Explicit processing of verbal and spatial features during letter-location binding modulates oscillatory activity of a fronto-parietal network

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ABSTRACT

The present study investigated the binding of verbal and spatial features in immediate memory. In a recent study, we demonstrated incidental and asymmetrical letter-location binding effects when participants attended to letter features (but not when they attended to location features) that were associated with greater oscillatory activity over prefrontal and posterior regions during the retention period. We were interested to investigate whether the patterns of brain activity associated with the incidental binding of letters and locations observed when only the verbal feature is attended differ from those reflecting the binding resulting from the controlled/explicit processing of both verbal and spatial features. To achieve this, neural activity was recorded using magnetoencephalography (MEG) while participants performed two working memory tasks. Both tasks were identical in terms of their perceptual characteristics and only differed with respect to the task instructions. One of the tasks required participants to process both letters and locations. In the other, participants were instructed to memorize only the letters, regardless of their location. Time-frequency representation of MEG data based on the wavelet transform of the signals was calculated on a single trial basis during the maintenance period of both tasks. Critically, despite equivalent behavioural binding effects in both tasks, single and dual feature encoding relied on different neuroanatomical and neural oscillatory correlates. We propose that enhanced activation of an anterior-posterior dorsal network observed in the task requiring the processing of both features reflects the necessity for allocating greater resources to intentionally process verbal and spatial features in this task.

Keywords:

Binding
Working memory
Episodic buffer
Oscillatory activity
Prefrontal cortex
Magnetoencephalography

The capacity to maintain and manipulate information in working memory (WM) is critical to higher cognitive functions. Despite its crucial role in a number of mental skills and abilities, WM capacity is surprisingly limited. Through the integration of individual features into “objects”, however, we are capable of processing larger amounts of information. Indeed, recent experimentation suggests the limit of WM capacity to be set at around three to four bound “objects” (Cowan, 2001; Todd & Marois, 2004; Vogel, Woodman, & Luck, 2001). The ability to integrate information involves “the reorganization of bits of information to create more complex but unified representations of previously distributed information” (Wheeler & Treisman, 2002), a phenomenon identified

in the memory literature as ‘chunking’ (Baddeley, 2000; Ericsson, Chase, & Faloony, 1980; Miller, 1956; Simon, 1974). In visual WM, the integration of different stimulus features into more complex representations or objects is most often referred to as ‘binding’ (Alvarez & Cavanagh, 2004; Bays & Husain, 2008; Eriksen & Yeh, 1985; Gray, 1999; O’Craven, Downing, & Kanwisher, 1999; Wheeler & Treisman, 2002; Wolfe et al., 1990), a process increasingly recognized as a critical determinant of memory performance (Cowan, 2001). A large part of the existing research on binding and WM has focused on the integration of visual features (Bodelon, Fallah, & Reynolds, 2007; Filbey, Holroyd, Carver, Sunderland, & Cohen, 2005; Friedman-Hill, Robertson, & Treisman, 1995; Luck & Vogel, 1997; Todd & Marois, 2004; Vogel & Machizawa, 2004; Zhang & Luck, 2008) and, to a smaller extent, auditory features (Maybery et al., 2009; Saito et al., 2005; Widmann, Gruber, Kujala, Tervaniemi, & Schroger, 2007). The integration of (visually presented) verbal and spatial features has attracted, in comparison,

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less scrutiny. However, interest has recently grown following the addition to the WM model of the episodic buffer, a new component, defined as “an interface between a range of systems, each involving a different set of codes” (Baddeley, 2000). The inclusion of this component mainly responded to the initial model’s limitations in accounting for the binding between representations handled by the WM’s visual and verbal subsystems, or the links between long-term language knowledge and WM (Allen, Baddeley, & Hitch, 2006). Recently, several behavioural studies have begun to investigate the mechanisms underpinning verbal–spatial binding (Cowan, Sauls, & Morey, 2006; Luck, Foucher, Offerlin-Meyer, Lepage, & Danion, 2008; Mitroff & Alvarez, 2007; Morey, 2009; Oberauer & Vockenberg, 2009). The neural bases of this type of binding have also been investigated by means of functional magnetic resonance imaging (fMRI) and magneto/electroencephalography (MEG/EEG) (Campo et al., 2005, 2008, 2010; Luck et al., 2010; Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000; Wu, Chen, Li, Han, & Zhang, 2007). All of these studies used modified versions of the single probe change-detection task developed by Prabhakaran et al. (2000), in which participants were asked to maintain both verbal (either letters or words) and spatial (locations) information presented either in an integrated (bound condition) or in an unintegrated fashion (separate condition). When contrasting bound and separate conditions, greater activations were typically found in anterior prefrontal cortex (PFC) in the former, suggesting a fundamental role of this region in the binding process. These results are in agreement with previous findings on object–location binding in animals (Rainer, Asaad, & Miller, 1998a, 1998b; Rao, Rainer, & Miller, 1997), and humans (Filbey et al., 2005; Mitchell, Johnson, Raye, & D’Esposito, 2000; Simon-Thomas, Brodsky, Willing, Sinha, & Knight, 2003). Additionally, greater involvement of posterior parietal cortex (PPC) during the maintenance of integrated verbal–spatial information has also been observed (Campo et al., 2005, 2008; Luck et al., 2010; Wu et al., 2007).

