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Functional neuroimaging studies of prospective memory: What have we learnt so far?

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ABSTRACT

The complexity of the behaviour described by the term "prospective memory" meant that it was not at all clear, when the earliest studies were conducted, that this would prove a fruitful area for neuroimaging study. However, a consistent relation rapidly emerged between activation in rostral prefrontal cortex (approximating Brodmann Area 10) and performance of prospective memory paradigms. This consistency has greatly increased the accumulation of findings, since each study has offered perspectives on the previous ones. Considerable help too has come from broad agreement between functional neuroimaging findings and those from other methods (e.g. human lesion studies, electrophysiology). The result has been a quite startling degree of advance given the relatively few studies that have been conducted. These findings are summarised, along with those from other brain regions, and new directions suggested. Key points are that there is a medial–lateral dissociation within rostral PFC. Some (but not all) regions of medial rostral PFC are typically more active during performance of the ongoing task only, and lateral aspects are relatively more active during conditions involving delayed intentions. Some of these rostral PFC activations seem remarkably insensitive to the form of stimulus material presented, the nature of the ongoing task, the specifics of the intention, how easy or hard the PM cue is to detect, or the intended action is to recall. However there are other regions within rostral PFC where haemodynamic changes vary with alterations in these, and other, aspects of prospective memory paradigms. It is concluded that rostral PFC most likely plays a super-ordinate role during many stages of creating, maintaining and enacting delayed intentions, which in some cases may be linked to recent evidence showing that this brain region is involved in the control of stimulus-oriented vs. stimulus-independent attending. Other key brain regions activated during prospective memory paradigms appear to be the parietal lobe, especially Brodmann Area (BA) 40 and precuneus (BA 7), and the anterior cingulate (BA 32). These regions are often co-activated with lateral rostral PFC across a wide range of tasks, not just those involving prospective memory.

1. Introduction

Prospective memory is a very new field of enquiry, but one in which there has been a startling increase of interest over the last few years. As Sellen, Louie, Harris, and Wilkins (1997) point out, a review approximately 20 years ago (Kvavilashvili, 1992) cited only twenty-four experimental studies of prospective memory. Yet there are now several entire books devoted to the topic (e.g. Brandimonte, Einstein, and McDaniel, 1996; Glicksohn & Myslobodsky, 2006; Kliegel, McDaniel, & Einstein, 2007; McDaniel & Einstein, 2007), and substantial international conferences occupied exclusively with research into prospective memory (the first International Conference on Prospective Memory was held in Hertfordshire, UK, in July, 2000). This explosion of interest has been accompanied by a change in the way that "prospective memory" has been viewed.

The earliest studies, which were largely behavioural only, tended to be concerned with the practical aspects of remembering intentions, often relating to everyday life situations, rather than experimental paradigms (e.g. Wilkins & Baddeley, 1978). Accordingly, the emphasis was very much on the study of situational and behavioural characteristics affecting delayed intentions. However as the field became more experimental, and with the help of a few key papers (e.g. Kvavilashvili, 1987) the notion grew that there might be cognitive processes or constructs unique to this form of memory (in the sense of not also being shared with memory for past events). From the viewpoint of a scientist trying to discover principles of behaviour, or of brain–behaviour relations, this would be fortuitous, making discovery simpler. However from a biologi-

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cal viewpoint, at the extreme at least, such an arrangement would likely be exceptionally inefficient: prospective memory is a highly complex and multi-componential behaviour so it is unlikely to have representations and brain structures dedicated entirely to it. Such a principle, carried across all cognitive functions would likely be far too costly, so it is always more likely that at both an information processing and functional level that processes and structures operate across psychological domains, or at least across our narrow definitions of subject fields. In this way it was clear to many from the outset that it would be implausible that the study of prospective memory would grow entirely independently from other fields of conceptual relevance (for review see Ellis, 1996).

And so, in large part has it transpired. However, there has been a particularly fortuitous finding for cognitive neuroscientists studying prospective memory: a consistent relation between activation in rostral PFC during prospective memory paradigms. This has given an invaluable inroad into a topic that at one time had little or no precedent within cognitive neuroscience. Moreover, as more information about this brain region from the study of other functions appears, the field is being encouraged to consider prospective behaviour more broadly, with the potential to encompass not just prospective memory, but many other forms of "prospection".

