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Autobiographical and episodic memory—one and the same? Evidence from prefrontal activation in neuroimaging studies

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Abstract

Laboratory investigations of episodic memory often require participants to encode and later retrieve lists of items (words, pictures, or faces). The underlying assumption is that recollection of items from the list is analogous to recollection of events from one's past, i.e. autobiographical re-experiencing. Functional neuroimaging studies of episodic memory have provided extensive evidence suggesting that regions of the prefrontal cortex (PFC) play a role in episodic memory retrieval. A review of PFC activations reported in imaging studies of autobiographical memory and matched sub-sets of list-learning episodic memory studies reveals patterns of similarity but also substantial differences. Episodic memory studies often report activations in the right mid-dorsolateral PFC, but such activations are absent in autobiographical memory studies. Additionally, activations in the ventromedial PFC, primarily on the left, are almost invariably found in autobiographical memory studies, but rarely occur in studies of episodic memory. It is suggested that these two regions mediate different modes of post-retrieval monitoring and verification. Autobiographical memory relies on quick intuitive 'feeling of rightness' to monitor the veracity and cohesiveness of retrieved memories in relation to an activated self-schema. Episodic memory for lists requires more conscious elaborate monitoring to avoid omissions, commissions and repetitions. The present analysis suggests that care and caution should be exercised in extrapolating from the way we recollect 'events' from a list learned in the laboratory to the way we recollect events from our lives.

Keywords: Dorsolateral PFC; Ventrolateral PFC; Ventromedial PFC; Monitoring; Self-schema; Intuition

1. Introduction

Episodic memory is a term that was proposed originally in order to distinguish personally experienced events from the general facts we know about linguistic concepts, the world and ourselves (Tulving, 1972, 1983). Episodic memory is conceptualized as a system that enables the conscious recollection of an event and the context in which it occurred. This conceptualization implies that autobiographical memory is either synonymous with episodic memory or is a specific case of it (e.g. Gardiner, 2001; Kopelman & Kapur, 2001; Tulving, 1972). By this view, recalling a discrete experimental stimulus and the context in which it was presented ('an event') has the same status as recalling autobiographical events; both should be retrieved by a similar set of cognitive processes and be supported by similar brain structures. However, some have questioned the assumption of equivalence between these modes of remembering on theoretical grounds (Conway, 2001; Conway & Pleydell-Pearce, 2000; Tulving, 2001; Wheeler, Stuss, & Tulving, 1997). Specifically, Wheeler et al. (1997) highlight the idea that episodic memory is primarily characterized by the type of awareness that accompanies retrieval whereas autobiographical memory is defined by the content of the material retrieved (i.e. self-related). Episodic memory involves remembering by re-experiencing and being aware of the continuity of the experiencing self across time; autobiographical memory refers to information that directly involves the rememberer but need not entail the same subjective awareness. Autobiographical re-experiencing, the ability to travel back in time and re-experience an event from the past, is only one (important) aspect of autobiographical memory and is thought to be uniquely human by this view. Conway and Pleydell-Pearce (2000); see also Conway (2001) distinguish the time frame within which these memory types operate, with episodic memory measured in seconds, minutes and hours, whereas autobiographical memory encompassing much longer

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periods. This view echoes an earlier distinction made by Brewer (1986) who suggested episodic re-experiencing aspects of autobiographical memory may only last for days to weeks. By this view, detailed event-specific remote autobiographical memory has little in common with episodic memory as measured in the laboratory. Nonetheless, laboratory investigations of episodic memory most commonly involve encoding and retrieval of lists of items, and findings are generalized and deemed pertinent to the way humans recollect specific events from the past. This is true of investigations in cognitive psychology and cognitive neuroscience.

Neuroscientific investigations, and in particular functional neuroimaging, have provided in extensive evidence that links episodic memory to functions of the frontal lobes. For example, studies of episodic retrieval using lists of items consistently find activations in the prefrontal cortex (PFC). Some have suggested that retrieval-related processes tend to be lateralized to the right (Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1998; Henson, Rugg, Shallice, Josephs, & Dolan, 1999a; Nyberg et al., 1996; Rugg, Fletcher, Chua, & Dolan, 1999) although this view has been challenged by suggestions that this asymmetry is related to the nature of the material (verbal versus non-verbal) rather than the nature of the process (retrieval) (Lee, Robbins, Pickard, & Owen, 2000; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999; Miller, Kingstone, & Gazzaniga, 2002; Wagner, Poldrack et al., 1998b). Either way, neuroimaging studies very often implicate the right PFC in episodic retrieval processes (see Cabeza & Nyberg, 2000; Fletcher & Henson, 2001 for recent reviews). The consistent involvement of the right PFC in early PET studies of memory retrieval was first noted by Tulving, Kapur, Craik, Moscovitch, and Houle (1994) who proposed the hemispheric encoding/retrieval asymmetry (HERA) hypothesis to account for this regularity. With regard to the right PFC, the HERA model asserts that it is involved in retrieval of episodic, as opposed to semantic, information and that it is more involved in retrieval of such information than the left PFC (see Habib, Nyberg, & Tulving, 2003 for slight revisions of the model which also attempts to accommodate the material specificity arguments).

Subsequent imaging research, which employed more sophisticated technologies and research designs, indicated that different regions within the PFC are differentially activated in response to different task demands at various stages of the retrieval process. For example, in relation to task demands, studies began to probe the episodic aspect of retrieval by employing source memory paradigms. In these studies, subjects were required to retrieve specific contextual information such as where, when or how an item appeared rather than simply the content, or occurrence of an item in the study list (Cabeza et al., 1997b; Cansino, Maquet, Dolan, & Rugg, 2002; Dobbins, Foley, Schacter, & Wagner, 2002; Henson et al., 1999a; Nyberg et al., 1996; Ranganath, Johnson, & D'Esposito, 2000; Rugg et al., 1999; Rugg, Henson, & Robb, 2003). Theoretically, these judgments require additional cognitive processes compared to simple recognition that can be performed based on familiarity alone or a conjunction of familiarity and recollection (Jacoby, 1991). Retrieval of items and their context in the above mentioned studies was indeed associated with increased activity on either left or bilateral anterior PFC and either right or bilateral dorsolateral PFC when compared to retrieval of context-free items. These paradigms more closely approximate the phenomenology of autobiographical re-experiencing and the neuroanatomical evidence derived from them is thought to reflect its functional neuroanatomy better.

