from 64 channels (sampling rate = 500 Hz; high-pass filter = 0.1 Hz, low-pass filter = 100 Hz; impedances kept below 11 kΩ) using Neuroscan SYNAMPS (Compumedics Inc., El Paso, TX). Recordings were initially referenced to Cz, then converted to an average reference off-line. BESA 5.06 (Electrical Geodesics Inc., Eugene, OR) was used to remove eye movements, blinks, and other artifacts from the continuous EEG data (Berg & Scherg, 1994). Trials in which muscle, movement, or other artifacts drove amplitude values above 100 μV were manually rejected. Artifact-free data were high-pass filtered with a 0.5-Hz zero-phase filter, spline-Laplacian transformed (estimated dura potential) (Nunez et al., 1997), and interpolated into an 81-electrode montage. Epochs from 1000 msec prestimulus to 2000 msec poststimulus then were exported into ASCII format.

Data Analysis with Brain Electrophysiology Analysis and Statistical Testing

All further data processing was performed with in-house MATLAB software written by CS. The code used for signal processing and analysis (brain electrophysiology

analysis and statistical testing [BEAST]) may be freely downloaded at www.columbia.edu/~cs2028/beast/beast.htm. A detailed explanation of the analysis technique has been described elsewhere (Summerfield & Mangels, 2005a). Under the framework of this analysis package, wavelet-transformed data are subjected to independent components analysis (ICA) to separate the data into spatially correlated sources of variance. Significance testing is carried out using random permutation testing on component activation scores, and component projections are visualized on a 2-D scalp map to show brain regions contributing maximally to the component activations. BEAST uses ICA code from EEGLAB (Delorme & Makeig, 2004).

Wavelet Power

All epochs were Morlet wavelet-transformed (Torrence, & Campo, 1998) between 4 and 13 Hz (theta/alpha analyses) and 14 and 55 Hz (beta/gamma analyses) in nine logarithmically spaced frequency bands (ω_o = 6). To reduce artifacts, wavelet values were windsorized at 5 standard deviations above the mean. Data were temporally smoothed with a Gaussian filter of width 50 msec, and averaged across adjacent frequency bands, to increase signal/noise ratio. Trials in each condition were subsequently averaged, yielding mean time–frequency (TF) information for each condition, at each electrode, for each subject. Averaged wavelet values were converted to z scores at each subject and electrode prior to ICA analyses and significance testing.

ICA and Significance Testing

Data were reduced to correlated spatial components with ICA, and significance testing was carried out at each component with nonparametric random permutation testing. Analyses of variance (ANOVAs) with planned comparisons were carried out in parallel at every TF pixel to derive point-estimate statistics, and then subject-condition values were shuffled 1000 times and this ANOVA repeated for each permutation. To provide a correction for ''familywise error'' multiple comparisons, the maximum value across the entire TF plot was then entered into a distribution that forms the null against which point estimate values are compared. Only those point estimates that fall within the top 5% of this distribution were considered significant. This technique has been described in more detail elsewhere (Burgess & Gruzelier, 1999).

The present factorial experimental design presented a unique challenge for this method, as the interaction term statistics cannot be reliably calculated using the method described above (Suckling & Bullmore, 2004). We thus used planned comparisons to derive regions of interest (ROIs) within TF space, and then tested mean wavelet power/coherence values falling within this ROI

using conventional parametric statistics. The planned comparisons used for mem and pre searched for voxels that varied for WC > miss or miss > WC, collapsed across pre; for pre, the search was for voxels that varied in a pre2 > pre1 > pre0 or pre0 > pre1 > pre2 fashion, collapsed across mem. For the Pre × Mem interaction, we searched for voxels that predicted later memory only at pre0, pre1, or pre2 separately, or that varied across pre for WC or miss trials separately. Because planned comparisons are mean driven, in some cases, voxels satisfied these conditions but did not achieve significance when the interaction term was calculated with conventional parametric statistics. These effects are not reported here.

