Introduction

When making the decision that the joke you have just been told is one you have heard before, you may recollect a number of details about the context in which the joke was previously encountered. These details may relate to where and when the joke was heard, who told it, and who else was present. For example, you might remember that you heard it before during a best man speech at a wedding last summer, or you might remember that in fact it was you who previously told the joke (and perhaps the person who told it just now stole the joke from you). Additionally, you may remember some of your thoughts and reactions at the time of previously encountering the joke: e.g. as is often the case when the author of the present chapter tells a joke, that it was not particularly funny.

Characterizing source memory and related functions

A number of cognitive theories have been proposed to describe the processes involved in retrieving these different kinds of contextual detail. Source monitoring theory proposes that there is a set of decision processes that are involved in making attributions about the origins of previously encountered information, and that a subset of these processes (termed reality monitoring processes) support the ability to discriminate information that was generated by internal cognitive functions such as thought and imagination from information that was derived from the outside world by perceptual processes (Johnson & Raye, 1981; Johnson, Hashtroudi, & Lindsay, 1993). Another line of research has focused on characterizing the functionally distinct, largely sequentially operating processing stages supporting recollection, including the specification of retrieval cues and criteria for success, and the monitoring and evaluation of retrieved information against the specified verification criteria (Tulving, 1983; Burgess & Shallice, 1996; Schacter, Norman, & Koutstaal, 1998; Rugg, 2006). A further area of interest relates to whether the act of remembering events from the past might share common processing characteristics with other cognitive functions (Tulving, 1983; D'Argembeau & Van der Linden, 2004; Buckner & Carroll, 2007; Schacter & Addis, 2007), such as thinking about events that might occur...
in the future (prospective memory; McDaniel & Einstein, 1992; Ellis, 1996) and attending to the mental states of oneself and other agents (mentalizing; Frith & Frith, 2003).

At present, no single cognitive theory that I am aware of encompasses all of these issues, but individually, these areas of investigation have received a great deal of attention from cognitive psychologists, who have explored the effects of experimental manipulations on behavioural measures such as accuracy and reaction time, and have provided numerous insights into the operating characteristics of remembering (Mandler, 1980; Tulving, 1983; Ratcliff, Van Zandt, & McKoon, 1995; Clark & Gronlund, 1996; Kelley & Wixted, 2001; Yonelinas, 2002; Rotello, Macmillan, & Reeder, 2004). Further constraints on theorizing have been obtained from the study of older adults as well as patients with brain lesions and other disorders affecting cognitive function. Such neuropsychological studies, often employing dissociation logic (Shallice, 1988), have provided support for a number of key conceptual distinctions such as the separation of source recollection and item recognition, general source attribution processes and those supporting reality monitoring, and cue specification and post-retrieval monitoring processes. Typically, these studies have highlighted the prefrontal cortex (PFC) as one of the critical structures for accurate recollection (Janowsky, Shimamura, & Squire, 1989; Schacter, Kasznia, Kihstrom, & Valdiserri, 1991; McDaniel & Einstein, 1992; Burgess & Shallice, 1996; Henkel, Johnson, & De Leonardi, 1998; Glisky, Rubin, & Davidson, 2001; Simons et al., 2002; Duarte, Ranganath, & Knight, 2005).

Using neuroimaging data to constrain cognitive theory

In recent years, an increasingly important contribution has been made by studies using functional neuroimaging techniques such as functional magnetic resonance imaging (fMRI). Such techniques offer high spatial resolution, sufficient temporal resolution to permit some (albeit limited) separation of sequentially occurring processes, and the ability to document activity patterns in networks of connected regions distributed across the whole brain (Fletcher & Henson, 2001; Simons & Spiers, 2003). This is not, of course, to say that imaging has become the only tool to be used in seeking to understand recollection. Many fundamental insights continue to be obtained without going anywhere near a scanner. Furthermore, good neuroimaging experiments tend to be those that are closely guided and constrained by cognitive theory, preferably seeking convergence with neuropsychological evidence relating to the necessity of activated brain regions.