In a recent fMRI study of autobiographical memory (Gilboa, Winocur, Grady, Hevenor, & Moscovitch, in press), we noted the absence of activation in the anterior and mid-dorsolateral right PFC (around Brodmann areas (BA) 46/10 and 9/46, respectively), which we had expected to observe based on evidence from laboratory tests of episodic memory described above. This was particularly remarkable since our paradigm emphasized re-experiencing as opposed to general autobiographical knowledge, and because even direct comparisons between context-rich and context-poor memories did not yield the expected activation. Recently, this absence was also noted in another study of autobiographical memory (Maguire & Frith, 2003) and in a laboratory-based study of episodic memory (Burgess, Maguire, Spiers, & O'Keefe, 2001; see also Burgess, Maguire, & O'Keefe, 2002). These authors have hypothesized that differences in PFC activation may be due to differences in the temporal context of autobiographical memory, which is more distinct across memories, and the diversity of events, which reduces interference susceptibility, compared to laboratory-based episodic memory studies.

Such discrepant data again raise the question of the equivalence of episodic memory for lists and autobiographical re-experiencing, this time on empirical grounds. The present review seeks to address the question of similarities and differences in patterns of activation of the frontal lobes in laboratory tests of episodic memory and autobiographical memory studies.

2. Method

2.1. Selection and categorization of studies

There are only a handful of neuroimaging studies of autobiographical memory. The experimental techniques they use to select and elicit memories differ on several dimensions. For example, some studies emphasize re-living and re-experiencing of personal events by allowing longer retrieval times or by selecting events that are particularly memorable and significant in the subjects' lives. Other studies allow less time for retrieval and thus are unlikely to elicit the same type of re-experiencing (Conway & Bekerian, 1987).

Studies may also differ with regard to the amount of strategic processes and effort required for retrieval. Cues that are sufficiently specific and distinctive and are strongly associated with the to-be-retrieved information (proximal cues) can elicit direct retrieval or ecphory, which may not require much prefrontal involvement (Moscovitch & Winocur, 2002). More distal or abstract cues would require more strategic or generative retrieval (Conway & Pleydell-Pearce, 2000; Moscovitch, 1992; Moscovitch & Winocur, 2002). For example, Conway et al. (1999) used the Crovitz cue-word test that requires subjects to retrieve personal memories in response to a cue-word (e.g. 'letter') whereas Maguire et al. (Maguire & Frith, 2003; Maguire & Mummery, 1999; Maguire, Vargha-Khadem, & Mishkin, 2001) use a sentence verification paradigm with sentences that are derived from a pre-scan interview ensuring the participants have good knowledge of the event. Moreover, instructions can have a great effect on what sort of processes are elicited. Subjects in Fink et al.'s (1996) study also heard sentences derived from a pre-scan interview, similar to the stimuli used by Maguire. However, their participants were required to imagine everything that happened in the events and had more prolonged recollection times, turning the paradigm into a cued-recall rather than yes/no recognition, which would again require different strategic processes.

For the purpose of the present analysis, contrasts within autobiographical studies were defined with relation to three aspects that are particularly pertinent for observing retrieval-related frontal lobe activity in neuroimaging. (1) *Information*: whether the paradigm stressed retrieval of contextual information, requiring subjects to re-activate and re-experience unique aspects of personal events, or related more to content as in personal semantic or generic knowledge. Many studies have collected either subjective (rating scales) or objective (interviews) measures of re-experiencing, to support the idea that contextual information was retrieved (Addis, Moscovitch, Crawley, & McAndrews, in press; Andreasen et al., 1995, 1999; Gilboa et al., in press; Levine et al., in press; Maguire & Frith, 2003; Niki & Luo, 2002; Piefke, Weiss, Zilles, Markowitsch, & Fink, 2003; Ryan et al., 2001). Sometimes, however, it was difficult to determine the extent to which contextual information was indeed retrieved. For example, Maguire and Mummery (1999) used sentences such as "You were Mike's best man at his wedding". This event is specific to time and place and can therefore be considered contextual in nature. However, although the event itself is specific to time and place, one may verify this sentence based solely on semantic self-knowledge, without re-experiencing Mike's wedding. In these cases, contrasts were categorized as 'context' or 'content' based on the specificity of the information required (i.e. time, place, etc.). (2) *Task*: contrasts were categorized according to whether the retrieval task was a cued-recall or a recognition task as an approximate index of cue proximity (i.e. direct versus generative retrieval). Unlike in episodic memory studies (see below), the type of retrieval task is only rarely made explicit in autobiographical memory studies. It is important to note that the type of task is determined not only by the type of cue, but also by what is required of the participant, as in the example described above. The same is true of episodic memory studies where a word can serve as a stimulus for recognition (old/new) or for cued-recall, as in the case of paired associate paradigms; the distinction however is made explicit. (3) *Baseline*: contrasts were also defined with relation to the type of baseline used for the cognitive subtraction. Studies vary greatly not only by the choice of target condition but also with regard to the baseline condition and the hypothesized cognitive processes for which this baseline serves as control. Thus, activation in a particular region depends not only on whether that region participates in the presumed cognitive function but also on whether it is active or not in the baseline condition. Many of the autobiographical memory studies use other memory tasks, mostly semantic but also some episodic memory baselines, which may conceal prefrontal activation. Others, however, use lower level baselines such as reading, which likely involve fewer strategic processes.

Different paradigms within the episodic retrieval literature may also induce different types of processes. For example, manipulation of the 'density' of targets to lures in a recognition or fragment completion can vary the amount of post-retrieval verification processes observed during a particular block (Allan, Dolan, Fletcher, & Rugg, 2000; Rugg et al., 1998). As well, asking participants to retrieve either content (item) or context/source (see above) may change both the extent of generative retrieval required and the aspect of mental time travel required. Similar manipulations can be achieved using the remember/know distinction (Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Henson et al., 1999a) or exclusion tasks (Dobbins et al., 2002; Henson, Shallice, & Dolan, 1999b; Rugg et al., 2003). The type of retrieval task may determine the extent to which strategic search processes are involved as in cued-recall versus recognition (e.g. Cabeza et al., 1997b; Fletcher et al., 1998; Rugg et al., 1998). Finally, here too, the baseline used is as important as the task itself in determining the pattern of activation that is observed.