RESULTS

Behavioral Results

Study-phase trials were classified on the basis of whether subjects, on a later retrieval test, (a) correctly judged the item to be old *and* correctly identified in which font color it had been presented ("word + color" or WC trials) or (b) either failed to correctly recognize the item, or recognized the item but failed to correctly recollect the font color in which it was presented ("miss" trials). In order to increase statistical power, we collapsed across high- and low-confidence responses for all analyses. Three subjects were excluded, as they failed to identify the font color with above-chance accuracy (leaving $n = 16$). Overall, font color was correctly recollected on 42–86% of trials (mean = $64 \pm 16\%$; chance = 25%) in the remaining subjects.

In order to investigate how memory performance varied with prestimulus time (pre) and poststimulus time (post) time, trials were labeled according to the number of crosshairs preceding and following the stimulus; for example, in the stimulus sequence A B + + C, where stimulus B followed directly on from stimulus A, but

two crosshairs intervened between stimuli B and C, stimulus B would be classified as "pre0" and "post2." A schematic diagram of the trial sequence can be seen in Figure 1A. Figure 1B shows memory performance (percent word–color associations learned) as a function of pre- and poststimulus time. Visual inspection shows an overall pattern of increasing memory performance with increasing time preceding the stimulus. Indeed, when memory performance was compared using factorial analysis of variance (pre [3] × post [3]), later memory for the word–color association varied reliably with pre ($F = 5.59, p < .01$) in a pre2 > pre1 > pre0 fashion (linear trend: $F = 9.0, p < .01$). A significant main effect of post ($F = 8.65, p < .01$) was also observed, again with later memory performance increasingly linearly across poststimulus time ($F = 13.8, p < .01$). No interaction between pre and post was found.

EEG Results

In order to explore how the memory advantage for predictable trials effect might be reflected in brain activity accompanying the study phase, we examined how neural synchrony associated with encoding trials varied as a function of both subsequent memory (mem) and expectation (pre). In order to provide full coverage of the EEG frequency spectrum, power information was measured in the theta/alpha (4–13 Hz) and beta/gamma (14–55 Hz) bands for an epoch lasting for 800 msec following stimulus presentation. ICA of gamma- and theta-band data were performed separately to facilitate the isolation of unrelated sources of variance in each frequency band. All EEG data presented here are from the encoding phase of the experiment, and only responses to study items (not to interspersed crosshairs) are shown.

Graphical displays of spectral power results (Figures 2 and 3) each consist of four panels: (i) Component weights are plotted on the scalp to show the spatial

