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Support for an auto-associative model of spoken cued recall: Evidence from fMRI

Greig de Zubicaray [a,*], Katie McMahon [a], Mathew Eastburn [a],
Alan J. Pringle [a], Lina Lorenz [b], Michael S. Humphreys [c]

[a] Centre for Magnetic Resonance, The University of Queensland, Qld 4072, Australia
[b] University of Applied Sciences, Hamburg, Germany
[c] Centre for Human Factors and Applied Cognitive Psychology, The University of Queensland, Qld, Australia

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Abstract

Cued recall and item recognition are considered the standard episodic memory retrieval tasks. However, only the neural correlates of the latter have been studied in detail with fMRI. Using an event-related fMRI experimental design that permits spoken responses, we tested hypotheses from an auto-associative model of cued recall and item recognition [Chappell, M., & Humphreys, M. S. (1994). An auto-associative neural network for sparse representations: Analysis and application to models of recognition and cued recall. *Psychological Review*, *101*, 103–128]. In brief, the model assumes that cues elicit a network of phonological short term memory (STM) and semantic long term memory (LTM) representations distributed throughout the neocortex as patterns of sparse activations. This information is transferred to the hippocampus which converges upon the item closest to a stored pattern and outputs a response. Word pairs were learned from a study list, with one member of the pair serving as the cue at test. Unstudied words were also intermingled at test in order to provide an analogue of yes/no recognition tasks. Compared to incorrectly rejected studied items (misses) and correctly rejected (CR) unstudied items, correctly recalled items (hits) elicited increased responses in the left hippocampus and neocortical regions including the left inferior prefrontal cortex (LIPC), left mid lateral temporal cortex and inferior parietal cortex, consistent with predictions from the model. This network was very similar to that observed in yes/no recognition studies, supporting proposals that cued recall and item recognition involve common rather than separate mechanisms.

Keywords: Cued recall; Episodic memory; STM; LTM; Memory models; Recognition

1. Introduction

This paper presents functional magnetic resonance imaging (fMRI) data associated with spoken cued recall, a task in which participants produce a target word when presented with a cue word learned from a study list (Chappell & Humphreys, 1994). While a considerable number of fMRI studies have been concerned with item recognition effects in episodic memory, few have investigated spoken cued recall in detail (cf., Henson, Shallice, Josephs, & Dolan, 2002). Such an exercise is doubly important as some theories of item recognition propose the involvement of a separate recall-like process, termed recollection. In fact, spoken cued recall is often considered an index of recollection in these theories (e.g., Clark, 1999; Mandler, 1980).

The mechanisms contributing to cued recall performance are still subject to debate within the psychological literature. For example, the model favoured by Shiffrin and colleagues assumes cued recall is achieved by a process of sequential search through memory with sampling until a relevant representation is located, while item recognition is achieved by a single-step parallel activation and matching process (e.g., Diller, Nobel, & Shiffrin, 2001; Nobel & Shiffrin, 2001). The issue of whether separate search and global matching processes are responsible for cued recall and recognition, respectively, has dominated the memory literature since Atkinson and Shiffrin (1968) suggested this might be the case (in fact, Clark, 1999 describes this issue as "one of the central controversies" p. 215). Other biologically inspired cognitive theories emphasise an auto-associative mechanism in

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[*] Corresponding author. Tel.: +61 7 3365 4250; fax: +61 7 3365 3833.
E-mail address: greig.dezubicaray@cmr.uq.edu.au (G. de Zubicaray).

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which the correct representation is converged upon using information elicited from both short and long term memory (e.g., Chappell & Humphreys, 1994; Rizzuto & Kahana, 2001; Tehan & Fallon, 1995; Tehan, Humphreys, Tolan, & Pitcher, 2004). These latter models also assume that item recognition and cued recall are accomplished by similar mechanisms, a view shared by a growing number of memory models (see Kahana, Rizzuto, & Schneider, 2005).

Rizzuto and Kahana (2001) note an auto-associative mechanism is consistent with computational neuroscience models of hippocampal function. A number of these models have attributed this mechanism to the CA fields in particular (primarily CA3 and CA1 plus subiculum; e.g., Becker, 2005; Lengyel, Kwag, Paulsen, & Dayan, 2005; Meeter, Murre, & Talamini, 2004; Treves & Rolls, 1994; Wiskott, Rasch, & Kempermann, 2006). Like the connectionist psychological models described above, these biological models assume memory is represented by patterns of sparse activations distributed throughout the neocortex. Given these as input, the auto-associator converges upon the one closest to a stored pattern and outputs a response. The major anatomical input and output area for the hippocampus is the entorhinal cortex within the parahippocampal region (via the perforant pathway), while the dentate gyrus is thought to perform a storage role (Becker, 2005; Wiskott et al., 2006). Further, the amygdala modulates information transfer into the hippocampus via the dentate gyrus (e.g., Nakao, Matsuyama, Matsuki, & Ikegaya, 2004; Vouimba & Richter-Levin, 2005).