The present analysis is an exhaustive review of prefrontal activations reported in fourteen studies of autobiographical memory (Table 1). It is selective in that an equivalent number of episodic memory studies were selected for comparison based on each of the three aspects described above. The first comparison involves fourteen episodic memory studies that are matched on the type of information that is targeted for retrieval (content versus context) (Table 2). It should be noted that the definitions of context in list learning paradigms is different from contextual information in autobiographical memory in two important ways. One is that episodic memory studies are often designed to dissociate contextual aspects of memory from other retrieval processes, which is only the case in three autobiographical memory studies (Addis et al.,

Table 1
Contrasts from autobiographical memory studies used for the review

Study	Modality	Contrast	Information	Task	Baseline
Addis et al. (in press)	fMRI	Episodic and generic recall vs. sentence completion and size discrimination	Context	Cued recall	Semantic
Andreasen et al. (1995)	PET	Episodic event recall vs. verbal fluency	Context	Cued recall	Semantic
Andreasen et al. (1999)	PET	Intentional vs. incidental episodic recall	Context	Cued recall	Episodic
Conway et al. (1999)	PET	Crovitz cue-word vs. paired associate	Context	Cued recall	Episodic
Fink et al. (1996)	PET	Personal event sentence vs. other's event (imagined scenario)	Context	Cued recall	Semantic
Gilboa et al. (in press)	fMRI	Personal photo recall vs. 'other' photo (imagined scenario)	Context	Cued recall	Semantic
		Failure to retrieve specific information vs. 'other' photo	Content	Cued recall	Semantic
Levine et al. (in press)	fMRI	Personal episodic vs. general semantic recordings	Context	Cued recall	Semantic
		Personal semantic vs. general semantic recordings	Content	Cued recall	Semantic
Maddock et al. (2001)	fMRI	Names of familiar people vs. names of unfamiliar people	Content	Cued recall	Reading
Maguire and Mummery (1999)	PET	Personal events vs. word strings with no personal pronouns	Context	Recognition	Reading
		Personal events vs. public events and personal facts	Context	Recognition	Semantic
Maguire et al. (2000)	fMRI	Personal events vs. word strings with personal pronouns	Context	Recognition	Reading
Maguire and Frith (2003)	fMRI	Personal events vs. word strings with no personal pronouns	Context	Recognition	Reading
Niki and Luo (2002)	fMRI	Memory for places visited recently vs. places visited >7 years ago	Context	Cued recall	Episodic
Piefke et al. (2003)	fMRI	Childhood and recent memories vs. reading instructions	Context	Cued recall	Semantic
Ryan et al. (2001)	fMRI	Personal recall in response to general cue vs. sentence completion.	Context	Cued recall	Semantic

Table 2
Contrasts from episodic memory studies that were matched by imaging modality and type of information retrieved

Study	Modality	Contrast	Information	Task	Baseline
Cabeza et al. (1997b)	PET	Temporal order vs. item memory	Context	Recognition	Episodic
Cabeza et al. (2003)	fMRI	Recognition (predominantly R responses) vs. fixation	Context	Recognition	Fixation
		Recognition (item and context) vs. cued recall (stems and paired)	Context	Recognition	Episodic
Dobbins et al. (2002)	fMRI	Source (semantic) vs. item recognition	Context	Cued recall	Episodic
Dobbins et al. (2003)	fMRI	Recognition of encoding context vs. recency	Context	Recognition	Episodic
		Recency vs. encoding context	Context	Recognition	Episodic
Eldridge et al. (2000)	fMRI	'Remember' responses vs. 'know'	Context	Recognition	Episodic
Fletcher et al. (1996)	PET	Random vs. semantically related paired associates	Content	Cued recall	Episodic
Fletcher et al. (1998)	PET	Cued recall from a categorized list vs. word repetition	Content	Cued recall	Reading
Henson et al. (1999a)	fMRI	'Remember' responses vs. 'Know'/new words	Context	Recognition	Episodic
Koehler et al. (1998)	PET	Forced choice recognition (obj/loc) vs. encoding/perceptual matching	Context	Recognition	Perceptual
Lepage et al. (2003)	fMRI	Intact + rearranged word pairs vs. new pairs	Context	Recognition	Episodic
Nyberg et al. (1996)	PET	Item identity vs. location/time	Content	Recognition	Episodic
		Location/time vs. identity	Context	Cued recall	Episodic
Rugg et al. (1999)	fMRI	Source (location) vs. item recognition high density	Context	Cued recall	Episodic
		Source (location) vs. item recognition low density	Context	Cued recall	Episodic
Rugg et al. (2003)	fMRI	Exclusion (color/location at encoding) vs. recognition task	Context	Cued recall	Episodic
Suzuki et al. (2002)	fMRI	Temporal context (between lists) vs. picture recognition	Context	Recognition	Episodic

in press; Gilboa et al., in press; Niki & Luo, 2002). However, as pointed out above, most autobiographical memory studies provide evidence for the predominance of contextual information. The other is that in episodic memory studies context is often defined by subtle differences such as the side of the screen on which a word appeared or to which list a word belongs. Nonetheless, these manipulations were designed to mimic the type of subjective experiential phenomenon associated with autobiographical re-experiencing. This point is further discussed later. The

Table 3
Contrasts from episodic memory studies that were matched by imaging modality and type of retrieval task

Study	Modality	Contrast	Information	Task	Baseline
Allan et al. (2000)	PET	Fragment completion recall (0-density) vs. fragment completion	Content	Cued recall	Episodic
Bäckman et al. (1997)	PET	Explicit stem completion vs. stem completion not from list	Content	Cued recall	Semantic
Burgess et al. (2001)	fMRI	Place (cued-recall) vs. width comparison	Context	Cued recall	Perceptual
		Person (cued-recall) vs. width comparison	Context	Cued recall	Perceptual
Cabeza et al. (2003)	PET	Cued recall (stems and pairs) vs. recognition (item and context)	Content	Cued recall	Episodic
Cansino et al. (2002)	fMRI	Correct vs. incorrect source (location) memory	Context	Cued recall	Episodic
Fletcher et al. (1995)	PET	Cued recall (category: exemplar) vs. semantic (category: exemplar)	context	Cued recall	Semantic
Henson et al. (1999b)	fMRI	Location exclusion task vs. simple visual-motor control condition	Context	Cued recall	Reading
Henson et al. (2002)	fMRI	Paired associates (all levels of interference) vs. word reading	Content	Cued recall	Reading
Kensinger et al. (2003)	fMRI	Successful retrieval (easy and hard encoding) vs. fixation baseline	Content	Recognition	Fixation
Ranganath et al. (2003)	fMRI	Recognition of faces vs. fixation	Content	Recognition	Fixation
Ranganath et al. (2000)	fMRI	Retrieval of specific (size) vs. general information (old/new)	Context	Cued recall	Episodic
Raye et al. (2000)	fMRI	Exclusion for presentation modality (picture and heard words) vs. recognition	Context	Cued recall	Episodic
Rugg et al. (1998)	PET	Zero-density stem completion vs. stem completion (first word comes to mind)	Content	Cued recall	Semantic
Slotnick et al. (2003)	fMRI	Source (location) vs. hits for item identity	Context	Cued recall	Episodic
		Hits vs. correct rejection of abstract figures	Content	Recognition	Episodic