Figure 1. Encoding phase trial sequence and behavioral data. (A) Subjects were presented with a visual event every 2 sec, one third of which was a study item (word in one of four font colors). Prior to and following each study item, zero, one, or two fixation crosshairs were presented. Study items were classified according to the number of crosses preceding and following the stimulus: For example, the word "acorn" here is preceded by 0 and followed by two crosshairs (pre0/post2). (B) Behavioral performance. On the *y*-axis, the percentage of trials on which the word–color association was subsequently remembered for each level of *pre* and *post*. On the *x*-axis, pre0 (left), pre1 (middle) and pre2 (right) represent trials preceded by zero, one, and two crosshairs, respectively. Post0, post1, and post2 are plotted with blue, green, and red lines, respectively.
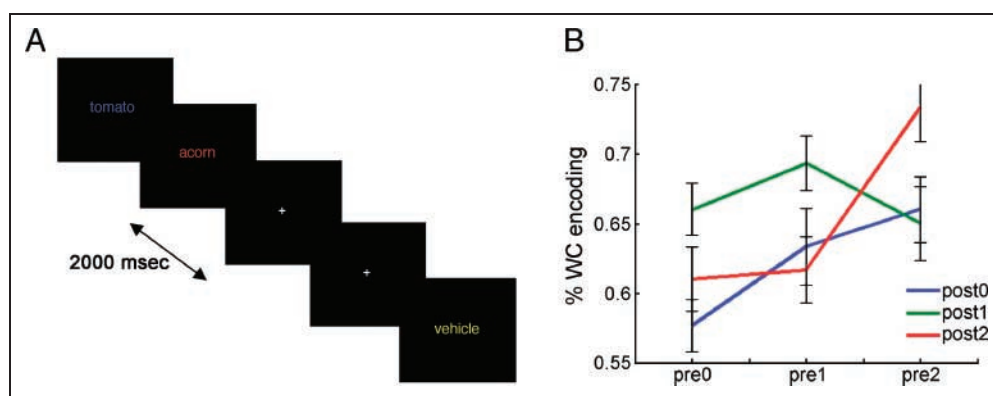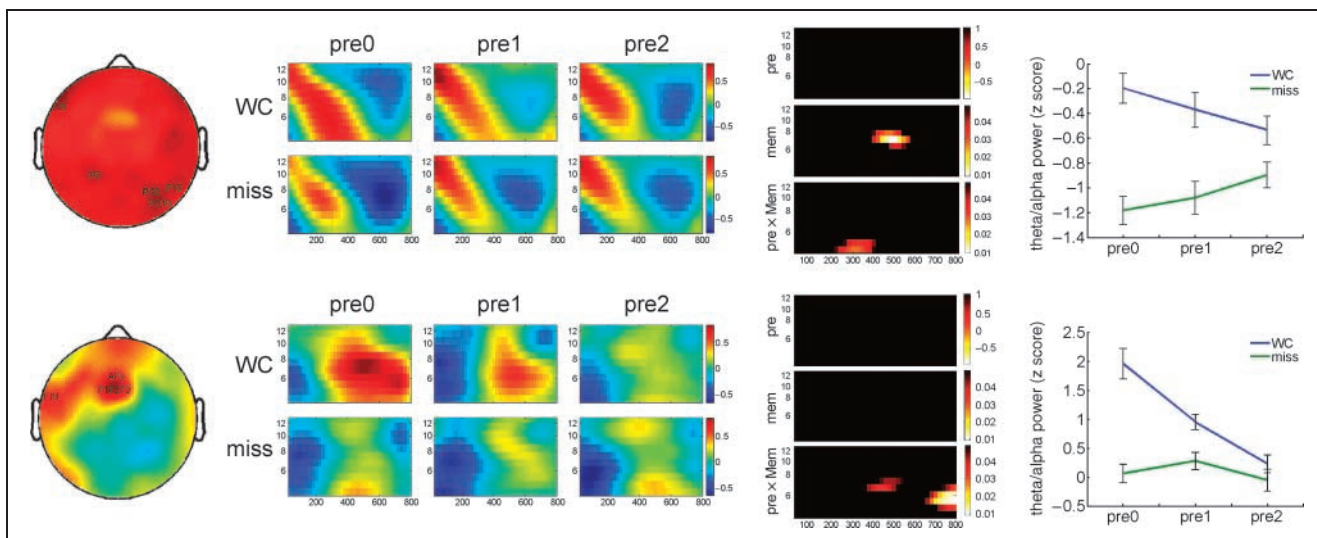
Figure 2. EEG results: 4–13 Hz. Left: component weights for each electrode. Middle left: TF plots (x-axis: time, 0–800 msec; y-axis: frequency, 4–13 Hz) for trials on which the word–color association was successfully learned (WC) and for which it was not (miss) for study trials preceded by zero (pre0), one (pre1), or two (pre2) crosshairs. Values are mean z scores across subjects. Middle right: significance plots for the main effect of pre (top), the main effect of mem (middle) and the Pre × Mem interaction (bottom). Only pixels significant at $p < .05$ (corrected for multiple comparisons) are shown; all other pixels are black. Right: mean spectral power values extracted from a mask in TF space corresponding to pixels exceeding $p < .05$ for the main effect of mem at Component 1 (top) and Mem × Pre at Component 2 (bottom). Mean spectral power across subjects is plotted on the y-axis; pre0, pre1, and pre2 are on the x-axis. The blue line represents WC trials, and the green line represents miss trials.