2. Characteristics of typical prospective memory paradigms

There are a very wide variety of situations in everyday life that require prospective memory. However, for experimental purposes in cognitive neuroscience the essential features of these situations have been simplified. The typical features of prospective memory paradigms are summarised by Burgess, Scott, and Frith (2003). These are:

(a) There is an intention, or multiple intentions to carry out a mental or physical act. A variant might be that the intention is to withhold an act that is performed routinely in a particular context.
(b) The intended act cannot be performed immediately after the intention to do it has been created.
(c) The intended act (or thought) is to be performed in a particular circumstance. This is known as the "retrieval context" (Ellis, Kvavilashvili, & Milne, 1999). In event-based studies, the retrieval context is signalled by a cue (the "intention cue", or "PM target"). In time-based tasks this is either at a particular time, or after a certain duration, and with activity-based PM tasks this might be after or during a particular ongoing activity or another task.
(d) The delay period between creating the intention and occurrence of the appropriate time to act (the "retention interval") is filled with activity known as the "ongoing task".
(e) Performance of the ongoing task prevents continuous, conscious rehearsal of the intention over the entire delay period. Typically this is because the activity is too demanding of competing cognitive resources (e.g. attention), or the delay period is too long. This is a feature which distinguishes a prospective memory paradigm from e.g. some "working memory" or vigilance paradigms.
(f) The intention cue (or retrieval context) does not interfere with, or directly interrupt, performance of the ongoing task. Intention enactment is therefore self-initiated, and the participant has to recognise the PM cue or retrieval context for themselves (e.g. rather than receiving a clear interrupt or instruction from an external source).
(g) In many situations involving prospective memory no immediate feedback is given to the participant regarding errors or other aspects of their performance.

This is not intended as an exhaustive characterisation. Variants upon these general themes have been created by experimental psychologists, and many aspects are hotly debated. However, these seven features, when occurring together in the same paradigm, are likely to describe a task which most theorists would recognise as engaging processes relevant to "prospective memory".

2.1. Neuroimaging studies of prospective memory – a very brief overview

There have not been a large number of neuroimaging prospective memory studies thus far. A determined reader could read them all in a day although the assimilation of their implications and significance would likely take very much longer, even for someone familiar with the behavioural literature. The first neuroimaging study of prospective memory was published only a dozen or so years ago (Okuda et al., 1998). So it is appropriate that we now ask (a) what we have learnt from these early years of neuroimaging of prospective memory, and (b) what the priorities might be for future study.

Considering the first question, it is likely that historians of the subject, perhaps turning their attentions to the growth of this field many years hence, might conclude that we learnt much more from the first dozen or so studies in the first dozen years than might ever have seemed likely at the outset. This has been facilitated by the fortuitous scientific discovery mentioned above: a consistent relation, first noted by Burgess, Quayle, and Frith, (2001) and Burgess et al. (2003), between activation of rostral prefrontal cortices (approximating Brodmann Area 10) and the performance of prospective memory tests. The reason why this finding has been so helpful is that, at the time of the first three studies around the beginning of this century (Burgess et al., 2001, 2003; Okuda et al., 1998), virtually nothing was known about rostral PFC. This has probably managed to throw the relation between PM and rostral PFC activations into sharp relief.

Prior to the emergence of neuroimaging, this large brain region (in fact the largest single cytoarchitectonic region of the prefrontal cortex) was almost completely ignored by cognitive neuroscientists. Whilst even from the earliest days of neuroimaging, a relation between *retrospective* memory and rostral PFC activations had been noted (see Grady, 1999 for review), the translation of these findings into an information processing account of the functions of rostral PFC had not been straightforward, resulting in broad post hoc characterisations that were not easy to falsify. The central problem was that whilst rostral PFC activations occurred consistently during episodic memory paradigms, they also occurred during many other paradigms which appeared to have little or no episodic memory component. These could be simple conditioning paradigms, or tasks involving semantic memory; language, visual perception, as well as functions more often associated with the frontal lobes such as attentional switching (see Burgess, Gilbert, & Dumontheil, 2007; Burgess, Simons, Dumontheil, & Gilbert, 2005 for review). However, other ideas about the contributions of rostral PFC to human cognition were just beginning to emerge (e.g. Christoff & Gabrieli, 2000; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999). These experimental papers, which attempted to link rostral PFC activations to particular cognitive operations (e.g. "branching"; the manipulation of self-generated information; see Burgess, Gilbert, et al., 2007 for review), provided some very useful information regarding the type of paradigm that might provoke rostral PFC activations. The findings (which have largely been replicated since) were also new enough that the field was open to new possibilities (as indeed it very much still is), and a small cadre of investigators worldwide began looking more carefully at the range of tasks which were found to have provoked haemodynamic changes in this large brain region.