When undertaken well, neuroimaging studies can produce data that may be thought of as another dependent variable for distinguishing between competing cognitive theories and generating hypotheses for further investigation (Henson, 2005). In particular, inferences based on significant region-by-condition interactions in patterns of brain activity can be considered analogous to the dissociation logic used in neuropsychology (Shallice, 2003; Henson, 2005, 2006). Another formalized strategy is the reverse inference, analogous to probabilistic association logic, according to which activity in the same specific brain region for two different tasks implies that both tasks must share one or more cognitive processes (Poldrack, 2006). The reverse inference relies for its usefulness on the anatomical specificity that can be obtained from neuroimaging but is not so readily available in
neuropsychological studies. By adopting one or both of these inferential strategies, it is possible for researchers to use neuroimaging data to constrain their cognitive theories, either by introducing further distinctions to a conceptualized cognitive system on the basis of observed dissociations in activity, or by expanding the scope of a cognitive model as a result of a reverse inference to include processes which may not have been predicted *a priori*.

In the last decade or so, a growing number of memory researchers have designed theoretically motivated functional neuroimaging experiments constrained by cognitive theory and neuropsychological data. The results of these studies have, in a number of cases, been interpreted on the basis of region-by-condition interactions and/or reverse inferences, providing additional insights into the functional organization of memory processes. Many of these developments, for example relating to important roles played by regions of the medial temporal lobe, are discussed in other chapters in the present volume. In this chapter, I describe some of the insights that have impacted on our conceptual understanding of source recollection, focusing on the areas of investigation outlined earlier: internally and externally generated context; pre- and post-retrieval processing stages; and commonalities between recollection, prospective memory, and mentalizing. These insights center on anterior PFC, a region for which accruing evidence suggests an important role in central cognitive control processes that are relevant to each of these functions. I go on to outline a cognitive hypothesis of these control processes and their operating principles, a hypothesis that has primarily been developed and constrained on the basis of deductive inferences drawn from functional neuroimaging data.

**Recollection of internally vs. externally generated context**

Functional neuroimaging studies of source memory, consistent with the neuropsychological literature, have supported the distinction made by cognitive theories between source recollection and item recognition. Early neuroimaging studies also echoed lesion evidence emphasizing the importance of PFC regions in the recollection of source information (Nyberg *et al.*, 1996; Nolde, Johnson, & D’Esposito, 1998; Rugg, Fletcher, Chua, & Dolan, 1999; Henson, Shallice, & Dolan, 1999; Ranganath, Johnson, & D’Esposito, 2000). Source-related activation was consistently observed in ventrolateral (Brodmann Area [BA] 45/47) and dorsolateral (BA 9/46) PFC, and was also reported in some studies (but not universally) in anterior PFC (approximating BA 10). Roles were ascribed for the ventrolateral region in the specification of retrieval cues (Dobbins, Foley, Schacter, & Wagner, 2002), and for dorsolateral PFC in the post-retrieval monitoring of recovered information (Rugg *et al.*, 1999; Henson *et al.*, 1999) (see next section for more on this).

Understanding the role in source memory played by anterior PFC has been less straightforward. This may be partly because of a long-running debate in the recognition memory literature over whether activation in this region during old/new recognition reflected the cognitive state (or ‘retrieval mode’) an individual was in prior to remembering (Nyberg *et al.*, 1995), the particular aspects of mnemonic information to which attention was directed (‘retrieval orientation’) (Rugg & Wilding, 2000), the amount of cognitive
resources (retrieval effort) expended during a retrieval attempt (Schacter, Alpert, Savage, Rauch, & Albert, 1996), or the level of accuracy (retrieval success) achieved in recovering the sought-after information (Rugg, Fletcher, Frith, Frackowiak, & Dolan, 1996). Another reason that the involvement of anterior PFC in source memory may have been difficult to characterize was that whereas a number of neuroimaging experiments reported activation in this region during the recollection of source details (Rugg et al., 1999; Ranganath et al., 2000; Dobbins et al., 2002; Kahn, Davachi, & Wagner, 2004), other equally well-conducted, apparently very similar studies failed to identify activation in this region (Nyberg et al., 1996; Henson et al., 1999; Suzuki et al., 2002).