distribution of each component (leftmost); (ii) mean component activations (TF plots, averaged across subjects) are shown for each level of pre and mem (middle left); (iii) planned comparisons (with appropriate correction for multiple comparisons) were used to isolate regions of TF space where activation scores for each component differed reliably as a function of pre, mem and Pre × Mem (middle right); and (iv) these regions were then used as masks to extract mean spectral power for each level of pre and mem from the component activation plots, and these effects are then displayed on separate axes (rightmost).
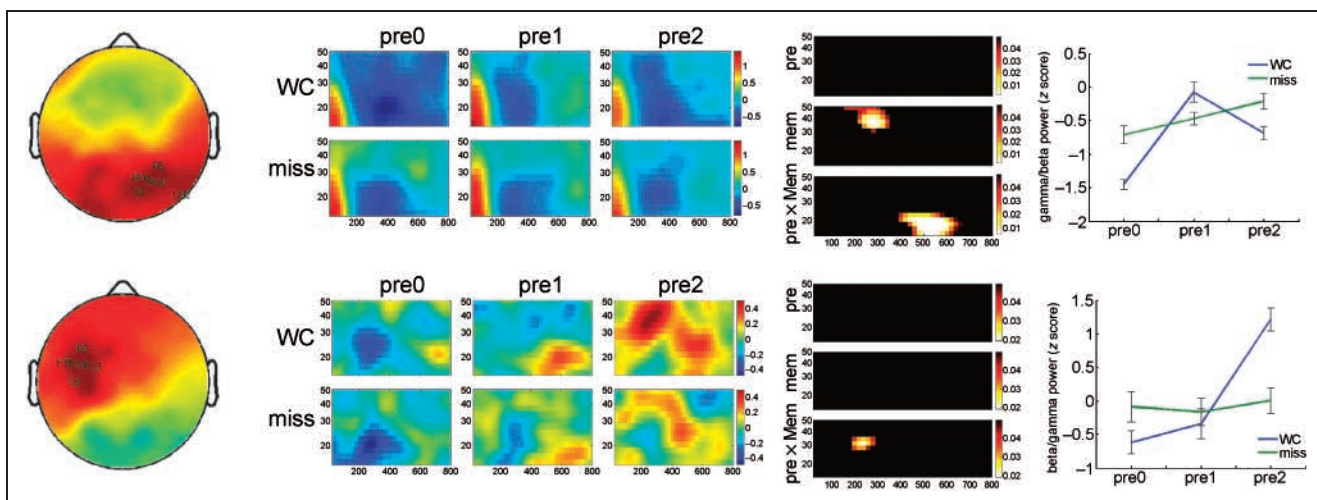

Figure 3. EEG results: 14–55 Hz. Left: component weights for each electrode. Middle left: TF plots (x-axis: time, 0–800 msec; y-axis: frequency, 14–55 Hz) for trials on which the word–color association was successfully learned (WC) and for which it was not (miss) for study trials preceded by zero (pre0), one (pre1), or two (pre2) crosshairs. Values are mean z scores across subjects. Middle right: significance plots for the main effect of pre (top), the main effect of mem (middle), and the Pre × Mem interaction (bottom). Only pixels significant at $p < .05$ (corrected for multiple comparisons) are shown; all other pixels are black. Right: mean spectral power values extracted from a mask in TF space corresponding to pixels exceeding $p < .05$ for the main effect of Pre × Mem at Component 1 (top) and Mem × Pre at Component 2 (bottom). Mean spectral power across subjects is plotted on the y-axis; pre0, pre1, and pre2 are on the x-axis. The blue line represents WC trials, and the green line represents miss trials.

EEG Results: 4–13 Hz Data

Characteristic EEG responses followed each visual event in the encoding phase of the experiment. Across the entire scalp, stimulus presentation triggered a steady slowing of the EEG response, leading to a characteristic diagonal "alpha–theta shift" in the TF plots throughout the first 400 msec of the epoch (Figure 2). Although this pattern of neural activity was widespread across the scalp, highest ICA weights were observed over the left (P3) and right (PO8, PO10, P10) parietal cortex, as well as over left frontal sites (F9). From ~400 msec onward, 4- to 13-Hz EEG responses at this component desynchronized, but deeper theta/alpha desynchronization was observed for miss trials, leading to a subsequent memory effect in the theta-band at 400–600 msec poststimulus ($F = 12.7$, $p < .003$). These effects were described by an ICA component that explained 28.6% of the variance in poststimulus theta/alpha-band activity (Figure 2, top).

A second component (variance explained = 4.7%) loaded on anterior midline electrodes (AFz, Fz, F1, F2) extending more widely over left frontal regions ventro-laterally as far as anterior temporal electrode FT9. At these electrodes, TBA (<8 Hz) onset was at ~300 msec and continued until the end of the epoch, and neural synchrony at >400 msec predicted later memory only for those study items that were immediately preceded by another study item (pre0 trials) (Pre × Mem interaction, $F = 3.4$, $p < .05$). A main effect of mem ($F = 9.7$, $p < .008$) was also observed for this late TBA, and an effect of pre approached significance ($F = 2.6$, $p < .09$). Results for this component can be seen in Figure 2 (bottom).

