Functional coupling between frontal and parietal lobes during recognition memory

Christopher Summerfield[CA] and Jennifer A. Mangels

Psychology Department, Schermerhorn Hall, Room 406, Columbia University, 1190 Amsterdam Ave, New York, NY 10027, USA

[CA]Corresponding Author: summerfd@psych.columbia.edu

Neuroimaging studies have suggested that the frontal and parietal lobes may be important for the process by which we remember information. However, little is known about how these regions exchange information during memory retrieval. We measured EEG synchronisation in the gamma-band (25–55 Hz), a putative measure of functional coupling between brain regions, while human subjects performed a recognition memory task. Fronto-parietal synchrony was increased for true old memories relative to false memories and new items. Our results suggest that synchronization of neuronal responses in the gamma-band may be an important mechanism by which frontal and parietal regions exchange information during the recognition of past events. *NeuroReport* 16:117–122 © 2005 Lippincott Williams & Wilkins.

Key words: DRM paradigm; Electroencephalography (EEG); False memory; Gamma-band activity (GBA); Independent components analysis (ICA); Retrieval

INTRODUCTION

Our understanding of how the brain distinguishes old from new events has been deepened by the advent of neuroimaging techniques that permit trial-by-trial sorting of neural responses, such as event-related fMRI and ERP. Using these techniques, researchers have observed that neural phenomena that are sensitive to whether a recognition probe is old or new ('old/new effects') tend to be localised to the frontal and parietal lobes [1]. Further information about the neural processes underpinning recognition memory has been provided by investigations of false memory, in which subjects report recognising (with high confidence) an item to which they were not previously exposed. Interestingly, although regions of frontal cortex that show robust old/new effects do not seem to be sensitive to whether the memory is true or false [2], this is not the case for posterior brain regions, which appear to track the veridicality of the memory ('true/false' effects) [3–6]. Consistent with the notion that posterior brain regions are required for recollection of sensory context or 'source', true memories may additionally involve re-activation of cortical regions that initially supported encoding of the sensory/perceptual features of the relevant stimulus ('sensory recapitulation') [4,5].

Whilst fMRI and ERP studies provide important information about the contribution of individual brain regions to a neural effect, other techniques are more suited to exploring how neural information is shared within a brain network during cognition. The phase-locking (coherence) of oscillatory neural responding between two brain regions, which may reflect functional coupling between neural assemblies, can be measured by signal processing techniques that involve decomposing the scalp EEG signal into its spectral components [7]. Initial explorations of high-frequency brain activity (gamma-band [25–55 Hz] activity or GBA) during recognition have suggested that 'local' synchrony over a single brain region may vary between old and new items [8], or as a function of the subjective experience which accompanies memory [9], however no study has yet explored whether long-range coherence between frontal and parietal lobes dissociates between old and new recognition or true and false recognition. In the present study, we compared both local and long-range GBA across the brain for recognition trials on which old events were judged to be old (hits) with new events judged to be new (correct rejections) and new events judged to be old (false alarms). Our data demonstrate for the first time that successful veridical recognition of visual stimuli requires long-range functional coupling between the frontal and parietal lobes, mediated in part by synchronisation of high-frequency neural responding.

SUBJECTS AND METHODS

Subjects: Nineteen neurologically normal right-handers (13 women; mean age 25.4 years, range 18–38 years) were paid $25 to participate in the study. All subjects gave informed consent and the study was approved by Columbia University Institutional Review Board.

Design and procedure: We employed a variant of the Deese-Roediger-McDermott (DRM) task [10]. In the typical DRM task, subjects study a list of words (e.g., candy, sugar, bitter…taste) that are all semantically associated to some degree with a non-present theme word (e.g., sweet). This theme word is called the lure because the semantic overlap

between it and the studied words induces subjects to falsely recognize this item as old with relatively greater frequency and confidence than non-associated foils. In our version of the DRM paradigm, subjects studied 18 lists of 10 visually-presented words that were moderately associated with a theme word. Later, recognition memory was tested with six of the list words (randomly selected), along with the lure, two of its highest associates, and three of its lowest associates as foils. No non-associated items were used as foils. This modification was done to increase further the likelihood that we would obtain a sufficient number of high-confidence false alarms for EEG analysis. In addition, to reduce the likelihood that subjects would adopt the heuristic that the lure and high associates were never actually presented, six of the 24 lists were reverse lists, in which high associates (including the lure) and low associates were studied and moderate associates served as foils.