It is always problematic to attempt a theoretical explanation that can account for null results. The lack of anterior PFC activation in the three studies cited above could be attributable to lack of experimental power or to susceptibility distortion in the fMRI signal due to the proximity of anterior PFC to the sinus area. However, a potentially more theoretically interesting account, which would require testing in a within-subjects experiment, is that the types of context used in all the previous studies tended to differ according to whether, at the time of encoding, they were derived from the outside world (e.g. when or where an event occurred) or were generated internally (e.g. one's thoughts about the event). The experiments that had tested recollection of which of two encoding tasks had been undertaken by participants with each target stimulus all observed significant activation in anterior PFC (Rugg et al., 1999; Dobbins et al., 2002; Kahn et al., 2004). However, studies that had focused on perceptual contextual features, such as the position or size on the monitor screen in which target stimuli had been studied, produced inconsistent results in anterior PFC with some reporting significant activation (Ranganath et al., 2000; Cansino, Maquet, Dolan, & Rugg, 2002) and others not (Nyberg et al., 1996; Henson et al., 1999; Suzuki et al., 2002). If anterior PFC were sensitive to the internal/external nature of recollection decisions, this would support the reality monitoring processing distinction made by cognitive theories of source memory between recollection of the cognitive operations engaged by participants in carrying out a study task versus recollecting perceptual details derived from the outside world relating to the study episode (Johnson & Raye, 1981; Johnson et al., 1993).

A number of recent studies have investigated whether neuroimaging evidence can be found to support the existence of reality monitoring processes, by manipulating within subjects the recollection of internally and externally generated source details. The emerging consensus from these studies is that anterior PFC is among the brain regions sensitive to reality monitoring distinctions, consistently exhibiting differential activation during the retrieval of aspects of context that were internally generated vs. perceptually derived at the time of encoding (Simons, Owen, Fletcher, & Burgess, 2005; Simons, Gilbert, Owen, Fletcher, & Burgess, 2005; Dobbins & Wagner, 2005; Simons, Davis, Gilbert, Frith, & Burgess, 2006; Vinogradov et al., 2006; Kensinger & Schacter, 2006; Simons, Henson, Gilbert, & Fletcher, 2008). For example, Simons, Owen et al. (2005 directly contrasted recollection of the encoding task carried out during initial presentation of stimuli with recollection of where on the monitoring screen the stimuli had been presented. They observed a significant region-by-condition interaction within anterior PFC, with lateral
regions associated with recollection of both task and position details, and a medial anterior region exhibiting significantly greater activation during recollection of encoding task than of stimulus position. Similar lateral-medial anterior dissociations have since been observed in a number of subsequent studies, with the lateral region activated consistently during all source conditions tested, and the medial region sensitive to reality monitoring manipulations (Simons, Gilbert et al., 2005; Dobbins & Wagner, 2005; Simons et al., 2008).

As shown in Figure 22.1, medial anterior PFC has been shown to exhibit differential activation during recollection of the encoding task undertaken contrasted with remembering where on the screen (Simons, Owen et al., 2005) or when in time (Simons, Gilbert et al., 2005) stimuli were presented, or remembering their size on the screen (Dobbins & Wagner, 2005). The same region is involved in remembering whether verbal phrases were previously presented in full on the screen (e.g. ‘bacon and eggs’), or whether a word was missing which participants had to imagine (e.g. ‘bacon and ?’) in order to complete the phrase themselves (Simons, Davis et al., 2006; Vinogradov et al., 2006). Likewise, medial anterior PFC is differentially engaged during recollection of whether an object was previously seen or imagined by participants (Kensinger & Schacter, 2006). Finally, medial anterior PFC has been shown to be associated with remembering whether oneself or another person previously performed a particular operation on stimuli (Simons et al., 2008). The sensitivity of this region to reality monitoring distinctions is apparent regardless of whether words, faces, or objects are being remembered (Simons, Owen et al., 2005; Simons, Gilbert et al., 2005; Dobbins & Wagner, 2005; Kensinger & Schacter, 2006), suggesting that the effect is independent of stimulus type. Moreover, medial anterior activation has been observed irrespective of whether the ‘internal’ or ‘external’ condition is associated with lower recollection accuracy and longer reaction times or vice versa, or whether such behavioural factors are matched between conditions (Simons, Owen et al., 2005; Simons, Gilbert et al., 2005), suggesting that an account in terms of differential task difficulty is unlikely to be sufficient.