In a recent study (Campo et al., 2010), we demonstrated implicit verbal–spatial binding effects that were dependent on the task-relevant feature. We used MEG to measure brain activity underpinning the maintenance of verbal and spatial features in two recognition tasks, based on a letter–location paradigm previously used in binding studies (Prabhakaran et al., 2000). In both the verbal and spatial tasks, participants were presented with four consonants appearing simultaneously in four distinct locations. Both tasks were identical in terms of their perceptual characteristics and only differed with respect to the task instructions. In the verbal task, participants attended to the consonants only (their locations were irrelevant), while in the spatial task they attended to the locations only (consonants identity was irrelevant). We observed that maintaining the verbal information (consonants) arranged in a spatially distributed manner resulted in the concurrent processing of the (task-irrelevant) location information—in other words, attending to consonant identity resulted in binding those consonants to their spatial locations. Interestingly, the reverse effect was not observed, supporting the notion of an asymmetric association between verbal and spatial features. This implicit or unintentional binding of verbal and spatial features was associated with greater oscillatory activity over PFC in “classical” frequency bands during the first half of the retention period and accompanied by greater activity in PPC and temporal regions.

Despite the fact that the processing of the spatial feature occurred in an involuntary manner, the pattern of brain activation was very similar to that observed in previous studies in which participants attended to, and intended to maintain, both verbal and spatial features (Campo et al., 2005, 2008; Luck et al., 2010; Prabhakaran et al., 2000; Wu et al., 2007). This similarity is intriguing considering evidence from neuroimaging studies establishing distinct neuroanatomical substrates for controlled and incident-

tal memory (Chiu et al., 2006; Dove, Manly, Epstein, & Owen, 2008; Fletcher et al., 2001; Lekeu et al., 2002; Noldy, Stelmack, & Campbell, 1990; Reber, Gitelman, Parrish, & Mesulam, 2003; Reber et al., 2002; Rugg, Fletcher, Frith, Frackowiak, & Dolan, 1997; Rugg et al., 1998; Russeler, Hennighausen, Munte, & Rosler, 2003; Schott, Richardson-Klavehn, Heinze, & Duzel, 2002; Schott et al., 2005). Brain areas showing greater responses in the controlled memory commonly include anterior PFC and posterior cerebral regions. Executive processes related to voluntary cognitive processing of information have been related to anterior PFC (Bor, Duncan, Wiseman, & Owen, 2003; Buckner & Koutstaal, 1998; Dove et al., 2008; Fernandez & Tendolkar, 2001; Wagner, 1999), while stimulus-specific enhanced activity in posterior areas has been suggested to be the result of frontally guided control processes (Dove et al., 2008).