Table 4
Contrasts from episodic memory studies that were matched by imaging modality and type of baseline

Study	Modality	Contrast	Information	Task	Baseline
Donaldson et al. (2001)	fMRI	Old vs. new words semantic judgement (abstract/concrete)	Content	Recognition	Semantic
Cabeza et al. (1997a)	PET	Cued recall word pairs vs. reading	Content	Cued recall	Reading
		Recognition of word pairs vs. reading	Content	Recognition	Reading
Düzel et al. (1999)	PET	Old/new vs. semantic judgment (living/non-living)	Content	Recognition	Semantic
Eyler Zorilla et al. (1996)	fMRI	Recency vs. reading/matching	Context	Recognition	Reading
Grady et al. (2001)	PET	Object recognition vs. object naming	Content	Recognition	Semantic
Hunkin et al. (2000)	fMRI	Cued recall (paired associate) vs. semantic association of target word	Content	Cued recall	Semantic
Kapur et al. (1995)	PET	Low target recognition vs. semantic judgment (living/non-living)	Content	Recognition	Semantic
		High target vs. semantic judgment (living/non-living)	Content	Recognition	Semantic
Konishi et al. (2000)	fMRI	Recognition hits (words) vs. correct rejections	Content	Recognition	Episodic
McDermott et al. (1999)	fMRI	Recognition old/new vs. semantic judgment (pleasantness of concepts)	Content	Recognition	Semantic
McDermott et al. (2000)	fMRI	Hits of studied compound words vs. correct rejection of non-studied	Content	Recognition	Episodic
Tsukiura et al. (2002)	fMRI	Newly learned names vs. famous names	Content	Cued recall	Semantic
Rugg et al. (1997)	PET	Recognition (deep) vs. semantic judgment (living/non-living)	Content	Recognition	Semantic
		Recognition (shallow) vs. semantic judgment (living/non-living)	Content	Recognition	Semantic
Saykin et al. (1999)	fMRI	Overlearned words vs. novel words	Content	Recognition	Episodic
Wagner et al. (1998a)	fMRI	Recognition (deep encoding) vs. reading	Content	Recognition	Reading

second comparison involved equal number of recognition and cued-recall paradigms, again under the limitation of slight differences in methodology between autobiographical and episodic memory studies (Table 3). Finally, the third group of episodic memory studies was selected to try to equate the types of baseline conditions used (Table 4). Overall, 42 episodic memory studies are reviewed.

Additionally, studies within each comparison were equated with respect to the imaging modality used (PET versus fMRI) to avoid differences in activation peaks that are due to different scanning methodologies (e.g. due to difficulty of scanning orbitofrontal cortex in fMRI or the lower spatial and temporal resolution of PET). The second column of each table indicates the imaging modality used. The third column of each table includes descriptions of each contrast. These descriptions are too brief to allow a proper account of the conditions involved, but should allow identification of the contrast within the corresponding article. The fourth, fifth and sixth columns identify the sought-after information (context or content), the memory task used (recognition or cued-recall) and the type of baseline for each of the contrasts.

Table 5
Number of activation peaks reported by episodic and autobiographical studies in the right prefrontal cortex

BA	Medial							Lateral								
	6	8	9	10	11	24	32	6	8	9	10	11	44	45	46	47
Autobio	3	–	3	2	3	–	3	4	–	1	2	1	–	9	2	1
Episodic 1	3	3	1	–	–	–	1	3	4	13	5	–	2	1	8	6
Episodic 2	1	1	–	–	–	1	1	5	1	9	7	–	2	2	8	4
Episodic 3	2	1	1	–	–	–	–	–	–	11	9	1	2	3	7	4

Note: Autobio, autobiographical; BA, Brodmann area; Episodic 1, first group of episodic memory studies, matched by type of information; Episodic 2, second group of episodic memory studies, matched by type of retrieval task; Episodic 3, third group of episodic memory studies matched by baseline used.

Table 6
Number of activation peaks reported by episodic and autobiographical studies in the left prefrontal cortex

BA	Medial							Lateral								
	6	8	9	10	11	24	32	6	8	9	10	11	44	45	46	47
Autobio	5	1	5	8	5	–	1	12	1	6	1	1	–	4	3	6
Episodic 1	3	4	6	–	–	–	1	7	5	8	6	–	3	10	2	7
Episodic 2	–	1	–	–	–	2	2	4	1	11	7	–	2	8	5	9
Episodic 3	2	2	1	–	–	–	4	6	1	4	6	1	3	–	1	2

Note: Autobio, autobiographical; BA, Brodmann area; Episodic 1, first group of episodic memory studies, matched by type of information; Episodic 2, second group of episodic memory studies, matched by type of retrieval task; Episodic 3, third group of episodic memory studies matched by baseline used.

3. Results

The results of the different contrasts are reported in Tables 5 and 6, for the right and left cerebral hemispheres, respectively. The total number of activation peaks is reported for each BA, separately for right and left lateral and medial aspects of the frontal lobes. If BA's were not provided in the paper they were determined according to the Talairach atlas coordinates (Talairach & Tournoux, 1988). In the text, regions are referred to in terms of their BA, and anatomical descriptions and qualifiers (e.g. right mid-dorsolateral PFC; left ventrolateral PFC) are added to better characterize the region of activation. The activation peaks of these contrasts, as identified by *xyz* coordinates in the articles, are plotted in Figs. 1 and 2. Peaks were offset to the nearest cortical surface for the purpose of representation in the figure. These relocations were mostly around 5(mm in magnitude, although some activation peaks had to be moved by up to 8(mm. Care was taken to ensure that the manipulated activations would fall in the BA described by the authors of the paper.