The experiment consisted of three blocks. In each block, subjects intentionally encoded items from six regular lists and two reverse lists. Words were presented centrally and sequentially on the screen for 1000 ms, followed by a blank screen for 1000 ms. After each list, subjects performed a brief distracter task (counting backwards) and were then prompted to freely recall words from that list. The next list was then presented. In the recognition test following each block, 96 words were presented (48 old, 48 new). During the recognition test, each probe word was presented centrally on the screen for 2000 ms, after which subjects pressed a key corresponding to one of four recognition/confidence options: sure old, think old, think new, and sure new. A 1000 ms blank screen preceded the next probe word.

For analysis, recognition trials were classified as hits, false alarms (FA), and correct rejections (CR). Misses were discarded due to low trial counts. Old/new effects were examined by testing for neural activity that was greater for hits than CR; true/false effects by testing for neural activity that was greater for hits than FA. We only included high-confidence responses in our analysis so that observed differences between trial types could not be attributable to variation in between-condition guessing rates.

EEG recording and artifact rejection: EEG was acquired during recognition from 64 channels (sampling rate 500 Hz, impedances $<11\,k\Omega$) using Neuroscan SYNAMPS (Compumedics Inc., El Paso, TX). BESA 5.06 (Electrical Geodesics Inc., Eugene, OR) was used to convert from the recorded Cz reference to an average reference, as well as to remove eye movements, blinks and other artifacts from the continuous EEG data [11]. Trials with muscle, movement or other visible artifacts were manually rejected. Artifact-free data were high-pass filtered with a 0.5 Hz zero-phase filter and then spline-laplacian transformed to obtain the estimated dura potential [12].

Data analysis: We explored two measures of GBA synchrony: local and long-range/coherence. Local GBA refers to increases in gamma band power detected at a single scalp electrode, which will generally be most sensitive to the synchronous oscillation of neurons within a relatively localised region of cortex proximal to that electrode. Long-range GBA or GBA coherence refers to the extent to which oscillations at two disparate electrodes maintain a constant phase relationship in the gamma band, and may indicate

that the cortical regions underlying these electrodes are engaged in some exchange of information.

In the present study, estimates of local spectral power were derived for each trial with a Morlet wavelet transform in the 25–55 Hz range (0–1500 ms). These estimates were trimmed and averaged at each electrode for each subject, in each condition. ICA was used to reduce data to correlated components, and statistical maps were drawn (using random permutation testing) to identify regions of time-frequency space for each component that exhibited significant differences between the component activation scores for each condition. Coherence was calculated at a subset of 20 electrodes, chosen for their spatial separation, for each condition, using a sliding fourier window of width 500 ms and 2 Hz frequency resolution (frequency range 25–55 Hz), to derive time-frequency estimates of coherence at each of 190 possible pairings. These coherence data were reduced with ICA in a similar manner to the spectral power data, yielding components that loaded on clusters of electrode pairings with a similar time-frequency coherence profile. Time-frequency significance maps were derived from component activations as for the local GBA data. A detailed description of the methods associated with each analysis stage, including caveats and comparison with conventional methods of EEG power and coherence analysis, have been described elsewhere [13]. Data were visualized using code adapted from EEGLAB [14].

RESULTS

Behavioural results: Mean hit rate was $82.8 \pm 8.4\%$ (range 66–99%), mean false alarm rate was $29.5 \pm 17.3\%$ (range 6–64%) and mean correct rejection rate was $70.5 \pm 17.3\%$ (range 36–94%). These values translated into a mean d' of 1.78 ± 0.62 (range 0.59–2.81) and a mean bias (beta) of -0.24 ± 0.32 (range −0.65–0.45). Overall, these data suggest that, consistent with other recognition memory studies employing the DRM paradigm, that subjects exhibited a bias to judge words to be old.