We were interested to investigate whether the patterns of brain activity associated with the incidental binding of letters and locations observed when only the verbal feature is attended (Campo et al., 2010) differ from those reflecting the binding resulting from the controlled/explicit processing of both verbal and spatial features. To this end, we used MEG to compare the neural oscillatory activity occurring in two tasks: one in which participants attended to the verbal features only, and one in which both letters and locations were intentionally processed. As recently highlighted by Voss and Paller (Voss & Paller, 2008), it is important to use similar memory tests and procedures in order to determine “the extent to which certain neural processing events uniquely contribute to only one type of memory”. Therefore, in line with our previous study, both tasks were identical in terms of their perceptual characteristics (participants were presented with four consonants appearing simultaneously in four distinct locations) and only differed with respect to the task instructions. One of the tasks required participants to encode both letters and locations, while in the other participants were instructed to memorize the letters only, regardless of their location. The presence of binding was measured behaviourally by comparing performance in two critical types of positive recognition probes: intact and re-combined probes. Intact probes consisted of a letter presented in the same location as at encoding. Re-combined probes involved a letter and location both presented at encoding but not together (i.e. a letter and location switch). As both probe types were identical in terms of their constituent features and only differed with respect to their original pairing (preserved or swapped), an advantage of recognizing intact over re-combined probes, in accuracy and/or reaction time (RT), would indicate that verbal and spatial features were maintained in an integrated fashion in WM. In contrast, if verbal and spatial features were held independently, intact and re-combined probes would be functionally equivalent and would yield similar levels of performance. Our rationale follows the so-called object-specific repetition effect, first described by Kahneman, Treisman, and Gibbs (1992), according to which the processing of a visual item is facilitated by its repetition as long as the relationship between visual identity and spatial location is maintained across repetitions (Elsley & Parmentier, 2009, see also Prabhakaran et al., 2000).

As binding was anticipated in both tasks, of interest was the pattern of neural activity in each based on the instruction relating to spatial location. In other words, would activations differ based on whether the encoding of spatial location was implicit (the verbal only task) or intentional (the verbal–spatial task)? Considering previous evidence (Kubler, Murphy, Kaufman, Stein, & Garavan, 2003), we hypothesized that the explicit requirement of processing both verbal and spatial features would impose greater demands, and that, accordingly, additional executive functions will be necessary. Therefore, we expected that greater engagement of strategic control processes would be associated with a greater neuronal

Fig. 1. Schematic illustration of both types of positive recognition probes. Trials in the verbal and verbal-spatial conditions were identical and differed only with respect to the instructions given to participants (to memorize either the consonants, regardless of their location, or both the consonants and the locations). The examples depicted on this figure are that of an intact probe (a letter that was in location) and recombined probe (both consonant and location were presented in the to-be-remembered array but not together). Probe consonants were always in lower case form.

oscillatory activity in various frequency bands, predominantly in the anterior PFC, and possibly also affecting oscillatory activity of posterior brain systems.

1. Materials and methods

1.1. Subjects

Eleven adult subjects (6 females), aged between 22 and 32 (mean age 24.36 years, SD of 2.99 years) participated in the present study. These participants had no history of neurological or psychiatric illness and had participated in our previous study (Campo et al., 2010). All gave their written consent, in accordance with the Declaration of Helsinki, after receiving a full briefing regarding the nature of the procedures involved in the experiment. They received 40€ upon completion of the experiment.

1.2. Stimuli and tasks

Experimental tasks were modelled on a letter-location paradigm developed by Prabhakaran et al. (2000) and adapted by Elsley and Parmentier (2009) consisting of a visual memory array of four consonants displayed in four locations (Fig. 1). The verbal stimuli comprised a set of eight consonants (arial font; 48 pt), selected so as to differ in appearance between upper- and lower-case forms (D, F, H, J, N, Q, R, T). The spatial stimuli were presented within a set of eight spatial locations, marked by squares, placed equidistantly in a circular manner and sustaining a visual angle of 3.63° from the center of each square to the central fixation cross. Both tasks used identical stimuli, but differed with respect to the features to be attended and memorized. In the verbal task, participants were asked to remember the identity of the consonants, irrespective of their location. In the verbal-spatial task, participants were instructed to remember both the identity and the location of the consonants. Each task began with a self-paced set of instructions, and five practice trials. At the beginning of each trial, participants first saw a 500 ms central fixation cross, followed by a sample memory array consisting of four consonants, displayed in white (against a black background) and in upper-case, selected at random (without replacement) from the above set of eight. Each consonant appeared in a distinct location randomly selected (without replacement) from the possible set of eight. The consonants were presented within a $1.87^\circ \times 1.87^\circ$ white frame to reduce variations in spatial configuration caused by the consonants perse (Delvenne, Braithwaite, & Humphreys, 2002). The to-be-remembered array remained on the screen for 2000 ms. After a 1200 ms delay interval, in both tasks, participants were presented with a single lower-case consonant in a location for 1000 ms, during which they were required to respond (a 1000 ms blank screen followed this response period before the onset of the next trial).