As indicated in Tables 5 and 6, there are observable similarities as well as differences between autobiographical and episodic memory studies with regard to the frequency with which activations are reported in different regions. Both types of studies report ventrolateral activations (BA 44/45/47) bilaterally. Although autobiographical studies tend to report more activations in area 45 on the right whereas episodic memory studies tend to report area 47 more frequently, the overall frequency is comparable. Similarly, superior frontal regions (areas 6 and 8) show comparable frequency of activation in the two types of studies and dorsal medial regions bilaterally also present similar patterns of activations (areas 6, 8 and 9), as well as 24/32 that only rarely are reported by both types of studies. On the other hand, there are noticeable differences in the frequency of activation reported in the right dorsolateral cortex (areas 9 and 46) and to a lesser extent polar area 10, occurring more frequently in episodic memory studies. These differences are not seen on the left dorsolateral cortex. Finally, ventromedial activation (areas 10 and 11) is reported very frequently on autobiographical memory studies and very rarely for episodic memory studies, primarily on the left. It is also noteworthy that when studies were selected based on their baselines, right superior cortex and left ventrolateral cortex are not as frequently reported.

4. Discussion

4.1. The prefrontal cortex and retrieval of episodic vs. autobiographical memories

Despite the obvious similarities in the pattern of activations reported by episodic and autobiographical memory studies, this review confirmed the initial observation from our study (Gilboa et al., in press); see also Burgess et al. (2001) and Maguire and Frith (2003). Activation of right dorsolateral PFC (BA 9/46, 9 and 9/10) rarely occurs in autobiographical memory studies although it is widely reported in episodic memory studies. When it does occur in autobiographical studies, it appears in the anterior (BA 10 and 10/46) or posterior (BA 6/9) part of this region (see Fig. 1) whereas episodic memory studies mostly report mid-dorsolateral PFC (BA 9 and 9/46).

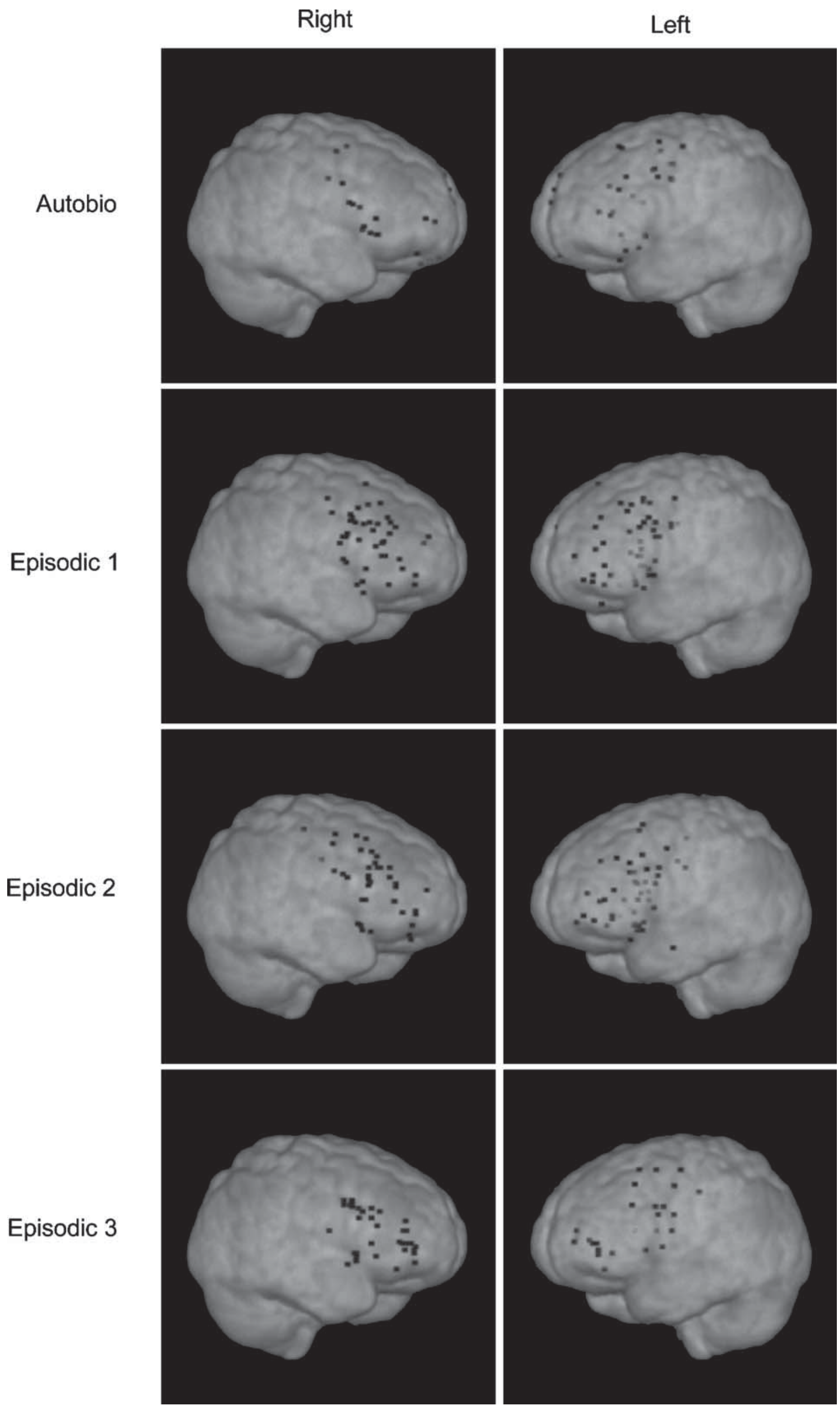

Fig. 1. Lateral activation peaks of the right prefrontal (left hand column) and left prefrontal (right hand column) cortices as reported in autobiographical and episodic memory studies. Autobio: autobiographical; Episodic 1: first group of episodic memory studies, matched by type of information; Episodic 2: second group of episodic memory studies, matched by type of retrieval task; Episodic 3: third group of episodic memory studies matched by baseline used.

