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Cortical pattern separation and item-specific memory encoding

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ABSTRACT

Pattern separation and pattern completion are fundamental brain processes thought to be critical for episodic memory encoding and retrieval, and for discrimination between similar memories. These processes are best understood in the hippocampus, but are proposed to occur throughout the brain, in particular in sensory regions. Cortical, as well as hippocampal, pattern separation may therefore support formation of event-unique memory traces. Using fMRI, we investigated cortical pattern separation and pattern completion and their relationship to encoding activity predicting subsequent item-specific compared to gist memory. During scanning, participants viewed images of novel objects, repeated objects, and objects which were both perceptually and conceptually similar to previously presented images, while performing a size judgement task. In a later surprise recognition test, they judged whether test items were 'same' 'similar' or 'new' relative to studied items. Activity consistent with pattern separation – responses to similar items as if novel – was observed in bilateral occipito-temporal cortex. Activity consistent with pattern completion – responses to similar items as if repeated – was observed in left prefrontal cortex and hippocampus. Curve fitting analysis further revealed that graded responses to change in image conceptual and perceptual similarity in bilateral prefrontal and right parietal regions met specific computational predictions for pattern separation for one or both of these similarity dimensions. Functional overlap between encoding activity predicting subsequent item-specific recognition and pattern separation activity was also observed in left occipital cortex and bilateral inferior frontal cortex. The findings suggest that extrahippocampal regions including sensory and prefrontal cortex contribute to pattern separation and pattern completion of visual input, consistent with the proposal that cortical pattern separation contributes to formation of item-specific memory traces, facilitating accurate recognition memory.

1. Introduction

Sensory information from a changing environment is continuously processed by the brain, often resulting in substantial overlap between incoming representations and traces already stored in long-term memory. In order to avoid interference, incoming episodes must therefore be assigned unique neural representations. In the hippocampus, this is thought to be achieved by pattern separation - the orthogonalisation of incoming relative to existing representations. Conversely, overlapping input is used at retrieval as a cue to drive reinstatement of existing traces via pattern completion, increasing overlap between incoming and existing representations (Marr, 1971; McNaughton and Morris, 1987; O'Reilly and McClelland, 1994). Although pattern separation is by definition an encoding process, and pattern completion a retrieval process, either or both can be elicited by a single event, whether novel or previously encountered (Hunsaker and Kesner, 2013). Efficient pattern separation at encoding is thought to contribute to later *mnemonic discrimination* between events with similar representations, while false recognition of similar events can result from inefficient pattern separation or dominance of pattern completion at encoding (Sahay et al., 2011; Stark et al., 2013; Wilson et al., 2006). However the precise mechanisms by which pattern separation and completion at encoding contribute to memory outcomes remain unknown, and it remains to be established whether and how neocortex complements the central role of the hippocampus in these computations. The present study investigated cortical pattern separation and completion, and asked whether regions showing these responses were also engaged during encoding leading to later item-specific memory.

Within the hippocampus, computational, electrophysiological and lesion evidence has implicated the dentate gyrus (DG) in

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pattern separation, and subfields CA3 and CA1 in pattern separation or completion, depending on the degree of overlap between incoming and existing representations (Gilbert et al., 2001; Guzowski et al., 2004; Leutgeb et al., 2007; Rolls, 2007; Vazdarjanova and Guzowski, 2004). High-resolution functional magnetic resonance imaging (fMRI) evidence from humans is consistent with these findings. Typically, these studies have examined responses to novel images of common objects, repetitions of these images, and images of perceptually and conceptually similar objects. By examining neural responses to similar images within regions showing differential activity between novel and repeated images, it is assumed that equivalent activity between similar and novel items is consistent with pattern separation, i.e., similar images are processed as if novel, whereas equivalent activity to similar items and repetitions is consistent with pattern completion, i.e., similar items are processed as if repeated. Examining regions showing repetition suppression (Henson and Rugg, 2003), such investigations have reported activity consistent with pattern separation in a region spanning DG/CA3, and pattern completion activity in CA1 and elsewhere in the medial temporal lobe (MTL) (Bakker et al., 2008; Lacy et al., 2011). Although pattern separation and completion investigations have focussed on the role of the hippocampus, networks throughout the brain are thought to perform similar functions, including sensory cortex (Aimone et al., 2011; Gilbert and Kesner, 2003). Rodent electrophysiological recordings have demonstrated pattern separation of odour cues in the olfactory bulb, and pattern completion in piriform cortex (Barnes et al., 2008; Wilson, 2009), but these functions in regions outside the MTL have received little attention in studies in humans.