While both cognitive and computational neuroscience models have employed auto-associative mechanisms to explain recall processes, the latter models necessarily make no predictions concerning the representation of lexical information involved in spoken cued recall, having been formulated primarily to account for results from studies of rats and non-human primates (e.g., Becker, 2005; Lengyel et al., 2005; Treves & Rolls, 1994; Wiskott et al., 2006). An important requirement for all models of spoken cued recall is that they explain how pre-existing semantic knowledge in long term memory (LTM) can affect the retrieval of an item that occurred in the study list (Nelson, McKinney, Gee, & Janczura, 1998; Tehan et al., 2004). To date, most attempts at model building have not attempted to do so (see Nelson et al., 1998; Tehan et al., 2004).[1]

The auto-associative model of spoken cued recall developed by Humphreys and colleagues (Chappell & Humphreys, 1994; Tehan & Fallon, 1995; Tehan et al., 2004) assumes that information from two patterns of activation is combined in order to retrieve an item from memory: a pattern representing the list context that elicits episodic information about the study items, and another eliciting information such as the meaning of the word and the category to which it belongs in semantic LTM. Intersecting or overlapping information elicited from these two patterns of activation is then fed to the auto-associator, and the list item's representation is converged upon. Tehan et al. (2004) have recently referred to this as the parallel-access-intersection (PAI) approach. Although this model was developed primarily to account for long term memory effects including recognition, Tehan and Fallon (1995) later proposed a minor update to account for short term cued recall effects. This amounts to ensuring that the pattern representing the list context elicits the phonological characteristics of the list items, because phonological similarity effects are observed more readily in verbal short term memory (STM). This assumption is shared by another prominent model that hypothesises a "phonological loop" comprising a short term store and an articulatory control system that refreshes the traces within it (Baddeley, 1986; Baddeley & Hitch, 1974).

There is now a considerable literature documenting the neocortical regions contributing to verbal STM. Converging evidence from neuroimaging, lesion and transcranial magnetic stimulation (TMS) studies indicates that phonological information is represented in STM via a predominantly left hemisphere network of regions including the posterior superior temporal and inferior parietal cortices (storage/maintenance) and the posterior inferior prefrontal cortex (pLIPC; articulatory control) (e.g., Becker, MacAndrew, & Fiez, 1999; Buchsbaum, Olsen, Koch, & Berman, 2005; Martin, Shelton, & Yaffee, 1994; Nixon, Lazarova, Hodinott-Hill, Gough, & Passingham, 2004; Ravizza, Delgado, Chein, Becker, & Fiez, 2004). Outside of these neocortical areas, the cerebellum has also been implicated in phonological STM, although its precise contribution in terms of storage or rehearsal remains to be clarified (e.g., Chen & Desmond, 2005; Justus, Ravizza, Fiez, & Ivry, 2005; Ravizza et al., 2006). Additional evidence suggests that phonological and semantic representations can be dissociated in verbal STM (e.g., Martin et al., 1994; Shivde & Thompson-Schill, 2004). The representation of semantic information, both in STM and LTM, has been attributed to left lateralised regions including the lateral middle temporal cortex and anterior inferior prefrontal cortex (aLIPC; e.g., Binder, Westbury, McKiernan, Possing, & Medler, 2005; Devlin, Matthews, & Rushworth, 2003; Shivde & Thompson-Schill, 2004). Long term semantic representations are known to effect performance on verbal STM tasks directly (e.g., Forde & Humphreys, 2002), and it has been suggested that verbal STM in fact corresponds to the temporary activation of semantic (and phonological) representations in LTM (Martin & Saffran, 1997). Assuming the PAI approach (Chappell & Humphreys, 1994; Tehan & Fallon, 1995; Tehan et al., 2004) is accurate, all of these neocortical regions should be observable in an fMRI experiment of spoken cued recall, as should hippocampal structures given they represent successful convergence and output areas for the auto-associator.

Results from positron emission tomography (PET) investigations of spoken cued recall have indicated variable engagement of bilateral frontal, temporal and parietal regions, and occasionally the hippocampus (e.g., Cabeza, Locantore, & Anderson, 2003; Fletcher et al., 1996; Nyberg, Forkstam, Petersson, Cabeza, & Ingvar, 2002). In addition, direct comparisons of item recognition and cued recall tasks in PET studies have shown common or differential recruitment of cerebral regions

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[1] The need to incorporate LTM representations in models of short term cued recall is indicated by findings that test cues linked to more associates in semantic memory result in poorer recall (i.e., the cue set size effect; e.g., Nelson, Schreiber, & Xu, 1999) and that related extralist cues produce successful recall of list words (Tehan et al., 2004).