**Distinct processing stages of source recollection**

A number of cognitive theories of retrieval have proposed that there are functionally distinct processing stages involved in retrieving a stored representation from memory (Tulving, 1983; Burgess & Shallice, 1996; Schacter et al., 1998; Rugg, 2006). These processing stages, illustrated in Figure 22.2, are considered to operate in a largely sequential, iterative fashion, beginning with the retrieval orientation stage of specifying retrieval cues and criteria for success on the basis of the task instructions and presented target stimulus. Once these pre-retrieval specification processes have been completed, a goal-directed search of mnemonic representations can be undertaken seeking concordance between the retrieval cue and stored information. If the search was sufficiently well-specified, potential target memories will be identified and their associated stored representations reactivated and maintained online in working memory. The retrieved information will be monitored and evaluated against the specified verification criteria and, if the criteria for
successful retrieval are satisfied, an appropriate behavioural response can be made. Alternatively, if the retrieved mnemonic information is insufficient or incorrect, the retrieval cues and verification criteria can be modified and further retrieval searches attempted.

Because it can be difficult in neuropsychological studies of memory dysfunction to establish which of the processing stages may be impaired in any one individual (Fletcher & Henson, 2001), much of the information on whether separable brain regions that might support each of these stages of retrieval comes from functional neuroimaging. Such studies have highlighted that different areas of PFC may support pre-retrieval and post-retrieval cognitive control processes. For example, Dobbins et al. (2002) identified a region of ventrolateral PFC which was activated during both semantic processing and source recollection tasks, but not during item recognition. On the basis of this pattern of activation, the authors interpreted the likely function of this region in recollection as reflecting the controlled semantic analysis necessary for the specification of effective retrieval cues. This region was differentiated from a more posterior region of ventrolateral PFC, which showed significant activity across semantic processing, source recollection, and item recognition tasks, consistent with previous suggestions of a role in lexical/phonological maintenance in working memory (Poldrack et al., 1999; Smith & Jonides, 1999).

The post-retrieval stage of monitoring recovered information against pre-specified verification criteria has also been examined in a number of neuroimaging experiments, with evidence suggesting the involvement of dorsolateral PFC regions (Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1998; Henson et al., 1999; Rugg et al., 1999; Henson, Rugg, & Shallice, 2000). For example, Henson et al. (2000) operationalized monitoring by contrasting situations in which participants expressed low confidence in their memory with situations in which they were highly confident, observing activation in right dorsolateral PFC. Similar results implicating dorsolateral PFC were also found when the higher monitoring demands of a source recollection task were contrasted with item recognition, considered to rely more on judgements of familiarity (Henson et al., 1999; Rugg et al., 1999). However, as described in the previous section, some studies contrasting source
recollection with item recognition also observed activation in anterior PFC (Rugg et al., 1999; Ranganath et al., 2000; Dobbins et al., 2002), which further investigation suggested may be determined by the internal vs. external nature of the source detail being recollected (Simons, Owen et al., 2005; Dobbins & Wagner, 2005). An unresolved question is which stage(s) of the retrieval process might be subserved by anterior PFC.

We have recently attempted to address this issue by teasing apart whether anterior PFC might show differential activity associated with pre- or post-retrieval processes. Focusing first on evidence for a role in pre-retrieval processes such as retrieval orientation and/or cue specification, we designed a source memory test phase in which each trial began with an instruction specifying which of two different source details were to be recollected on that trial, presented prior to the onset of a previously-studied target stimulus. We hypothesized that retrieval orientation processes might be expected to be recruited when the retrieval instruction was presented, continuing to be engaged on presentation of the target stimulus and as the retrieval search ensued. In one experiment (Simons, Gilbert et al., 2005), a manipulation was employed whereby a recollection instruction was either followed by a target stimulus (which would provoke a retrieval search) or followed by a control stimulus (in which case a retrieval search would not be undertaken). Any activation that was observed in both conditions could be considered to reflect processes occurring prior to the inception of a retrieval search. A conjunction contrast, identifying regions of significant activation common to both search and no-search conditions, revealed significant activation in left lateral anterior PFC, as well as in the ventrolateral region attributed to cue specification by Dobbins et al. (2002).

This result was replicated in a subsequent study in which the onsets of the retrieval instruction and the target stimulus were separated by a randomly varying number of
seconds (similar to the method used by Sakai & Passingham, 2003). Activity associated specifically with the retrieval instruction rather than the target stimulus was seen in the same region of left lateral anterior PFC as in the previous study (Simons et al., 2008). Similar findings were also reported by Dobbins and Han (2006), although the lateral anterior PFC region they implicated in pre-retrieval processes was located on the right, perhaps reflecting the use of pictorial stimuli in that study (although stimulus-specific asymmetries in anterior PFC have not been noted previously; Simons, Owen et al., 2005; Simons, Gilbert et al., 2005). In all three studies examining retrieval orientation processes, no significant pre-retrieval activity was observed in medial anterior PFC; moreover, significant region-by-condition interactions in the studies from Simons et al. confirmed the specific nature of the lateral anterior PFC role in these processes.