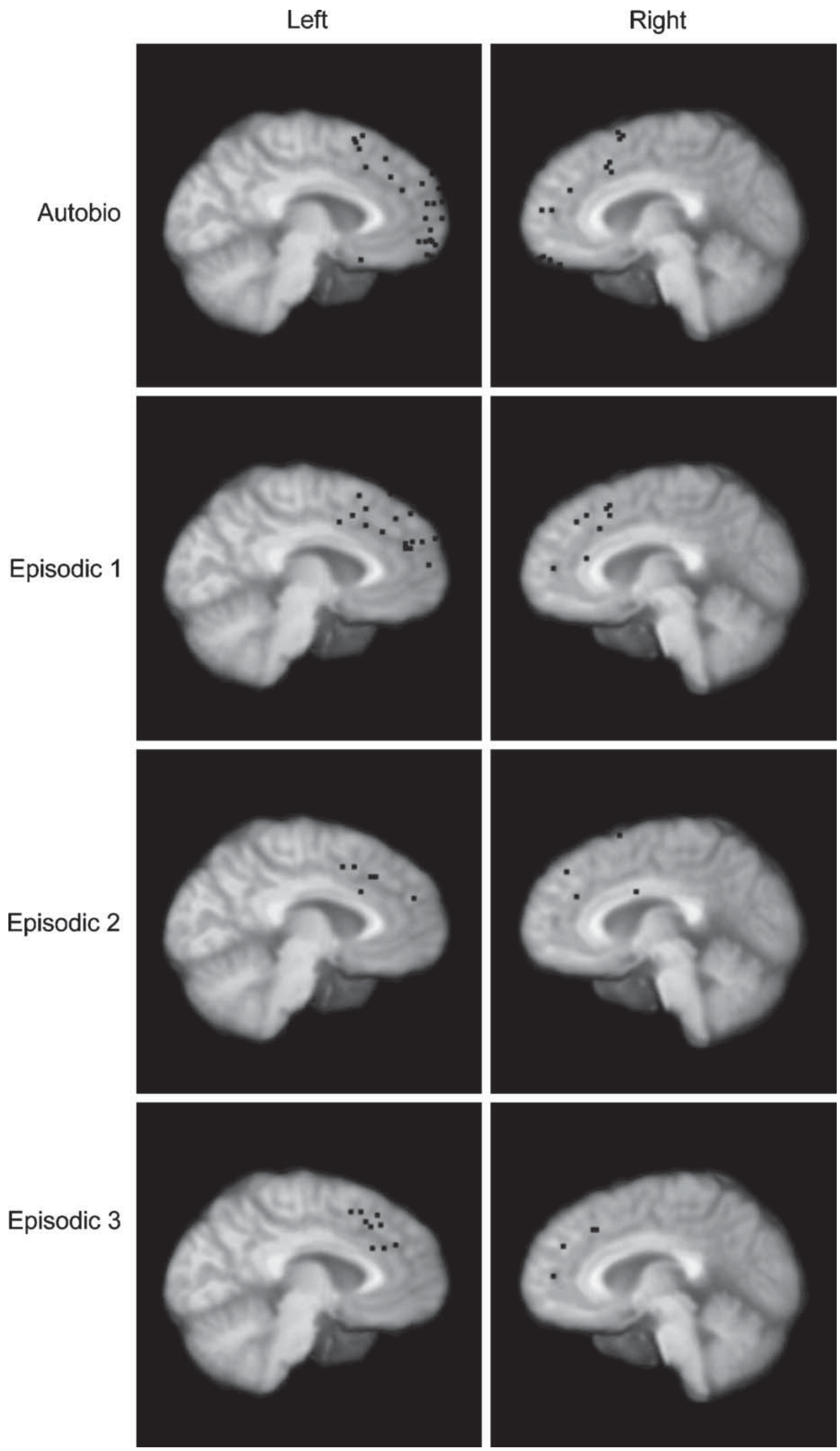

Fig. 2. Medial activation peaks of the left prefrontal (left hand column) and right prefrontal (right hand column) cortices as reported in autobiographical and episodic memory studies. Autobio: autobiographical; Episodic 1: first group of episodic memory studies, matched by type of information; Episodic 2: second group of episodic memory studies, matched by type of retrieval task; Episodic 3: third group of episodic memory studies matched by baseline used.

In addition, noticeable differences between episodic and autobiographical studies were observed in the medial PFC. Both types of studies report comparable activations in the dorsal medial PFC. Activations within the ventral medial PFC (BA 10/11) primarily on the left appear in all autobiographical memory studies, but not in any of the episodic memory studies. As a general rule, conclusions based on the absence of activations in any single imaging study should be interpreted cautiously as many variables, including cross-study differences in statistical power, the threshold at which activations are reported and most importantly the type of baseline used may affect such patterns. In the present review, studies were compared also with regard to the type of baseline used, and the same pattern of absence of activation emerged. In addition, a review of 61 episodic memory retrieval studies (Cabeza & Nyberg, 2000), also reported no activations in the ventromedial PFC, suggesting this finding is robust. More data need to be accumulated with regard to retrieval of autobiographical memory to determine the robustness of the observed 'silence' of the mid-dorsolateral cortex. In the meantime, a hypothesis regarding the functional significance of the current findings is offered below. The different patterns of activation in the right dorsolateral and left ventromedial PFC in episodic and autobiographical memory studies may reflect different modes of memory retrieval monitoring.

4.2. The right ventrolateral and mid-dorsolateral prefrontal cortex

One influential hypothesis regarding the role of right PFC regions in episodic memory retrieval is the monitoring hypothesis (e.g. Fletcher et al., 1998; Henson et al., 1999b; Rugg et al., 1998; Rugg et al., 2003; but see Lepage, Ghaffar, Nyberg, & Tulving, 2000; Nyberg et al., 1995 for the alternative 'retrieval mode' hypothesis). According to the monitoring hypothesis, the right PFC is thought to be involved in the continual checking of responses in order to avoid omissions and repetitions in free recall tasks. During cued-recall and recognition, it is involved in monitoring responses to avoid false positives and false negatives. By comparison, the ventrolateral PFC (around BA 45 and 47) is believed to be involved in specification of retrieval cues prior to a retrieval attempt when an indirect retrieval cue is available (Moscovitch & Winocur, 2002) and active retrieval is required (Petrides, 2002). The dorsolateral cortex (BA 9, 46 and 10) on the other hand, is engaged in monitoring of information in memory (Petrides, 2000), which is critical at the post-retrieval stage, primarily under conditions of uncertainty (Henson, Rugg, Shallice, & Dolan, 2000; Moscovitch & Winocur, 2002).

The dissociation between ventrolateral and dorsolateral PFC is reflected in the present analysis: ventrolateral cortex is associated with both autobiographical and episodic studies while dorsolateral PFC seems to be specific to episodic memory studies. Assuming basic equivalence of functional neuroanatomy between memory tasks, this suggests that similar pre-retrieval processes are implicated, but possibly different post-retrieval ones. A review of studies of episodic retrieval shows that activation of the right ventrolateral PFC is sensitive to the nature of retrieval task, being more involved in cued-recall than in recognition (Fletcher & Henson, 2001). Presumably, in cued-recall, each cue defines a new 'search space' from which the correct response could be retrieved.