The task in the verbal condition was to indicate, by button press, whether the probe consonant was part of the to-be-remembered array, regardless of its location. In the verbal-spatial task, participants were required to decide whether both the probe consonant and location appeared in the to-be-remembered display (regardless of whether these consonant and locations had been presented together). Two

types of critical positive-recognition probes (requiring a "yes" response) were presented constituting our measure of binding: intact and re-combined probes. Intact probes consisted of a letter presented in the same location as at encoding. Recombined probes involved a letter and location both presented at encoding but not together (i.e. a letter and location switch). The negative recognition probes (requiring a "no" response) were as follows: a new consonant in a new location (in the verbal task only); an old location occupied by a new consonant (in both the verbal and the verbal-spatial tasks); and an old consonant in a new location (in the verbal-spatial task only). In both tasks, instructions emphasized the importance of both accuracy and speed.

1.3. Procedures

MEG scans were obtained during the verbal and the verbal-spatial tasks. A total of 480 trials were presented in each task. Experimental conditions were completed in different sessions lasting 45 min approximately. Tasks were purpose-written using E-prime (Schneider, Eschman, & Zuccoloto, 2002).

The stimuli were projected through a LCD video-projector (SONY VPL-X600E), situated outside the shielded room on-to a series of in-room mirrors, the last of which was suspended approximately 60 cm above the subject's face ($19.8^\circ \times 26.1^\circ$).

1.4. Data collection and analysis

All MEG recordings were carried out using a whole-head neuromagnetometer containing an array of 148 magnetometers (4-D WHS 2500[®], San Diego) and situated in a magnetically shielded room. The data were collected using a sample rate of 254 Hz and band pass filtered between 0.1 and 50 Hz. MEG data were submitted to an interactive noise reduction procedure that helped reduce environmental noise as part of the signal analysis package. Vertical and horizontal bipolar electro-oculograms (EOG) were also recorded by bipolar montages using a Synamps amplifier (NeuroScan, El Paso, Texas) with Ag/AgCl electrodes (same sample rate and online filters as mentioned previously). Trials containing eye movement or blinks (as indicated by peak-to-peak amplitudes in the EOG channels in excess of 50 μV) or other myogenic or mechanical artifacts were removed using the automated artifact rejection algorithm implemented in the Brain Electrical Source Analysis software suite (BESA 5.1; Megis Software). Analyses were limited to the retention period of trials in which participants responded correctly (hits and correct rejections), as our aim was to examine the maintenance of information in WM.

Time-frequency (TF) representation of MEG data based on the wavelet transform of the signals (Mallat, 1998; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1997) was calculated on a single trial basis for a 1700 ms time window starting from 500 ms before the onset of the stimulus presentation, and 1200 ms starting from the beginning of maintenance period. Wavelet transform is a dynamical alternative to Fourier, used to perform time spectral analyses for non-stationary time series. The continuous wavelet transform (WT) of a signal $x(t)$ (MEG recordings in our case) suppose its projection onto a set of basic functions obtained from mother wavelet ψ by rescaling and translating it along the time axis. Wavelet coefficients

of the $x(t)$ signal in the time-spectral plane (p, z), $W(p, z)$, were obtained as follows:

$$W(p, z) = \frac{1}{\sqrt{p}} \int_{-\infty}^{\infty} x(t) \psi \left(\frac{t-z}{p} \right) dt$$

where parameters z and p play the role of localization and period of the rhythmic component, respectively. To study rhythmic components of a signal the Morlet wavelet mother function is well suited:

$$\Psi(y) = \exp(j2\pi) \exp \left(\frac{-y^2}{2k_0^2} \right)$$

where k_0 is a parameter that can be chosen according to the research aim, in this case we set to 10.