EEG Results: 14–55 Hz Data

Results for the gamma/beta frequency ranges are shown in Figure 3. The most characteristic feature of rhythmic EEG activity in the beta/gamma ranges was a powerful desychronization following stimulus presentation, which was maximal over right parieto-occipital electrodes (O2, CB2, PO4, PO8, and P6). This desynchronization succeeded a burst of beta/alpha power concurrent with stimulus presentation, which persisted in the lower beta range until ~100 msec poststimulus. Encoding success modulated this response in the higher frequency range, as for WC trials, the 40–50 Hz response tapered off very early in the epoch, but for miss trials, it continued until >300 msec poststimulus. This led to reliable differences in 40–50 Hz activity as a function of later memory, with *reduced* neural synchrony over posterior scalp sites at >150 msec observed for later remembered trials ($F = 8.0$, $p < .02$). This effect can be seen in the second from the top significance plot ('mem') in Figure 3 (top, middle right panel). No main effect of pre ($p = .22$) or interaction ($p = .54$) were observed within this mask.

However, later in the epoch, beta-band activity varied in an interacting fashion with subsequent memory and anticipation time, with a deeper desynchronization predicting later memory only for pre0 trials ($F = 6.3$, $p < .01$) (Figure 3, bottom right). This effect was reliable from 400 to 600 msec, at 14–25 Hz (Figure 3, bottom, middle right). This ICA component explained 13.1% of the variance in poststimulus beta/gamma activity.

A second component (variance explained = 12.2%) exhibited a broad frontotemporal topography, with maximal weights observed at electrodes F5, FT7, FC5, C3, and C5. Neural activity onset over these regions in the beta/gamma range with or shortly after stimulus presentation, and frontal ~40 Hz synchrony from ~200–300 msec predicted subsequent memory, but only in the pre2 condition, where the study item was preceded by two crosshair stimuli. This effect was statistically reliable (Pre × Mem interaction, $F = 4.43$, $p < .03$) although the focus of the statistical differences was slightly lower, at 30–35 Hz. No main effect of mem ($p = .68$) was observed within this mask over these frontal sites, although there was a trend for GBA to increase in concert with anticipation time ($p = .06$).

DISCUSSION

Subjects performed a version of the DM paradigm in which the times that preceded and followed each study item were independently manipulated. As predicted, a longer poststimulus period facilitated later memory, presumably because it permitted more time for strategic conceptual processing (such as phonological rehearsal or semantic elaboration) that is well known to lead to "deep" encoding (Craik & Lockhart, 1972). However, the novel behavioral result presented here is that time *prior to* the stimulus is a robust and independent predictor of encoding success, with longer intervals prior to presentation of a study item leading to improved later memory for that item. Moreover, we identified dissociable subsequent memory effects over the left prefrontal cortex for predictable study items (which subjects were 100% sure were about to occur) and unpredictable study items (which there was only a 33% chance would occur) in the gamma (>25 Hz) and theta (4–8 Hz) bands, respectively. These findings complement previous research into the functional role of gamma- and theta-band neural synchrony in memory and attention, and describe, for the first time, functionally dissociable correlates of top-down and bottom-up attention orienting during successful episodic encoding.

Neural Synchrony: Theta Band (4–8 Hz)

Compelling evidence indicates that TBA plays a role in short-term memory maintenance (Sarnthein et al., 1998)

but the precise nature of that role remains poorly understood (Bastiaansen & Hagoort, 2003). A further role in intermediate- and long-term memory formation is suggested by the finding that long-term potentiation, the candidate cellular–molecular basis for the formation of new memories, seems to depend on the phase of hippocampal theta activity (Huerta & Lisman, 1993), and blocking theta activity by lesioning the medial septum causes spatial memory impairments (Givens & Olton, 1990). Moreover, during serial learning of words, increases in neocortical theta-band synchrony, particularly over the frontal cortex, are a robust predictor of later memory (Summerfield & Mangels, 2005a; Sederberg et al., 2003; Klimesch et al., 1996). Neocortical TBA may thus play an important role in memory formation, perhaps by ''informing'' the hippocampus what should be bound with what during declarative memory formation (Buzsaki, 1996).