The lack of activations in the right mid-dorsolateral cortex (BA 9/46) and scarcity of activations in the anterior part (BA 10/46) in studies of autobiographical memory is more difficult to interpret. Fletcher et al. (1998) originally suggested that the dorsolateral region is required for 'complex, high level planning' of intended acts and the monitoring of the retrieved information within working memory. Thus, it is involved in tasks where there is a demand for the monitoring of one's own responses in order to guide the next response. It is also activated in recognition memory but only when post-retrieval processing demands are increased, for example on tasks that require a judgment of relative recency of two items (Cabeza et al., 1997b), when correct recognitions are made with low confidence (Henson et al., 2000) and when source judgments are required (Henson et al., 1999b).

Most tasks of autobiographical retrieval also require complex high-level processes that would involve monitoring of the products of retrieval, and some present very high demands on such processes (e.g. Conway et al., 1999; Gilboa et al., in press; Ryan et al., 2001), yet activation of the right dorsolateral PFC is not observed. There are three possible reasons for the absence of activations in the right dorsolateral PFC despite the cognitive requirement for monitoring.

(1) Activation by the target task is cancelled out by the baseline task, which also activates this region. This explanation is unlikely because diverse baselines are used in autobiographical memory studies, some of which require very low-level processing such as reading instructions, sentence completion, listening to taped general semantic information or word strings, paired-associates, imaginary scripts, etc. Moreover, when episodic memory studies were equated with autobiographical memory studies with regard to the baselines employed, the same pattern of mid-dorsolateral activation is found as in other episodic memory studies, despite the diversity of baseline conditions.

(2) Another possibility is that by emphasizing response selection, episodic memory studies lead to greater necessity for verification and monitoring (Petrides, 2000) than do autobiographical studies. The latter 'allow' subjects to have repetitions, and do not require them to sequence the events in any logical order or to ensure that they retrieve all of the relevant details from the particular event ('omissions'). Although this hypothesis cannot be dismissed entirely, there is evidence that speaks against it. Maguire and colleagues used sentence

verification that required response selection, but they also do not report activity in dorsolateral PFC; however, their paradigm leaves little room for uncertainty, which may be an important factor in verification processes (Henson et al., 2000; Moscovitch & Winocur, 2002). Moreover, behavioral data indicate that autobiographical memory retrieval does involve verification and sequencing processes. Burgess and Shallice (1996) suggest that even when no explicit requirement is made, subjects very commonly engage in verification analysis and self-corrections, while repetitions are relatively rare (see also Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002).

(3) A third possibility is that the right dorsolateral PFC is only recruited as part of a fine-grained control mechanism under conditions of uncertainty. Autobiographical memories are characterized by a very strong belief value (Brewer, 1986) that is not necessarily directly related to their actual veracity. This strong belief value is the result of a set of processes that determine the subjective sense of the veracity and coherence of retrieved self-related memories; it is distinct from the type of processes the right dorsolateral PFC mediates and may even override it in cases of conflict. As will be argued below, this system is crucially mediated by the ventromedial PFC, which shows activation in autobiographical memory studies but rarely in studies of episodic memory.

4.3. The medial prefrontal cortex

Medial PFC has been associated with several seemingly disparate cognitive processes. It is often implicated during processing of self-referential stimuli, such as self-referent encoding of trait adjectives (Craik et al., 1999; Gusnard, Akbudak, Shulman, & Raichle, 2001; Kelley et al., 2002) or focusing on internal reactions to stimuli (Gusnard et al., 2001). Craik et al. (1999) suggest that activation of a general schematic representation of the self, mediated by medial left PFC, influences encoding and is responsible for the superiority in retrieval of items encoded with relation to the self. Similar kinds of processing may be involved during retrieval of self-referential information (Andreasen et al., 1999; Maguire, 2001; Stuss & Levine, 2002).

Moscovitch and Winocur (2002) use the term ‘felt rightness in context’ to describe the possible role of the ventromedial PFC and the frontal pole in “working with memory” processes. ‘Felt rightness’ refers to the ability to rapidly or intuitively appreciate the appropriateness, suitability and accuracy of a response with relation to the goals of the memory task and/or current personal goals. It precedes any elaborate cognitive verification of the truthfulness of the memory and the context in which it is retrieved. Evidence of confabulation following ventromedial PFC lesions further supports the idea that this region is important in monitoring aspects of the veracity of autobiographical memories. Confabulating patients tend to accept indiscriminately strong memory cues irrespective of the appropriateness of their content or the context of retrieval. They can sometimes cognitively appreciate the inconsistencies between their memories and the goals of the memory task, but will often cling to their confabulatory ideation. Although the lesion in confabulation is often more posteromedial (Gilboa & Moscovitch, 2002), the anterior and posterior ventromedial PFC may play complementary roles of positive and negative criterion setting for accepting or rejecting a memory (Moscovitch & Winocur, 2002).

Similar ideas have been raised in an apparently unrelated context. The anterior ventromedial PFC has been implicated in situations where a response needs to be made under conditions of uncertainty and/or guessing rather than based on a deliberate selection process (Maguire, Frith, & Morris, 1999; Nathaniel-James, Fletcher, & Frith, 1997, see Elliott, Dolan, & Frith, 2000 for review). For example, Nathaniel-James et al. (1997) presented their participants with sentences where the last word was missing and required them to complete the sentence with a word that was either compatible or incompatible with the meaning of the sentence (cf. the Hayling Test (Burgess & Shallice, 1997). Activation in anterior ventromedial PFC was observed when participants were required to complete sentences that had many possible correct completions compared to conditions where only a few possible correct responses existed. The effect was also observed in the incompatible response condition (Nathaniel-James et al., 1997). Elliott and colleagues (Elliott et al., 2000) suggest that what is common to tasks that produce activation of the ventromedial PFC is the requirement to select stimuli and responses based on a general ‘feeling of rightness’.

An interesting convergence exists between the study by Nathaniel-James et al. (1997) described above and the performance of the confabulating patient HW with damage to the ventromedial PFC (Moscovitch, 1989). HW confabulated in response to non-specific cues during semantic retrieval but gave correct responses when the same questions were re-phrased to provide him with a proximal retrieval cue. When providing these correct responses, he insisted he was guessing, i.e. he had no ‘feeling of rightness’ even when he was right. Thus, when neurologically intact individuals respond to non-specific cues, they activate ventromedial PFC and rely on a general feeling of rightness (Nathaniel-James et al., 1997) while patient HW with extensive lesion to this region was unable to perform under similar conditions and evidently lacks that ‘felt rightness’ intuition.

