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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.

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, & Faloon, 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, Saults, & 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 incidental 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 stimuli-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