Turning to post-retrieval monitoring processes, we hypothesized that even if the retrieval process does iterate, post-retrieval monitoring should typically occur later in time than pre-retrieval cue specification. Therefore, regions that subserve such post-retrieval processes may be those that are associated with source recollection, but in which activity peaks significantly later than that in retrieval orientation-related regions. As shown in Figure 22.3, when the time-courses of lateral and medial anterior PFC regions involved in source recollection were extracted, the peak of activity in the medial region occurred significantly later than that in the lateral region associated with pre-retrieval processes (Simons, Gilbert et al., 2005). This latency difference did not merely reflect possible differences in vasculature between regions, because there was no difference in latency between lateral and medial anterior PFC regions associated with performance during a semantic retrieval baseline condition. Instead, this result suggests that medial anterior PFC contributes to a later stage of retrieval than cue specification, such as post-retrieval monitoring.

The suggestion that medial anterior PFC is involved in a late stage of retrieval is not direct evidence for a role in monitoring specifically. However, the proposed association with post-retrieval monitoring was given additional support by recent evidence of task-dependent differences in functional connectivity between medial anterior PFC and right dorsolateral PFC during source recollection (Simons et al., 2008). As noted above, numerous studies have linked dorsolateral PFC with post-retrieval monitoring processes (Fletcher et al., 1998; Henson et al., 1999; Rugg et al., 1999; Henson et al., 2000). When activity in medial anterior PFC was entered into a psychophysiological interaction analysis, the region of the brain to show the most significant task-specific covariation in activity was right dorsolateral PFC (Simons et al., 2008). This connectivity pattern indicates that, during source recollection, medial anterior PFC may modulate activity in right dorsolateral PFC during the monitoring of retrieved contextual information.

**Commonalities between recollection, prospective memory, and mentalizing**

One of the cardinal features of episodic memory is the concept of mental time-travel (Tulving, 1983), the idea that the act of remembering involves projecting oneself to a different time to
recollect details of a previous experience. Other cognitive functions share this characteristic of mentally projecting oneself into another time or place (Tulving, 1983; D’Argembeau & Van der Linden, 2004; Buckner & Carroll, 2007; Schacter & Addis, 2007). For example, prospective memory involves thinking about the future, considering events that might occur or keeping in mind intentions to act (McDaniel & Einstein, 1992; Ellis, 1996). In addition, forming a theory of mind, or mentalizing, involves considering a situation from another person’s perspective, in essence projecting oneself into that person’s mind (Frith & Frith, 2003; Saxe, Carey, & Kanwisher, 2004). In recent years, evidence has accumulated to suggest that the cognitive functions of recollection, prospective memory, and mentalizing may share neural substrates, as well as common processes. Damage to regions of PFC has been associated with source recollection deficits (Janowsky et al., 1989; Simons et al., 2002; Duarte et al., 2005), with impairment to prospective memory (Burgess, Veitch, de Lacy Costello, & Shallice, 2000), and with difficulties on reasoning tasks requiring a theory of mind (Stone, Baron-Cohen, & Knight, 1998; Stuss, Gallup, & Alexander, 2001; although see Bird, Castelli, Malik, Frith, & Husain, 2004).

One region that has been suggested to be particularly critical is the medial area of PFC, and reverse inference evidence from functional neuroimaging substantiates the view that
this area plays an important role. The consistent, reproducible involvement of medial anterior PFC in source recollection has already been discussed in this chapter. A number of studies have implicated a very similar region in performance of prospective memory tasks (see Figure 22.4), with activity being seen when participants undertake a cognitive task while maintaining a delayed intention to act in the future (at a particular time in the future or when a particular cue event occurs) (Okuda et al., 1998; Burgess, Quayle, & Frith, 2001; Burgess, Scott, & Frith, 2003; Simons, Schöölvinck, Gilbert, Frith, & Burgess, 2006). In a recent study, we examined just how critical this region is to prospective memory by manipulating both the salience of the cue event signaling that the intended action should be performed, and the complexity of the intention to be retrieved (drawing on distinctions made in the cognitive literature by McDaniel & Einstein, 1992). Despite significant effects of these manipulations on behavioural performance, strikingly similar patterns of activation were observed in anterior PFC (Simons, Schöölvinck et al., 2006).