To conclude, the Ventromedial PFC is involved in: (i) processing of self-related information; (ii) decision-making under conditions of uncertainty when multiple possible answers are available and (iii) memory control processes providing a ‘feeling of rightness’. Considering autobiographical memory, these processes may converge to provide a system that monitors the veracity of retrieved memories. It does so by establishing a self-related retrieval template that sets up the parameters against which retrieved memories are evaluated based on (or which give rise to) a general intuitive 'feeling of rightness'. Thus, the monitoring of the veracity and perhaps cohesiveness of autobiographical memories is primarily mediated by the ventromedial PFC.

Monitoring may involve two separate processes. One is closely akin to general problem-solving procedures applied to the memory domain and entails keeping track of actions and of expected events so as not to repeat them. This may is mediated by mid dorsolateral prefrontal region. The other is a component that supplies the person with a general immediate sense regarding the veracity of a memory. In the context of memory retrieval, "felt rightness", is an intuitive, quick endorsement or rejection of recovered memories with respect to the goals of the memory task (Gilboa & Moscovitch, 2002; Moscovitch & Winocur, 2002).

The ventromedial PFC also acts to integrate cognitive processes with emotional somatic signals in order to bias decision making at a pre-conscious level (Bechara, Damasio, & Damasio, 2000; Bechara, Damasio, Tranel, & Damasio, 1997). It is well situated anatomically to integrate visceral cues with information from limbic and neocortical heteromodal regions, in order to allow for such biasing (Barbas, 1995). It may accomplish a similar goal in the memory domain, particularly in autobiographical memories where such processes are pertinent, as memories carry emotional meaning or personal significance. Early, rapid emotionally-based decisions to endorse or reject an item may be followed by a more thorough, cognitive assessment of the memory's plausibility if for example the initial response is incompatible with other knowledge or memories. It is this latter function that is mediated by the dorsolateral cortex, but is probably recruited only infrequently in normal retrieval of autobiographical memories and thus is unlikely to appear in imaging studies.

4.4. Autobiographical and episodic memory

Tulving (2001) describes episodic memory as '... the kind of memory that allows one to remember past happenings from one's life' (p. 1505) including what happened, where and when. However, not all past happenings share the same status in the memory system. Although there are a lot of commonalities in the way retrieval processes of episodic and autobiographical memory are mediated by the brain, there may also be fundamental differences. Certain characteristics of autobiographical memory and episodic memory for lists of items may give us a clue as to why some of their functional neuroanatomy differs.

For one thing, the time frame of these two types of memory differs greatly. Laboratory tasks involving lists of items usually test subjects within minutes of encoding whereas autobiographical memory studies use memories formed over time periods of months, years or even decades. Brewer (1986) suggests that only retrieval of very recent autobiographical memories (in the order of days to weeks) involves re-creation of copy-like information from the original experience. With time, however, schema-based processes transform the retrieval process into a reconstructive cognitive process that may still retain the phenomenal characteristics of more recent personal memories (e.g. strong visual imagery, strong belief value). Similarly, Conway and coworkers (Conway, 2001; Conway & Pleydell-Pearce, 2000) suggest episodic memory is quite a rare type of memory that serves as a bridge between working memory and long-term memory, and is measured in the order of minutes to hours. Only a subset of these memories gets incorporated into more general autobiographical knowledge structures and is available for later retrieval, endowing the memory with its recollective experience. It is possible that immediate retrieval of this subset of episodic memories would recruit the same set of regions that are generally involved in retrieval of autobiographical memory; however, it seems more likely that time *per se* is not the primary factor determining the functional neuroanatomy of episodic and autobiographical memory. Interestingly, the only autobiographical memory study in the present review that reported activation in area 9 of the right dorsolateral cortex is a prospective study that involved retrieval of trivial every-day memories recorded over a few months preceding the scanning session (Levine et al., in press). Most of these events are unlikely to be incorporated into long-term autobiographical memory of the sort that is sampled in other autobiographical memory studies. It remains to be seen whether other studies that use prospective short-term methods to investigate autobiographical memory (e.g. by using mini-events or records of everyday occurrences) would show recruitment of regions associated with list-learning paradigms.

A related issue is the type of 'context' within which memories are embedded. When subjects are probed for contextual information related to their recollective experience in episodic memory paradigms, the context is very limited in scope and the search space very defined with relation to time and circumstance. In the studies reviewed above, subjects are asked to distinguish between contexts of two lists studied recently, two sides of the monitor where an item may have appeared or try to recall specific associated events (internal or external) that may have occurred during encoding in remember/know paradigms. Autobiographical memories on the other hand, even when they also involve vivid episodic recollective experience, are complex multi-faceted representations involving information at different levels of specificity that may be drawn from an infinitely large collection of experiences. This may be related to the involvement of the ventromedial PFC during decision-making under ambiguous conditions, and the reliance on a general sense or intuition regarding the truthfulness of the memory. As discussed above, Moscovitch and Winocur (2002) term this function 'feeling of rightness'.

Finally, memory for items in a list, compared to autobiographical memory differs with relation to the significance they bear for the rememberer in terms of personal goals, self-identity and emotional salience, to name just a few aspects. Elaborate definitions of episodic memory consist of three basic constructs: the self, subjectively sensed time and awareness of one's own continual experience in time (autonoetic awareness; Wheeler et al., 1997). Such definitions clearly allude to autobiographical memory, with its influence on the way we perceive ourselves. Studies that use remember/know judgments or exclusion tasks in order to address the characterization of episodic memory as memory that includes contextual information may capture the subjectively sensed time and autonoetic awareness. However, it is not clear that even these paradigms are able to capture all of the basic structures posited for episodic memory, and in particular the construct of self (Conway, 2001). As clearly seen in this review, the functional neuroanatomy associated with these distinctions within episodic memory studies is quite different from the one observed in autobiographical studies.

Currently, within the framework of memory systems (Schacter & Tulving, 1994; Squire, 1992), declarative memory is thought of as comprising only two sub-systems: semantic memory and episodic memory. It may be useful to think of declarative memory as encompassing three systems: semantic memory, episodic memory and self or autobiographical memory. Conway and coworkers (Conway, 2001; Conway & Pleydell-Pearce, 2000) have proposed the 'self memory system', and have argued convincingly for its distinction and characterization as a separate memory system. The present review provides some functional neuroanatomical evidence that distinguishes episodic memory from autobiographical memory, and suggests the need to consider the latter in its own right.

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