Overall, $67.8 \pm 13.2\%$ of all hit trials, $38.7 \pm 19.1\%$ of all false alarms trials, and $50.1 \pm 22.8\%$ of all correct rejection trials were made with high confidence (HC). As we wished to confine all analyses to HC trials, it was important that all subjects had sufficient numbers of HC trials in each category for robust statistical analysis. We thus excluded six of the 19 subjects who exhibited HC trial counts in any of the three conditions (hits, false alarms, correct rejections) of <20, leaving 13 subjects for all EEG analyses.

EEG results: local gamma-band synchrony: All inferential analyses were conduced on an epoch beginning at stimulus presentation and continuing for 1500 ms. ICA was used to determine the major sources of variance in the local GBA data, and planned comparisons were used to determine areas of TF space for these spatial components that showed old/new or true/false effects. As can be seen in Fig. 1a, the two derived components that accounted for the greatest percentage of the variance between conditions demonstrated topographies corresponding to right frontal and parieto-occipital cortical zones. The time-frequency profiles of component activations for these components are plotted in Fig. 1b, and a map of the (corrected) p-values corresponding to differences between conditions is provided in Fig. 1c.
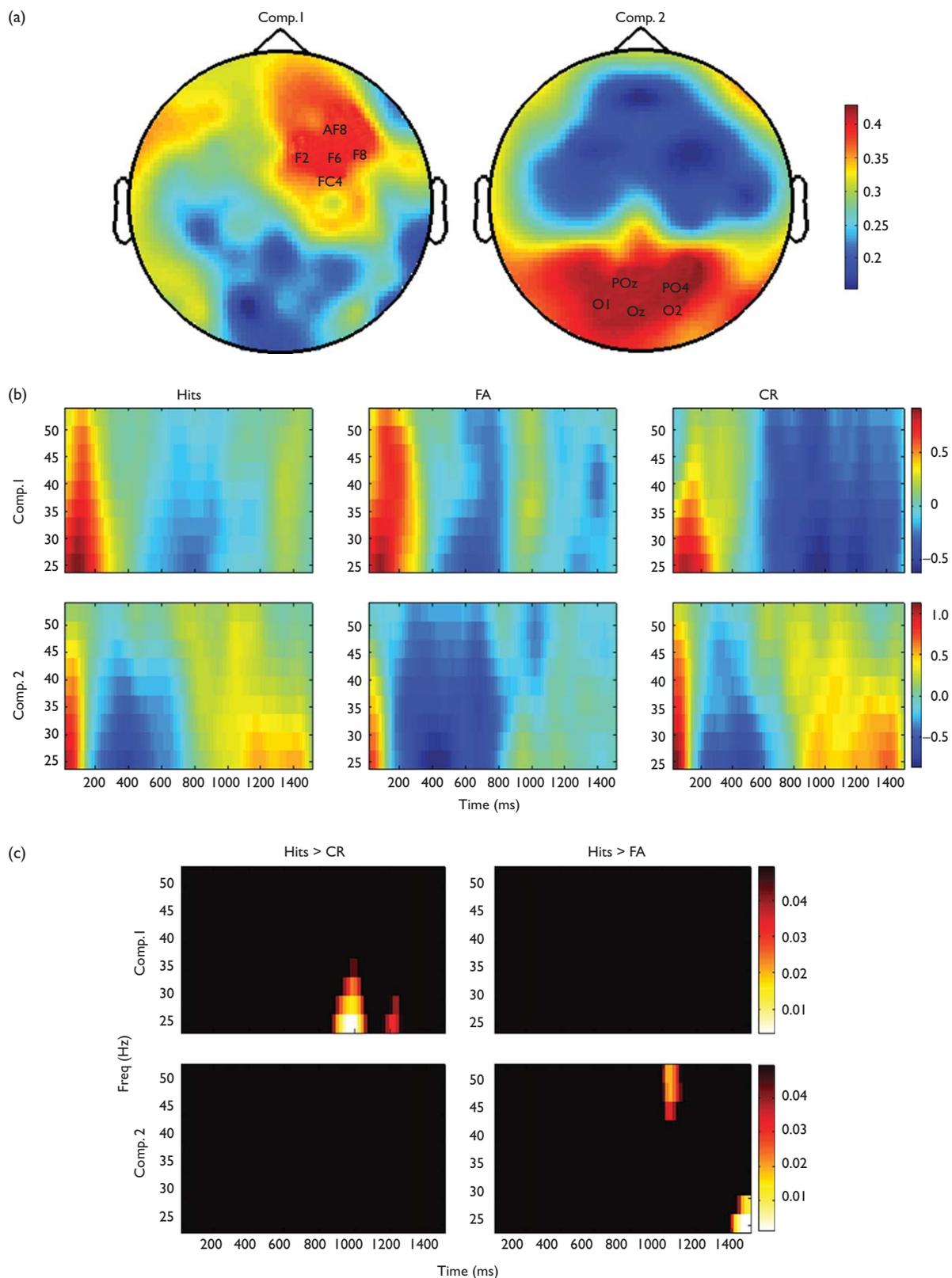
Fig. I. Local GBA data. (a) ICA derived components loading on right frontal (left) and parieto-occipital (right) electrode sites. (b) Component activations (time-frequency plots) for components I and 2 for each condition. Time is on the x-axis, and frequency on the y-axis. Values are z-scores. (c) Areas of time-frequency space in which significant differences are observed for the comparisons Hits > CR and Hits > FA. Scale refers to corrected p-values. Only p-values < 0.05 are shown.
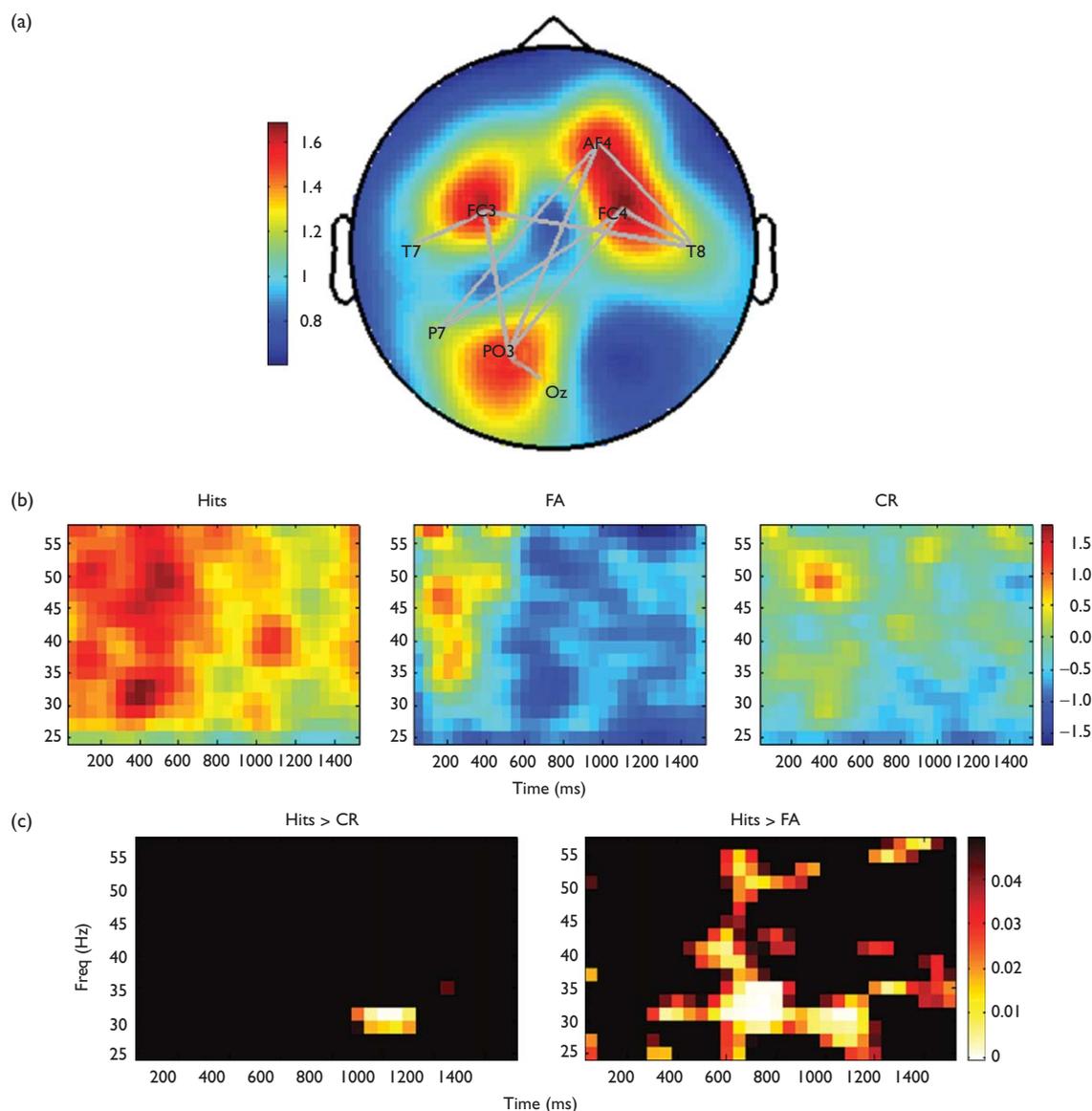
Fig. 2. Long-range GBA data. (**a**) ICA on coherence derived a fronto-parietal component. The top ten weighted electrode pairings (grey lines) are plotted on top of summed ICA weights for each electrode (coloured background). (**b**) Time-frequency distribution of coherence values (component activations) at each condition. Values are z-scores. (**c**) Areas of time-frequency space showing significant differences for comparisons Hits > CR and Hits > FA.