Dipolar magnetometer topographies are difficult to interpret with respect to the underlying generator sources. The mixing of signals from different sources in a single sensor, as well as artificial interactions generated by two sensors picking up a signal from a single source are probable causes of confound (Fan et al., 2007; Palva, Monto, & Palva, 2010). Accordingly, we decided to model frequency changes in the source space (Palva et al., 2010). The minimum-norm estimation procedure (MNE) was used to perform the source localization of the TF MEG signals corresponding to the retention period neuronal response. A tessellated cortical mesh template surface derived from the Montreal Neurological Institute (MNI) phantom brain and implemented in SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm5/>) served as a brain model to estimate the current source distribution. This MNI dipole mesh (3004 nodes) was used to calculate the forward solution using a head model based on overlapping local spheres (Huang, Mosher, & Leahy, 1999). The inverse solution was calculated by applying 12 MNE, with standard Tikhonov regularization, implemented in BrainStorm (<http://neuroimage.usc.edu/brainstorm/>). Tikhonov regularization is needed to control for the effect of the noise on the solution (Bouhamidi & Jbilou, 2007). Jensen and Vanni (2002) have demonstrated that by transforming the real and imaginary parts of the Fourier components in the source domain by means of MNE and combining them it is possible to identify source areas of rhythmic activity in the frequency domain. Accordingly, in our study the underlying current source density (the source strength at each node of the MNI phantom brain) of four frequency bands (theta, 4–8 Hz; alpha, 8–12 Hz; beta, 13–30 Hz; gamma, 30–50 Hz) was estimated by calculating the MNE in the frequency domain (Jensen & Vanni, 2002; Moratti, Rubio, Campo, Keil, & Ortiz, 2008). Here, the real and imaginary parts of each wavelet component averaged within each of the four frequency bands was submitted to the MNE analysis. Thereafter, the MNEs of the real and imaginary parts were combined by using the root square of the sum of squares of the two wavelet parts as an estimate of absolute amplitude. The change in amplitude was calculated with respect to a baseline period before the beginning of each epoch. For each frequency band, the mean time-frequency amplitude of the prestimulus period (between 500 and 0 ms before stimulus onset) was considered as a baseline and subtracted from the time-frequency representation in order to normalize it. In order to exclude baseline differences between conditions a baseline comparison was performed. No significant differences were found in this pre-stimulus period of time. The amplitude values at each dipole location of the brain surface mesh corresponding to the TF-values were statistically analyzed by using a Student *t*-tests to compare the verbal and verbal-spatial conditions. A nonparametric permutation test was conducted to explore differences in brain activity (Maris & Oostenveld, 2007). This test controls for the false alarms in a situation involving multiple comparisons. MNE source strength values were shuffled within each condition (verbal and verbal-spatial) under the null hypothesis of no differences between them. The statistic employed in the permutation test was the maximum statistical value across time and frequency dimensions. 511 permutations were computed in which condition labels (verbal and verbal-spatial) were randomly assigned to data sets from both groups. For each source, the *p*-value was approximated by a Monte Carlo estimate and calculated according to the proportion of the permutation distribution exceeding the observed maximum source test statistic. Sources exceeding a corrected *p*-value of .05 were considered significant. Given that the corrected values are very conservative, we also present significant differences in activated brain regions (corrected) at more a liberal threshold ($p < .001$, uncorrected) for the purposes of describing the timing of activation.

2. Results

2.1. Behavioural data

Data from two participants containing MEG signals with noise levels that prevented further analysis data were excluded from behavioural and *T-F* analysis. Performance was assessed in terms of accuracy (% correct) and reaction time (RT), for correct responses, for both positive probe trials (intact and recombined) in each task.

We conducted separate repeated-measures analysis of variance (ANOVA) for accuracy and for RT measures. The ANOVAs con-

tained two within-subjects factors, task (verbal vs. verbal-spatial), and probe type (intact vs. recombined). Greater accuracy on intact probes ($M = 90.16\%$; $SD = 9.26$ for the verbal task; $M = 87.56\%$; $SD = 7.56$ for the verbal-spatial task) than on recombined probes ($M = 84.01\%$; $SD = 7.17$ for the verbal task; $M = 83.39\%$; $SD = 7.82$ for the verbal-spatial task) led to a significant main effect of probe-type ($F(1,8) = 24.54$; $p < .001$). No significant effect of task ($F(1,8) = .16$; $p > .60$), nor task by probe type interaction ($F(1,8) = .172$; $p > .40$) were found. Participants were faster on intact probes ($M = 906.22$ ms; $SD = 181.86$ for the verbal task; intact: $M = 956.33$ ms; $SD = 204.90$ for the verbal-spatial task) compared to recombined probes ($M = 927.78$ ms; $SD = 175.7$ for the verbal task; $M = 989.67$ ms; $SD = 224.85$ for the verbal-spatial task) as indicated by a main effect of probe-type ($F(1,8) = 9.85$; $p < .02$). Neither the main effect of task nor the interaction approached significance ($F(1,8) = 1.43$; $p > .20$; $F(1,8) = .83$; $p > .30$, respectively).

Thus, statistical analyses of our behavioural data indicated that significant and equivalent verbal-spatial binding effects were observed in both tasks. Having established the existence of binding in both tasks at the behavioural level, we proceeded to compare the source localization of oscillatory activity between the two tasks.