![Figure 22.4](image)

**Figure 22.4** Anterior PFC regions important for source recollection (e.g. retrieving details of the encoding task undertaken when stimuli were previously encountered) closely resemble those involved in prospective memory (e.g. retrieving a delayed intention to act when a particular target stimulus is presented). Figures adapted from Simons, Owen et al. (2005 and Burgess et al. 2003), with permission from Elsevier.
These activations closely resembled those linked to source recollection, attesting to the importance of this region for both cognitive functions.

A related line of research has involved directly contrasting activity associated with recalling events from the past versus imagining events in the future (Okuda et al., 2003; Addis, Wong, & Schacter, 2007; Szpunar, Watson, & McDermott, 2007). For example, Okuda et al. (2003) scanned participants while they were talking about events that had occurred in the past or would occur in the future. Activation common to both conditions was observed in medial anterior PFC, among other areas. Similar results were observed recently by Addis et al. (2007) and Szpunar et al. (2007), who presented participants with cue words and asked them to recall a past event or imagine an event in the future related to each word. These investigators endeavoured to control phenomenological characteristics of the target recollections such as level of detail, personal significance, and specificity in time, factors on which narrative accounts of past and future events often differ (D'Argembeau & Van der Linden, 2004). Just as in the study by Okuda et al., striking commonalities were observed by Addis et al. and Szpunar et al. in medial anterior PFC across the elaboration of past and future events. Together, the results of these studies provide within-subject evidence confirming that the processes supported by medial anterior PFC are central to both recollection and prospective memory.

Another cognitive function that has been suggested (e.g. Buckner & Carroll, 2007) to require similar processes of self-projection is ‘mentalizing’, the ability to understand and represent another individual’s perspective (Frith & Frith, 2003; Saxe et al., 2004; Amodio & Frith, 2006). This ability is considered to involve the utilization of a theory of mind, the mental projection of oneself into another individual’s mind to understand what that individual thinks or believes about the world (Premack & Woodruff, 1978). Much research has concentrated on the development of theory of mind in children (Frith & Frith, 2003), but in recent years neuroimaging studies have characterized the neural substrates of mentalizing. These studies have consistently observed medial PFC activation during such tasks as inferring the emotional states of oneself and others (Ochsner et al., 2004), evaluating personality traits relating to the self or other people (Kelley et al., 2002; Macrae, Moran, Heatherton, Banfield, & Kelley, 2004), and interpreting, on the basis of stories or cartoons, the beliefs or intentions held by other people (Fletcher et al., 1995; Brunet, Sarfati, Hardy-Bayle, & Decety, 2000).

Although neuroimaging studies of mentalizing have typically reported activation in medial anterior PFC, the precise locus of activity has often been more caudal than the area linked with source recollection and prospective memory (Gilbert, Spengler et al., 2006; see also Gilbert et al., 2007). One account for this variation could be that source and prospective memory tasks usually relate solely to one’s own personal experience, projecting oneself to a different time from the present, whereas mentalizing tasks often require judgements to be made from the perspective of another person, projecting oneself into that person’s mind. In a recent study (Simons et al., 2008), we attempted to test this hypothesis by contrasting a form of source recollection previously linked with the more rostral region of medial anterior PFC (‘Did I previously perceive or imagine that stimulus?’) with a form
that might require consideration of another person’s perspective (‘Did I or the experimenter previously perform the encoding task with that stimulus?’). The sole activation difference between the two kinds of judgement lay in greater activity in medial anterior PFC when recollecting whether the participant or the experimenter had carried out an operation during prior encoding as compared to recollecting whether an item had been perceived or imagined. Critically, this activation was located in a relatively caudal region of medial anterior PFC, with a coordinate on the rostro-caudal axis that was significantly closer to the anterior commissure origin than the coordinates from previous source recollection and prospective memory studies. This relatively caudal activation associated with recollection requiring consideration of one’s own and another person’s perspective lay instead in the center of the distribution of mentalizing-related anterior PFC activations reported in a recent meta-analysis (Gilbert, Spengler et al., 2006).