However, a broader role for TBA in cognition has been suggested by the finding that sensorimotor and attentional mechanisms are associated with increases in theta-band synchrony. In particular, frontal midline TBA seems to reflect control processes that are activated when a subject is required to orient attention or prepare to respond (Makeig, Delorme, et al., 2004), and ERP components implicated in detection of novel or salient events, such as the positive-going P2 and P300 waves observed over midline frontal and parietal electrodes, may reflect event-related spectral perturbation (ERSP) of ongoing theta rhythms at the cortex (Makeig, Westerfield, et al., 2002). According to this theory, bottom-up stimulation may lead to a ''phase reset'' of the theta rhythm, such that during event-related averaging, amplitude maxima and minima of ongoing theta activity are aligned to form the characteristic positive- and negative-going deflections of the ERP (although this view of the relationship between neural synchrony and the ERP remains controversial) (Yeung, Bogacz, Holroyd, & Cohen, 2004). Here, we argue that a theta-band phase-reset may form part of a mechanism by which attention is oriented to an unpredicted stimulus, invoking executive control processes required to flexibly accommodate novel or unexpected information within the current set of goals and plans. Accordingly, decades of ERP research have shown that positive-going deflections at 200–400 msec over the frontal and parietal cortices are enhanced during the processing of oddball stimuli (McCarthy & Donchin, 1981), are suppressed under divided attention (Mangels et al., 2001; Wickens, Kramer, Vanasse, & Donchin, 1983), and predict subsequent memory (Otten & Donchin, 2000), precisely as would be predicted if these early ERP/ERSP effects reflect attentional effects that gate successful encoding. The idea that frontal midline TBA reflects a general attentional orienting mechanism can explain why it has been found to vary over a wide range of attentional, memory, and motoric tasks, and why abnormalities in TBA are a hallmark of disorders of attention such as ADHD (Barry, Clarke, & Johnstone, 2003).

Regardless of whether the stimulus was predictable (pre2) or not (pre0), we observed increases in TBA all over the scalp, and notably over parietal electrodes, on trials on which the word–color association was successfully encoded (WC trials) compared to those on which it was not (misses). We thus replicated previous reports implicating TBA in successful encoding (Summerfield & Mangels, 2005a; Sederberg et al., 2003; Klimesch et al., 1996). More importantly, however, both at this broad scalp component and at another component that loaded heavily on midline frontal scalp sites and extended over the left frontal cortex, a significant interaction was observed whereby theta synchrony predicted later memory to a greater extent on pre0 trials, that is, where one study item unexpectedly succeeded another. This activity was initially observed as early as ∼200 msec poststimulus at posterior electrodes, and slightly later (>400 msec) over the frontal cortex, falling well within the time frame of observed theta-band ERSP effects. It seems likely that where the appearance of a forthcoming stimulus cannot be predicted, the effectiveness with which attention is disengaged from the prior study item and oriented toward the current item will be a robust predictor of subsequent memory. By contrast, on well-spaced, predictable trials, TBA is a poorer predictor of later memory, as subjects are able to orient their attention to the forthcoming study item in a top-down fashion even before the stimulus arrives. Moreover, the topography of the ICA component at which this activity was observed, loading maximally on frontal midline electrodes, is highly consistent with previous studies showing that frontal dorsomedial areas (and the underlying anterior cingulate cortex) are an important part of a network underlying the orienting of attention to spatial locations, features, or representations (Corbetta & Shulman, 2002). These data thus provide support for the idea that TBA predicts later memory because it subserves the disengagement and reengagement of attention during the unfolding of an unpredictable sequence of stimuli or events.

Neural Synchrony: Gamma Band (>25 Hz)

We also found increases in GBA over the left prefrontal cortex during successful encoding. This is consistent with recent reports that increased neocortical gamma-band synchrony during encoding is associated with later recall (Sederberg et al., 2003) and recognition memory (Gruber, Tsivilis, et al., 2004). Does neocortical GBA directly contribute to the formation of a new declarative memory trace, or does it covary with attentional factors that facilitate encoding? The former is suggested by data from intracranial recordings in humans, which noted that phase-locking of gamma-band responses between the hippocampus and nearby rhinal cortex (Fell, Klaver,

Lehnertz, et al., 2001), through which major afferent pathways to the hippocampus pass (Amaral & Witter, 1989). However, accumulating evidence suggests a role for neocortical GBA in the top-down orienting of attention to an expected or target stimulus (Herrmann et al., 2004; Debener et al., 2003; Engel et al., 2001). Consistent with this view, we observed that on trials where the presentation of a study item was predictable (i.e., when subjects had time to orient attention in a top-down fashion to a forthcoming event) the ∼40 Hz response was earlier and stronger as a function of later memory.