2.2. Distributed source localization and time course of oscillatory activity during the maintenance period

2.2.1. Theta frequency band (4–8 Hz)

Significant differences indicating greater activation during the verbal-spatial task were observed in premotor areas. Source amplitudes were greater in the verbal-spatial task compared to the verbal task in right premotor area, reaching their maximum at around 220 ms ($p < .05$, corrected). Using an uncorrected *p* value of .001, we observed that this activity lasted from 170 ms to 300 ms post-stimulus offset. Left premotor area also showed greater activity during the verbal-spatial task, reaching its peak at around 1150 ms ($p < .05$, corrected). This activity extended between 1050 and 1190 ms ($p < .001$, uncorrected) (Fig. 2A and B).

2.2.2. Alpha frequency band (8–12 Hz)

Distributed source localization of alpha-range activation revealed that the right occipito-temporal region was more activated ($p < .05$, corrected) during the verbal-spatial task compared to the verbal task, showing a peak latency of 340 ms. This activity was evident from 330 to 370 ms ($p < .001$, uncorrected). A greater oscillatory response was found during the verbal task in left inferior temporal lobe, peaking at around 780 ms ($p < .05$, corrected). This activity was observed in a time range between 730 and 850 ms ($p < .001$, uncorrected). Left occipital region also showed an enhanced alpha oscillatory activity, peaking around 930 ms ($p < .05$), that extended between 890 and 960 ms ($p < .001$, uncorrected) (Fig. 2B).

2.2.3. Beta frequency band (13–30 Hz)

Significantly greater oscillatory activity in the verbal-spatial task compared to the verbal task was observed over PPC, bilaterally, peaking at around 180 ms (left PPC) and 210 ms (right PPC) ($p < .05$, corrected). Left inferior parietal lobe also showed greater oscillatory activity during the verbal-spatial task, showing a peak latency of 530 ms ($p < .05$, corrected). These activations lasted from 160 to 220 ms ($p < .001$, uncorrected) and between 490 and 540 ms ($p < .001$, uncorrected), respectively. *T-F* analysis also showed a greater activity in sources located in right DLPFC in the verbal-spatial task, peaking at around 310 ms ($p < .05$, corrected), extending from 290 to 350 ms ($p < .001$, uncorrected) (Fig. 2A and B).

Fig. 2. (A) Grand average time-frequency (*T-F*) representations, including evoked and induced oscillations, for the two tasks are depicted, *T-F* plots for a left anterior sensor for both tasks are shown on the upper panel; *T-F* plots for a left posterior sensor for both tasks are shown on the bottom panel. (B) Shows the result of the group analysis projected onto a tessellated cortical mesh template surface derived from the Montreal Neurological Institute (MNI) phantom brain. The figure depicts sources indicating maximum statistically significant difference in amplitude between tasks in specific time bins for different frequency ranges by means of *p* values ($p < .05$ corrected). Only *p* values exceeding the critical *p* value of .05 are shown. Colorbar indicate the *p* values.

2.2.4. Gamma frequency band (30–50 Hz)

Source differences in gamma band activity were detected in left DLPFC, indicating greater activation in the verbal–spatial task compared to the verbal task ($p < .05$, corrected). This activity showed a first peak latency of 195 ms ($p < .05$, corrected), and lasted from 180 to 215 ms ($p < .001$, uncorrected). A second significant peak was observed at around 670 ms ($p < .05$, corrected), lasting between 660 and 700 ms ($p < .001$, uncorrected). Topographical distribution of the source estimates for oscillatory activity in gamma band also showed significant greater activation in posterior regions during the verbal–spatial task. Specifically, differences were observed over left and right occipito-temporal regions ($p < .05$, corrected), peaking at around 210 and 650 ms, respectively. Right premotor cortex and bilateral medial PFC showed significantly greater oscillatory activity in the verbal task as compared to the verbal–spatial task. Activations in premotor cortex peaked at around 330 and 970 ms ($p < .05$, corrected), and were observed between 315 and 370 ms and between 960 and 1000 ms ($p < .001$, uncorrected). Activity in medial PFC showed a peak latency of 990 ms ($p < .05$, corrected), and was evident between 970 and 1000 ms ($p < .001$, uncorrected). The verbal task was also associated with greater activity over left and right occipital cortex in three different time windows ($p < .05$, corrected), peaking at around 235 ms, and 540 ms in the right hemisphere, and around 1140 ms in the left hemisphere (Fig. 2B).