From neuroimaging findings to cognitive hypothesis

The neuroimaging findings reviewed in this chapter have converged to suggest that regions of anterior PFC support processes that: (a) are central to source recollection, and in particular reality monitoring, discriminating information that was generated by internal cognitive functions from information perceived from the outside world; (b) make distinct contributions to pre-retrieval cue specification and post-retrieval monitoring operations; and (c) are common to functions such as prospective memory and mentalizing, in addition to source recollection. These findings, some of which are based on region-by-condition interactions and some on reverse inference, are difficult to fit into any single extant account of source recollection. Instead, they have contributed to the formulation of a new cognitive hypothesis of the general processing operations supported by anterior PFC, characterized as an information processing gateway (see Figure 22.5) that serves to bias attention between stimulus-oriented and stimulus-independent thoughts (Burgess, Simons, Dumontheil, & Gilbert, 2005). This hypothesis is based almost entirely on inferences drawn from neuroimaging data, as patients with focal lesions selectively affecting anterior PFC are extremely rare and the region is structurally very different in even the closest non-human primates (Semendeferi, Armstrong, Schleicher, Zilles, & Van Hoesen, 2001).

According to the ‘gateway’ hypothesis, source memory relies on the differential allocation of attention between internally represented mnemonic information and the currently-perceived stimuli that provoke its retrieval (Simons, Gilbert et al., 2005). Taken one stage further, the hypothesis provides an account for reality monitoring in terms of sensitivity to the internal versus external nature of the original source of stored mnemonic representations (e.g. internally generated imaginings versus externally derived perceptions). The available evidence indicates that activity in medial anterior PFC is consistently greater during recollection of internally-generated than externally-derived source details (Simons, Owen et al., 2005; Simons, Gilbert et al., 2005; Dobbins & Wagner, 2005; Simons, Davis et al., 2006; Vinogradov et al., 2006; Kensinger & Schacter, 2006). Intriguingly, the dominance in activity for processing of information that was previously
internally generated is typically inverted during tasks that require the processing of currently perceived or imagined stimuli. For example, Gilbert et al. (2005) observed greater activation in medial anterior PFC when participants performed tasks on the basis of visually-presented stimuli than when they performed the same tasks ‘in their heads’ (see also Janata et al., 2002; Small et al., 2003; Gilbert, Simons, Frith, & Burgess, 2006). Although the reasons for the polarity reversal in processing of remembered and current information are not yet fully understood, taken together the results do suggest a general, low-level set of processes that are responsible for discriminating between internally and externally generated information.

A full account of the proposed operating characteristics of the gateway hypothesis are beyond the scope of this chapter (readers may refer to Burgess et al., 2005, for further details). However, the general cognitive control function of biasing attention between internally generated thoughts and stimulus-oriented perceptions is likely recruited to the benefit of a number of the processing stages of recollection (Simons, Gilbert et al., 2005; Simons et al., 2008). For example, pre-retrieval operations may involve the transformation of a visually presented retrieval instruction specifying the type of recollection required on an upcoming trial from an externally derived perceptual representation into stimulus-independent task parameters that orient attention towards particular contextual details, and generate, select, and initiate retrieval strategies and verification criteria. Stimulus-oriented processing of a presented target stimulus, about which details of previous

**Figure 22.5** Diagram illustrating the Gateway Hypothesis, describing a cognitive control system, supported by anterior PFC, that biases attention between stimulus-oriented and stimulus-independent thought (adapted from Burgess et al., 2005, with permission from Oxford University Press). Adjustment of gates 1 and 2 to position A will favour stimulus-independent thought, whereas if both gates are at position B, attention is oriented towards interacting with external stimuli. Different configurations of the gates are proposed to account for empirical observations of sensitivity to internally and externally generated context; distinctions between pre- and post-retrieval processing stages; and commonalities between recollection, prospective memory, and mentalizing. See main text for details.
exposure context are to be retrieved, can operate to direct searches of the internal mnemonic store, from which matching stored representations can be evaluated against the specified verification criteria. If the retrieved information does not meet the criteria for a response, further stimulus-oriented processing may be used to identify other properties of the presented stimulus as a basis for modifying the retrieval strategies and criteria for further searches to be undertaken. Alternatively, if the criteria for successful retrieval are met, an appropriate behavioural response can be output through effector systems.