A number of fMR adaptation (fMRA) studies are also relevant to pattern separation and completion processes. These have assessed the information represented in specific regions by measuring stimulus-specific repetition suppression. Repetition suppression to exact repetitions but not perceptually and conceptually similar images has been reported in visual cortical regions including fusiform and lateral occipital cortex (LOC) (Chouinard et al., 2008; Koutstaal et al., 2001). Such responses resemble pattern separation in that similar items elicit a response which is distinct from that of repetitions. Repetition suppression to similar images which differ perceptually from previously viewed items has also been observed in other occipito-temporal regions and in left inferior frontal gyrus (LIFG) (Chouinard et al., 2008; Fairhall et al., 2011; Horner and Henson, 2011), resembling pattern completion. Such findings together suggest that cortical regions contribute to the degree to which visual inputs are coded as perceptually and semantically similar or distinct. However, evidence for pattern separation or completion from these studies is incomplete. Some studies have reported repetition suppression for repeated relative to both novel and similar items within the same anatomical region without showing that these responses actually overlap (Bakker et al., 2008; Kumaran and Maguire, 2009). Similarly, it has not yet been demonstrated that the regions showing repetition suppression to similar items also show attenuated activity to repetitions, as expected for pattern completion. One fMRA study however demonstrated occipito-temporal responses more clearly consistent with pattern separation. Kim et al. (2009) reported release from repetition suppression in bilateral LOC and fusiform in response to images which differed in shape but not basic-level concept relative to previous images. LOC activity also did not differ between conceptually similar and conceptually novel images equated in shape similarity with previously viewed images. Results were interpreted as sensitivity of LOC to change in shape information, but can also be interpreted from a pattern separation perspective, i.e., reduced activity for repetitions relative to both novel and similar images, but activity for novel and similar items did not differ, providing the most direct evidence to date of responses consistent with pattern separation in visual cortex.

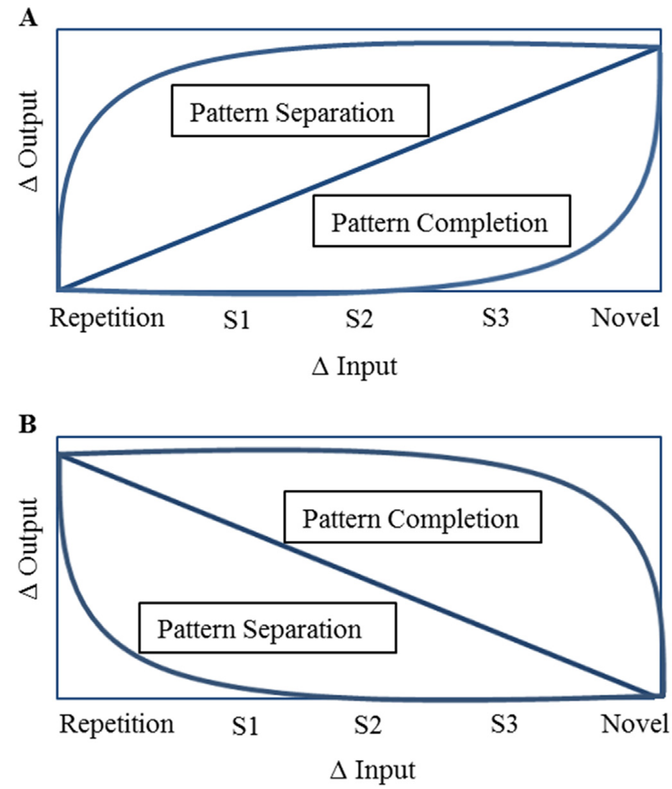

Fig. 1. Predicted input-output response functions for pattern separation and pattern completion regions. S1 = high similarity items, S2 = medium similarity items, S3 = low similarity items. (A) In regions showing repetition suppression, pattern separation is predicted to show a power function with decreasing slope in response to change in input, falling above the diagonal. Pattern completion regions are expected to fit an increasing slope power function, falling below the diagonal. (B) In regions where repetitions show increased activity relative to novel items, functions in the opposite direction are predicted. Pattern separation is predicted to show a decreasing slope power function falling below the diagonal, and pattern completion an increasing slope power function falling above the diagonal. In (A) and (B), the linear diagonal represents cases where change in input and change in output are equal. Adapted from Motley and Kirwan (2012).

Although the fMRA findings are suggestive of cortical pattern separation and completion, these processes are computationally defined in terms of their responses to parametrically varied input similarity (e.g., Treves and Rolls, 1992; Vazdarjanova and Guzowski, 2004). Therefore, examination of neural responses to graded change in input, i.e., to stimuli of varying similarity relative to previously presented items, can provide further support for their presence (Hunsaker and Kesner, 2013; Kumaran and Maguire, 2009). Pattern separation is defined as reduction in overlap of output representations from a region relative to the degree of overlap of input representations received by the region (Rolls, 1996; Treves and Rolls, 1992). The resulting changes in output in response to increasing input similarity can therefore be approximated by a power function with decreasing slope, i.e., a large difference in activity occurs between repeated and the most similar items (Fig. 1A; Motley and Kirwan, 2012). In contrast, pattern completion *increases* the representational overlap at output relative to input representations (O'Reilly and McClelland, 1994), approximated by a power function with increasing slope, i.e., very slight differences in activity occur between repeated and similar items, with only highly dissimilar items processed as if novel (Fig. 1; Vazdarjanova and Guzowski, 2004). In regions showing repetition enhancement, the functions are the same but their direction is inverted (Fig. 1B). A linear function represents the case where overlap is equal between input and output representations, i.e., neither pattern separation nor completion occurs (Guzowski