The first component, which explained 21.3% of the variance (eigenvalue=25.6), loaded maximally on right superior dorsolateral frontal regions (AF8, F8, F6, F2, FC4; Fig. 1a, left). GBA was maximal shortly after stimulus presentation in all three conditions, but increased for hit and FA conditions, relative to CR trials, later in the epoch (>750 ms). Statistically reliable old/new effects (hit > CR) were observed at this component beginning at ∼1000 ms in the lower gamma band (25–30 Hz). FA > CR effects were also observed at the same time-frequency location (not shown). However, GBA did not differ between true (Hit) and false (FA) recognition trials.

The component loading principally on parieto-occipital electrodes (Oz, O1, O2, POz, PO4; Fig. 1a, right) explained the second greatest percentage (10.3%) of the variance

(eigenvalue=7.2) and exhibited time-frequency activations which appeared to increase for hit and CR trials relative to FA trials, beginning around 750 ms (Fig. 1b). Inferential analysis confirmed that GBA differed between Hits and FA trials at >1000 ms in both lower (∼25–30 Hz) and upper (∼40–50 Hz) portions of the gamma frequency band (Fig. 2c). No old/new effects (hits > CR) were observed over parietal electrodes.

EEG results: long-range gamma-band coherence: Coherence across the scalp was calculated for hits, FA and CR trials. ICA was conducted to define spatially separable sources of variance contributing to these data. As illustrated in Fig. 2a, the only component we found that accounted for

>5% of the variance (7.7%; eigenvalue=2.9) loaded on electrode pairings within a triangular network of right fronto-temporal (AF4, FC4, T8), left frontal (FC3,T7) and parieto-occipital (P7, PO3, Oz) electrode sites. The highest five weights were observed for the pairings PO3-FC3, PO3-AF4, PO3-FC4, AF4-T8, and AF4-P7. In all three conditions, increases in GBA were observed in the early portion of the epoch (<400 ms), but this response was stronger and more sustained on Hit than FA or CR trials (Fig. 2b). Accordingly, significant differences were observed for the comparisons hit>CR and hit>FA, particularly in the middle and later portions of the epoch. Old/new effects (hit>CR) were maximal at 900–1200 ms post-stimulus, at close to 30 Hz. True/false effects (hit>FA) began earlier, at ∼300 ms, and peaked in the 600–800 ms range at ∼35 Hz, continuing until the end of the epoch (Fig. 2c).