3. Discussion

In the present study, we reported the first attempt to study verbal–spatial binding under conditions where only the verbal feature was to be attended (verbal task) – known to produce spontaneous verbal–spatial binding (Campo et al., 2010) – compared to a task where both the verbal and spatial features were attended. The comparison was carried out using with MEG, by contrasting the patterns of neural oscillatory activity in ‘classical’ frequency bands as a function of whether participants attended and memorized the verbal features only (verbal task) or both verbal and spatial features (verbal–spatial task). The two tasks we compared were identical in terms of their perceptual characteristics, and only differed with respect to the instructions given to participants, resulting in different processing demands. The behavioural results revealed significant and equivalent cross-code binding effects in both tasks, both with respect to accuracy and response latencies. Of interest were any differential patterns of neural activity evidenced between the two tasks.

The results of the oscillatory neural activity showed that verbal–spatial binding relied on partially distinct neuroanatomical substrates when one and both features were attended and encoded. As our behavioural measures indicated binding effects in both tasks, and no differences in terms of accuracy or speed response, we can conclude that differences between tasks in oscillatory activity were due to the requirement to intentionally process *both* verbal and spatial information classes. It was found that maintenance during the verbal–spatial task was associated with the activation of a dorsal processing stream including DLPFC, premotor areas and PPC, mainly during the first half of the retention period. Activity in these areas were found in the theta, beta and gamma frequency ranges. Maintenance during the verbal task was associated with gamma activity in anterior dorsal areas, including premotor cortex and medial PFC. Contrary to the verbal–spatial task, the majority of these activations were observed later in the retention period (i.e. second half). Activity in the occipital and left temporal cortices in gamma and alpha frequency bands were observed during the maintenance period in both tasks.

In sum, differences between tasks were observed in frequency, location and time. Interestingly, oscillatory activity in the theta

and beta bands was only observed during the verbal–spatial task. Using the same paradigm, Wu et al. (2007) showed greater oscillatory activity in theta band over frontal sites during intentional maintenance of integrated letter–location features as compared to unintegrated features. Summerfield and Mangels (2005) reported a similar pattern of anterior theta activation during intentional encoding of word–color association as compared to word-only encoding. As results from these studies were based on data analyzed at sensor level, which do not allow a precise localization of the effect, we are not able to compare the anatomical localization (i.e. premotor cortex) of the theta activity observed in our study with that reported in the above mentioned studies. Nonetheless, theta oscillations in anterior areas appear to be a common finding. As pointed by some authors (Deiber et al., 2007; Payne & Kounios, 2009; Sauseng, Hoppe, Klimesch, Gerloff, & Hummel, 2007) the amplitude of frontal theta activity depends on the attentional level required to deal with the task rather than on the amount of information being manipulated. While task difficulty, and therefore mental effort, is “intrinsically linked to the highest memory load” (Deiber et al., 2007), the finding, in our data, of equivalent behavioural binding effects irrespective of whether participants encoded one or both features, could then be considered as reflecting different task demands – if we assumed that the intentional processing of the consonants and locations in the verbal–spatial task may have required the allocation of more cognitive resources – but equivalent memory loads. Thus, the greater oscillatory activity observed over premotor areas in the verbal–spatial task is consistent with previous findings that linked central executive functions to theta oscillations in anterior sites during the retention period of a WM task (Deiber et al., 2007; Schack, Klimesch, & Sauseng, 2005).

When considering differences in the brain regions activated in both tasks, it appears that activity in PFC and PPC was mediated by the manipulation of processing demands. On the one hand, enhanced activity in posterior regions requiring intentional control has been observed in previous studies (Dove et al., 2008). Focusing attention or intentional processing have been shown to increase activation in modality specific regions (Ranganath, DeGutis, & D’Esposito, 2004). Thus, the increased oscillatory activity in beta band in PPC during the verbal–spatial task could be reflecting the intentional processing of spatial locations in this task (Corbetta & Shulman, 2002). Alternatively, this enhancement could indicate that more attentional resources were deployed in the verbal–spatial task than in the verbal task. Interestingly, a prior study (Deiber et al., 2007) described a higher parietal beta activity for a demanding WM task, which was interpreted as reflecting enhanced attention. The time window in which we observed the effect is consistent with the so-called N2pc (an ERP component) the amplitude of which is considered to reflect the attentional requirements of performing a task (Luck & Hillyard, 1994). Interestingly, recent evidence shows that the amplitude of N2pc was greater in a feature–location binding condition as compared to a simple feature detection condition (Hyun, Woodman, & Luck, 2009). On the other hand, prefrontal gamma band oscillatory activity has been related to attention driven top-down processes (Cho, Konecky, & Carter, 2006; Engel, Fries, & Singer, 2001; Fan et al., 2007; Klimesch, Freunberger, & Sauseng, 2010), and may also extend to neural activity in the beta frequency range (Klimesch et al., 2010). While activity in frontal areas was observed in both tasks, the time course of the frontal beta and gamma activity during the verbal–spatial task is consistent with findings from a recent study exploring the frequency components of an executive control network (Fan et al., 2007). Specifically, it was shown that the executive attentional network was associated with a strong early increase in gamma band power, along with beta band, during the 100–300 ms period after target onset. Enhancement of early anterior components of the ERP (140–160 ms) has also been reported