The functional significance of high-frequency brain activity (>25 Hz) in human cognition remains controversial (Kaiser & Lutzenberger, 2005). Early reports arguing for a role in bottom-up perceptual grouping according to gestalt principles (Singer & Gray, 1995) were quickly complemented with findings that GBA is observed to vary with experimental manipulations of attention (Muller, Gruber, & Keil, 2000; Gruber, Muller, Keil, & Elbert, 1999; Tallon-Baudry, Bertrand, Delpuech, & Permier, 1997) and working memory (Tallon-Baudry, Bertrand, & Fischer, 2001). Accordingly, a role in top-down attentional control has been proposed (Engel et al., 2001). According to one model, GBA may be involved in "matching" a top-down prediction to bottom-up sensory information in order to facilitate recognition of an expected (Miltner et al., 1999) or relevant (Debener et al., 2003; Fries, Reynolds, Rorie, & Desimone, 2001) stimulus once it arrives. This model has been called memory match and utilization (MUM) theory (Herrmann et al., 2004) and argues that "early" gamma activity (occurring at ∼150 msec poststimulus) reflects the confluence of incoming information with a top-down representation or preestablished schema. Intuitively, it makes sense that such a mechanism should be deployed where the to-be-learned stimuli are expected and a reliable top-down prediction can be formed of the forthcoming stimulus (Friston, 2003), as was the case on pre2 ("predictable") trials. Furthermore the time and frequency at which we observed subsequent memory effects (40 Hz, ∼200 msec poststimulus) show very close convergence with those conjectured to underlie the confluence of top-down and bottom-up activity. Our data are thus highly consistent with the MUM model, and extend it to suggest that in addition to facilitating recognition of the stimulus, these top-down attentional mechanisms may increase the likelihood that it is encoded into long-term memory. Interestingly, a recent study of sentence comprehension has shown that GBA predominates when sentences contain semantically correct or expected items, whereas theta-band responses are evoked by semantic violations, data that clearly mimic the theta/gamma dissociation reported here (Hald, Bastiaansen, & Hagoort, 2005).

Over posterior electrodes, however, a different pattern was observed whereby gamma-band synchronization at 40–50 Hz was reliably greater during unsuccessful

encoding, an effect that occurred at ∼300 msec post-stimulus. Although it may at first appear contradictory, "negative" subsequent memory effects (i.e., desynchronization associated with successful encoding) have been reported previously in the gamma band (Sederberg et al., 2003; Fell, Klaver, Lehnertz, et al., 2001). Indeed, recordings from within the hippocampus have shown that enhanced gamma-band spectral power at 100–400 msec is a correlate of encoding trials that are later "missed," a time course that closely matches that observed here.

Left Anterior Cortex and Episodic Encoding

Neural activity that varied in an interacting fashion between both top-down and bottom-up attentional orienting and episodic encoding extended over scalp electrodes that were positioned to capture neural activity from the left prefrontal cortex. Left dorsolateral prefrontal regions have been previously shown to be a robust predictor of the learning of word–color associations (Ranganath et al., 2004), and more ventral regions are among the most frequently implicated in subsequent memory studies where item-context binding is criterial for successful encoding (Davachi, Mitchell, & Wagner, 2003; Cansino, Maquet, Dolan, & Rugg, 2002). Moreover, activity in the left prefrontal cortex fails to predict later memory when attention is divided with a demanding secondary task, indicating that the contribution of this region to successful encoding is attention dependent. This result, coupled with the established theory that left frontal regions support semantic retrieval (Cabeza & Nyberg, 2000), and the finding that it is recall and conscious recollection (retrieval criteria that benefit most from "deep" encoding) that suffer most under divided attention (Craik et al., 1996), forms the basis for the view that reducing attentional resources impairs later memory because it leaves subjects less opportunity to engage in deep semantic elaboration of the study item.