DISCUSSION

Previous neuroimaging studies have shown that frontal and parietal cortical regions are recruited when we recognise past events [1]. Using the complementary approach of EEG wavelet and coherence analysis, we confirmed the involvement of these regions in recognition memory. Our analysis technique (ICA) is a blind separation technique that is applied to reduce independent, linearly mixed input channels into a smaller number of correlated components, without further knowledge of their distribution or dynamics [14]. Despite the fact that local synchrony and long-range coherence data are mathematically independent of each other, in both instances, ICA derived components accounting for the greatest percentage of the variance that loaded maximally on separate frontal and parietal electrode sites. We also extend these results by demonstrating that functional coupling between these regions may be required for true recognition of past events.

Local right anterior and parietal GBA: Observed increases in local spectral power bore a close spatio-temporal resemblance to results reported by previous studies of recognition memory. Consistent with neuroimaging studies, GBA over the right dorsolateral prefrontal cortex exhibited a hit>CR profile of responding [15–17] that occurred late in the epoch and did not discriminate true from false memories [2]. The functional significance of this right frontal activity remains unclear, although it may be associated with retrieval success [17], monitoring the source of a memory [15], or detection of old words as salient targets [16].

We observed that parietal activity, which has been associated with vivid conscious recollection of old items, was attenuated during false relative to true recognition, as reported by previous studies [6,18]. These data thus offer support for a recent theory hypothesizing that true and false recognition trials differ in that only true recognition trials permit a recapitulation of the sensory processing that accompanied encoding [4,5].

Fronto-parietal gamma-band coherence: Parietal cortical zones phase-locked their GBA responses with left and right anterior cortex early in the epoch in all three conditions, but beginning at ∼400 ms post-stimulus, GBA on FA and CR trials began to diminish, such that hits differed reliably from

these conditions >600 post-stimulus. This period coincides with the time during which parietally-mediated conscious recollection processes are proposed to occur (500–800 ms) [19] and continues into portions of the epoch during which late frontal and parietal effects were observed in the present study. In addition, the spatial topography of this activity, which includes left/midline parietal and right dorsolateral prefrontal electrode sites, closely corresponds to spatial topographies identified as exhibiting late old/new (right anterior) and true/false (midline posterior) effects in the local GBA data. Finally, it is notable that the timing of the effect also overlaps (at 850 ms) with a peak in inter-electrode GBA covariation observed in association with subjectively reported recollection [9].

One interpretation for the functional significance of this fronto-parietal activity comes from the working memory literature. Working memory, like recognition memory, is thought to recruit both frontal and posterior parietal cortical sites [20]. Fronto-parietal coherence has been observed during working memory tasks [21,22], and several models of working memory maintain that posterior sensory representations may be activated in a sustained fashion by a frontally located control mechanism [23]. One possibility is that during veridical recognition, a frontally mediated executive control mechanism participates in the tonic reactivation (or recapitulation) of posteriorly represented sensory detail from the encoding episode.

CONCLUSION

Our data suggest that process by which past events are recognised involves a complex dialogue between the frontal and parietal lobes. Beginning at ∼400 ms, high frequency phase locking between these regions occurs preferentially for true old recognition. This sustained phase-locking may subserve an increase in neural integration between these cortical zones, facilitating recognition memory for past events.