An account in terms of a processing ‘gateway’ can also be applied to other cognitive functions that have been hypothesized to share functional properties with source recollection, such as prospective memory and mentalizing. Prospective memory can be considered to involve the biasing of attention between stimulus-oriented processing of the cognitive task being undertaken and stimulus-independent processing of the delayed intention to act (Burgess et al., 2003; Burgess et al., 2005; Simons, Schölvinck et al., 2006). During performance of the ongoing cognitive task, attention must be oriented towards the task stimuli both so satisfactory behavioural performance can be maintained, and so that a prospective memory cue stimulus can be detected when it is presented. Once the cue is identified, attention must be disengaged from the external stimuli and oriented towards internal representations so that the relevant intention can be retrieved from memory and the specified action effected. Similarly, mentalizing can be conceived as involving the disengagement of attention from the external world in favour of stimulus-independent processing to generate a representation of the world that simulates the perspective that may be held by another person (Amodio & Frith, 2006; Buckner & Carroll, 2007). Generating such a representation may involve both stimulus-oriented processing of the current behaviour of that person in relation to other salient people and/or objects in the world, as well as stimulus-independent processing of any prior experience that may be available of that person (or, indeed, of oneself) in related previous circumstances, in order to construct a sufficiently detailed representation of what the person’s beliefs, motives, and intentions are likely to be that their future behaviour can be predicted.

It should be noted that the gateway hypothesis is at present considered very much to be a work in progress. There are still a number of areas that are poorly understood. For example, further work is required to establish the dynamics by which the processing of previously experienced and currently perceived internally and externally generated information appears to differ. One possible means of investigating this issue might be by examining activity associated with recollecting source details about stimuli that, in the test phase, are being imagined by participants rather than being presented externally. In addition, it has yet to be established whether precisely the same processes are involved in the prospective functions of maintaining a delayed intention to act and imagining an event that might occur in the future. Future studies can investigate whether the same regions of anterior PFC are involved in both forms of projection into the future. Moreover, our understanding of the processes that may be common to source recollection, prospective memory, and mentalizing is somewhat vague and underspecified. These processes require more detailed exposition, and future studies should be undertaken to identify
other, as yet unconsidered, cognitive functions that may also rely on these common processes. Such studies will need to consider the means by which attending to stimulus-oriented and stimulus-independent information might contribute to an account of other cognitive functions (e.g., mentalizing processes as a component of source recollection), as well as seeking to understand the roles in these control processes played by other brain regions that almost certainly interact with anterior PFC, such as the medial temporal lobe (Simons & Spiers, 2003).

Finally, the hypothesis makes predictions about the manner in which cognitive functions such as source memory might break down in neurological or psychiatric disorders. For example, it has not so far been shown in the same patients that focal anterior PFC lesions impair performance on reality monitoring, prospective memory, and mentalizing tasks, as would be predicted if all of these functions rely on attentional switching between stimulus-oriented and stimulus-independent processing. Furthermore, reduced ability to distinguish information perceived in the outside world from imagined information might be one explanation for the hallucinations and delusions often seen in schizophrenia (Frith, 1992; Johnson & Raye, 2000). We have some evidence that tentatively supports such an account (Simons, Davis et al., 2006; Simons et al., 2008), but the relationship between reality monitoring deficits and psychotic phenomena, or indeed between impairments to recollection, prospective memory, and mentalizing, remain to be fully tested.

**Conclusions**

I have tried in this chapter to describe a number of neuroimaging studies of source memory and related functions, conducted in our laboratory and by other investigators that have been motivated and constrained by cognitive theories and which have, in turn, informed the development of a new cognitive theory, the gateway hypothesis. This hypothesis, which has been shaped considerably by neuroimaging data, can account for empirical observations such as differential sensitivity of medial anterior PFC to the recollection of source details that were previously internally generated or externally derived; the distinct contribution made by lateral and medial anterior PFC towards pre- and post-retrieval stages of the retrieval process; and the common involvement of medial anterior PFC regions in prospective memory and mentalizing, as well as source recollection. Hopefully, these studies provide just one example of how neuroimaging results can inform cognitive theories of memory. If neuroimaging studies are designed with the primary aim of testing predictions derived from cognitive theories, and inferences about the resulting patterns of brain activity are based on significant region-by-condition interactions or probabilistic designations of cognitive processes to specific brain regions, there seems no reason why neuroimaging should be considered as anything other than one more form of evidence for adjudicating between competing psychological theories. Presumably, most investigators would agree that the ultimate aim of our scientific discipline is to provide the fullest possible understanding of how we remember. In which case, seeking convergent evidence from all available experimental techniques can only take us further towards that goal.
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References


REFERENCES