in an spatial WM task (Awh, Anillo-Vento, & Hillyard, 2000). On this basis, the distinct patterns of activity we observed in the beta and gamma bands over anterior PFC might reflect differences in the strategic/attentional control processes between tasks. Additionally, the topographical distribution of frontal beta and gamma activity specifically observed during the verbal-spatial task is also consistent with several proposals about the crucial role played by lateral PFC in strategic recoding (Bor, Cumming, Scott, & Owen, 2004; Bor et al., 2003; Bor & Owen, 2007; Savage et al., 2001) and with functional neuroanatomical findings of previous neuroimaging studies comparing controlled and incidental memory processes (Buckner & Koutstaal, 1998; Buckner et al., 1995; Chiu et al., 2006; Fletcher et al., 2001; Hall, Gjedde, & Kupers, 2008; Kapur et al., 1996; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999; Noldy et al., 1990; Reber et al., 2003; Rugg et al., 1997; Schott et al., 2002, 2005), which collectively indicated a greater activation of DLPFC during controlled memory. In contrast, the medial PFC (activated late in the retention period in the verbal task) has been associated with spontaneous object and object-location memory in rats (Ennaceur, Neave, & Aggleton, 1997). Considered together, the greater engagement of a dorsal fronto-parietal attentional network (Corbetta & Shulman, 2002) in the task in which both features were required to be intentionally processed might reflect the allocation of spatial attention to locations held in WM (Awh et al., 2000), or the greater executive/attentional resources that were necessary in order to accomplish the task (Chun & Turk-Browne, 2007). These two alternatives are not mutually exclusive as selective spatial attention is at the core of models invoking cross-modal influences of spatial attention in multisensory integration (Corbetta & Shulman, 2002; Macaluso & Driver, 2005; Marois & Ivanoff, 2005; Senkowski, Talsma, Herrmann, & Woldorff, 2005).

One might tentatively propose that participants in the verbal-spatial task may have used binding as a strategy for making more efficient use of short-term memory by recoding information. However, this interpretation should be reconciled with recent findings (Morey, 2009; Wheeler & Treisman, 2002) suggesting that verbal and visuospatial features can be simultaneously maintained in their respective modality-specific buffers or in a domain-general store, depending on what information is necessary to complete the task. In the current experiment, we are unable to exclude that letter-location binding was also implicit in the verbal-spatial task.

Oscillatory activity in alpha and gamma bands were observed in similar brain regions, specifically occipital and left temporal cortices, across the verbal and verbal-spatial tasks. Colocalized neural responses in posterior brain regions comparing implicit and explicit have been previously shown. This finding has been suggested to "reflect perceptual processes common to the two forms of memory" (Turk-Browne, Yi, & Chun, 2006). In our case, occipital and temporal regions could be signaling processing of the verbal component of the stimuli, which is common for both tasks.

In summary, the present study provides, for the first time, evidence that behaviourally equivalent binding effects yielded by single and dual feature encoding conditions rely on different neuroanatomical and neural oscillatory correlates. Our results show a complex pattern of frequencies, neural generators and timing. Thus, the specific T-F patterns and different neural generators found during the retention period of each task provide evidence for the distinction of the processes supporting intentional and unintentional letter-location binding in WM. Since both tasks were identical in all respects except instructions, we propose that enhanced activation of an anterior-posterior dorsal network observed in the verbal-spatial task reflected the greater allocation of attentional resources to the intentional processing of both verbal and spatial features in this task (Chun & Turk-Browne, 2007).

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