REFERENCES

1. Buckner RL and Wheeler ME. The cognitive neuroscience of remembering. *Nature Rev Neurosci* 2001; **2**:624–634.
2. Duzel E, Yonelinas AP, Mangun GR, Heinze HJ and Tulving E. Event-related brain potential correlates of two states of conscious awareness in memory. *Proc Natl Acad Sci USA* 1997; **94**:5973–5978.
3. Gonsalves B and Paller KA. Mistaken memories: remembering events that never happened. *Neuroscientist* 2002; **8**:391–395.
4. Fabiani M, Stadler MA and Wessels PM. True but not false memories produce a sensory signature in human lateralized brain potentials. *J Cogn Neurosci* 2000; **12**:941–949.
5. Cabeza R, Rao SM, Wagner AD, Mayer AR and Schacter DL. Can medial temporal lobe regions distinguish true from false? An event-related functional MRI study of veridical and illusory recognition memory. *Proc Natl Acad Sci USA* 2001; **98**:4805–4810.
6. Curran T, Schacter DL, Johnson MK and Spinks R. Brain potentials reflect behavioral differences in true and false recognition. *J Cogn Neurosci* 2001; **13**:201–216.
7. Lachaux JP, Lutz A, Rudrauf D, Cosmelli D, Le Van Quyen M, Martinerie J *et al.* Estimating the time-course of coherence between single-trial brain signals: an introduction to wavelet coherence. *Neurophysiol Clin* 2002; **32**:157–174.
8. Duzel E, Habib R, Schott B, Schoenfeld A, Lobaugh N, McIntosh AR *et al.* A multivariate, spatiotemporal analysis of electromagnetic time-frequency data of recognition memory. *Neuroimage* 2003; **18**:185–197.

9. Burgess AP and Ali L. Functional connectivity of gamma EEG activity is modulated at low frequency during conscious recollection. *Int J Psychophysiol* 2002; **46**:91–100.

10. Roediger HL and McDermott KB. Creating false memories: remembering words not presented in lists. *J Exp Psychol Learn Mem Cogn* 1995; **21**: 803–814.

11. Berg P and Scherg M. A multiple source approach to the correction of eye artifacts. *Electroencephalogr Clin Neurophysiol* 1994; **90**:229–241.

12. Nunez PL, Srinivasan R, Westdorp AF, Wijesinghe RS, Tucker DM, Silberstein RB *et al*. EEG coherency. I: Statistics, reference electrode, volume conduction, Laplacians, cortical imaging, and interpretation at multiple scales. *Electroencephalogr Clin Neurophysiol* 1997; **103**:499–515.

13. Summerfield C and Mangels JA. Coherent theta-band EEG activity predicts item-context binding during encoding in press. *Neuroimage* 2004; in press.

14. Delorme A and Makeig S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods* 2004; **134**:9–21.

15. Henson RN, Rugg MD, Shallice T, Josephs O and Dolan RJ. Recollection and familiarity in recognition memory: an event-related functional magnetic resonance imaging study. *J Neurosci* 1999; **19**:3962–3972.

16. Herron JE, Henson RN and Rugg MD. Probability effects on the neural correlates of retrieval success: an fMRI study. *Neuroimage* 2004; **21**: 302–310.

17. Rugg MD and Yonelinas AP. Human recognition memory: a cognitive neuroscience perspective. *Trends Cogn Sci* 2003; **7**:313–319.

18. Heun R, Jessen F, Klose U, Erb M, Granath DO and Grodd W. Response-related fMRI of veridical and false recognition of words. *Eur Psychiatry* 2004; **19**:42–52.

19. Rugg MD and Coles MGH. The ERP and cognitive psychology: conceptual issues. In: Rugg MD and Coles MGH (eds). *Electrophysiology of Mind: Event Related Potentials and Cognition*. Oxford: Oxford University Press; 1995, pp. 132–170.

20. Wager TD and Smith EE. Neuroimaging studies of working memory: a meta-analysis. *Cogn Affect Behav Neurosci* 2003; **3**:255–274.

21. Babiloni C, Babiloni F, Carducci F, Cappa S, Cincotti F, Del Percio C *et al*. Human cortical EEG rhythms during long-term episodic memory task. A high-resolution EEG study of the HERA model. *Neuroimage* 2004; **21**:1576–1584.

22. Sarnthein J, Petsche H, Rappelsberger P, Shaw GL and von Stein A. Synchronization between prefrontal and posterior association cortex during human working memory. *Proc Natl Acad Sci USA* 1998; **95**:7092–7096.

23. Petrides M. Specialized systems for the processing of mnemonic information within the primate frontal cortex. *Philos Trans R Soc Lond B Biol Sci* 1996; **351**:1455–1461; discussion 1461–1462.