However, it has also been suggested that suppression of semantic elaboration may not be sufficient to account for the impairment to later memory observed following divided attention (Naveh-Benjamin, Guez, et al., 2003). For example, DA-related impairments in later recall persist even when items were matched with respect to subjective ratings of how well they were elaborated at study (Craik & Kester, 2000). One explanation for this discrepancy is that over and above any role in semantic retrieval, left anterior regions may form part of a wider network that contributes to successful encoding by mediating the control of attention toward the study item. A more direct role for the left anterior cortex in attention processing has been suggested by a previous DM study that found "state-related" effects predicting later memory in the left inferior frontal lobe (Otten, Henson, & Rugg, 2002). State-related effects index neural activity that does not vary with the temporal onset of the

stimulus, such as slow fluctuations in vigilance, or attentional control processes that begin prior to stimulus presentation. This study, taken together with others positing a direct role for the left anterior cortex in the controlled biasing of attention (Brass & von Cramon, 2004; MacDonald, Cohen, Stenger, & Carter, 2000), offers an alternative explanation for our data: that the contribution of left frontal regions to episodic encoding relates to controlled orienting of attention to predictable and unpredictable verbal events. This view is consistent with recent approaches to understanding the function of the left prefrontal cortex that eschew domain specificity in favor of a wider role in the regulation of mental activity (Thompson-Schill, Bedny, & Goldberg, 2005).

Neural Synchrony: Other Results

Although we observed increases in gamma-band synchronization over left frontal regions in association with later memory, the general trend for high-frequency (>14 Hz) neural activity across more posterior cortical regions was to desynchronize upon stimulus presentation. Neural activity in the beta and gamma bands exhibited a characteristic prestimulus synchronization that tapered off earlier at higher frequencies, continuing in the lower beta band until about ~100 msec poststimulus, but then gave way to a powerful desynchronization that was prominent across the scalp. ICA analyses in our laboratory (Summerfield & Mangels, 2005b) and conventional analyses from other laboratories (Bastiaansen, van der Linden, Ter Keurs, Dijkstra, & Hagoort, 2005) have previously identified this trend in the beta frequency range, although it is most often observed following a voluntary movement (Pfurtscheller, 1992). The extent of beta synchrony varied with expectation and memory, with a deeper desynchronization on pre0/WC trials, where subjects successfully learned the second of two sequentially presented word–color associations. Beta desynchronization at >500 msec has been previously observed in association with subsequent memory (Sederberg et al., 2003), although, in general, little is known about its role in attention and memory. However, a recent report employing rapid serial visual presentation has argued that beta-band synchronization may reflect a state of increased vigilance for behaviorally relevant stimuli (Gross et al., 2004). It could be, thus, that in conditions where bottom-up attention is not captured by the stimulus (i.e., where the study item is predictable, or where subjects fail to orient and thus encode), processing resources are freed up for vigilant anticipation of the forthcoming stimulus. One explanation for our observation of a beta-band "rebound" in a nonmotoric task is thus that it reflects generalized anticipation processes relating to the forthcoming stimulus, rather than the neural sequelae of voluntary movement execution.

Summary

Our data thus argue for a functional dissociation in the role of theta (4–8 Hz) and gamma (25–55 Hz) activity in successful episodic encoding. One way of interpreting the data presented here is that multiple attentional processes, dependent on the activation of the frontal cortex (and in particular left frontal cortex) sites, facilitate the formation of new memories. Where the to-be-encoded information is unexpected, the extent to which attention is disengaged from the current focus and oriented to the relevant information is likely to be highly predictive of later memory. This mechanism is mediated by transient neural synchrony in the theta (4–8 Hz) band, particularly over dorsomedial frontal regions previously implicated in endogenous attentional orienting. Predictable information, however, is encoded in a different way. Top-down attentional mechanisms mediated by neural synchrony in the gamma (>25 Hz) band increase early in the poststimulus epoch as a function of expectancy and memory, in concert with increasing behavioral performance on trials where study items were well spaced and expected. Left frontal GBA thus constitutes an excellent candidate for the neural substrate of a top-down attentional orienting mechanism that facilitates the encoding of new episodic memories.

Acknowledgments

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