Autobiographical memory and the self in time: Brain lesion effects, functional neuroanatomy, and lifespan development

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Abstract

Autobiographical remembering reflects an advanced state of consciousness that mediates awareness of the self as continuous across time. In naturalistic autobiographical memory, self-aware recollection of temporally and spatially specific episodes and generic factual information (both public and personal) operate in tandem. Evidence from both laboratory and real-life studies, however, suggests that these two processes can be dissociated. This paper reviews aging, lesion, and functional neuroimaging research on the anatomical substrates of autobiographical memory processes using a new measure, the Autobiographical Interview, and prospective collection of autobiographical material. Results indicate that autobiographical recollection is mediated by a distributed fronto-temporo-parietal system, with the anteromedial prefrontal cortex positioned to integrate sensory information with self-specific information. The emergence of autobiographical recollection at around age four coincides with the timing of prefrontal regressive cortical and progressive white matter changes that may support the development of this high-level capacity.

1. Introduction

A good storyteller weaves setting, players, antecedents, story line, and implications together in a tapestry. Embellishments, like novelist Richard Ford’s uncanny descriptions of his characters’ clothing and appearance, enhance the story with richness of detail. Tangents may crop up here or there, but the central story is never in doubt. Even when the sequence of events is altered as a literary device, as in Pulp Fiction, the end leaves us with a sense of order.

Just like the stories that enlighten and entertain us, stories about our own personally experienced episodes are embedded in a historical context that assists in shaping our recall. What makes autobiographical memory truly compelling, however, is the uniquely human ability to recall a sequence of events specific in time and place leading to a conclusion, with a juicy detail or two thrown in to make it seem real. These elements are not just for benefit of the story’s recipient; they also enhance the conscious experience of the storyteller, even when the story unfolds only in his or her mind.

Now imagine having unlimited access to personal and public factual information, but restricted access to events as experienced—the perceptual, cognitive, and emotional detail that marks an event as part of your own personal past. We have studied patients with just that profile of autobiographical strengths and weaknesses. In extreme cases, they can provide perfectly accurate autobiographical information, such as old school names, addresses, and names of friends, but they cannot retrieve a single event linked to one of those autobiographical signposts (e.g., Levine et al., 1998). In this paper, I will review research that has extended this observation to groups of individuals with a profile similar in quality, if not in degree. I will also discuss functional neuroimaging findings from healthy adults that follow from the behavioral studies.

The classic distinction between episodic and semantic memory has provided a useful framework for characterizing our patients’ autobiographical deficits. In making
this distinction, we focus not just on recognition or recall of events from a specific time and place as specified in the original definition of episodic memory (Tulving, 1972), but rather on “autonoetic” or self-knowing awareness by which information, when successfully retrieved, is experienced as part of one’s past (Tulving, 2002; Wheeler, Stuss, & Tulving, 1997). In this paper, the terms episodic or autobiographical recollection will be used to indicate these highest-level capacities of memory and consciousness (see Conway, 2001 for a related, but alternative definition of these terms).

Episodic recollection is an advanced, late-appearing (both evolutionarily and ontogenetically) mnemonic capacity that relies on coordination across multiple brain systems and can be selectively affected by brain damage. It supports behaviors such as self-reflection and planning for the future that are uniquely present in humans. The scientific study of this capacity advances our understanding of human consciousness and human behavior in ways that cannot be accomplished in studies of animal memory or even many human laboratory studies.

This paper begins with a review of some of the outstanding issues in the assessment of autobiographical memory. I will then describe our work contrasting older and younger adults’ autobiographical memory and that of patients with focal frontal brain disease. Convergent evidence from functional neuroimaging studies of healthy adults follows. I conclude with some comments on the relevance of these findings to normal human development.

2. Assessing autobiographical memory

In a typical study of autobiographical memory, participants are asked to list or describe events that happened in their past. While researchers may ask participants to recall events from a particular time frame, there is often no experimental control over characteristics of the events recalled such as their importance, emotional content, prior rehearsal, or the quality of recollective experience. In any other domain of memory research, participants would not select the memoranda in this way. On the contrary, there is a wealth of data on characteristics such as frequency, imageability, or length of words from which experimenters draw when, for example, carefully constructing lists for memory research. Moreover, in most such experiments, the investigator is present at the time of encoding, which is conducted under highly controlled circumstances.

The degree of control in a typical memory study is, of course, impossible to achieve with autobiographical memory, which is by definition unique to one person. Any study of autobiographical memory must therefore represent a compromise between experimental control and real-life relevance. We have developed two techniques for the study of autobiographical memory: prospective collection of autobiographical stimuli by our research participants and text-based segmentation and classification of autobiographical stimuli collected with the Autobiographical Interview (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). For the first technique, participants document personal events with a micro-cassette recorder for later selection by the investigator, much the same way words would be drawn from a list in a laboratory memory study, circumventing many of the problems that occur when memories are wholly self-selected. This technique is fairly invasive and, thus far, has been limited to our functional neuroimaging research (see below).

In contrast to the first technique, in which the goal is to produce well-defined, randomly selected stimuli for later exposure, in our Autobiographical Interview the participant selects and describes an event in which any and all components of autobiographical memory may be expressed. These components are then quantified from the transcribed protocol, achieving a standardized and rigorously scored measure for assessment of the various types of event details (e.g., emotional details, semantic, and episodic content) recalled by participants.

3. Episodic and semantic autobiographical memory

The main distinction of interest for both techniques is between episodic and semantic autobiographical memory. Episodic autobiographical memory is defined as conscious recollection of a temporally and spatially specific event from one’s personal past. This conscious state of “mental time travel” is achieved through recollection of events, sensory-perceptual details, thoughts, and feelings such that the rememberer becomes aware of an event as belong to his or her own past (Tulving, 1985, 2002; Wheeler et al., 1997). Semantic autobiographical memory contains the knowledge and facts of one’s past, including knowledge of one’s identity, personal characteristics, historical data, and the facts supporting awareness of personal past events, including knowledge that an event has occurred. Unlike episodic autobiographical memory, semantic autobiographical memory is time-independent; it can be accomplished without mental time travel. In this sense, autobiographical semantic knowledge is no different from public semantic knowledge. Indeed, similarities between personal and public semantic knowledge suggest that the neurocognitive processes mediating knowledge that Paris is the capital of France, for example, are shared with those mediating the knowledge that I was born in Detroit and that I toured Germany in 1985 (Kapur, 1999; Wheeler et al., 1997).

The general distinction between episodic and semantic memory is supported through decades of
experimental research (Gardiner, 1988; Tulving, 1972, 1983; Wheeler et al., 1997). In laboratory studies, episodic and semantic memory can be assessed by asking participants to classify memoranda according to the quality of their conscious experience using the remember/know technique (Gardiner, 1988; Tulving, 1985). Support from neuropsychological research has come from the study of anterograde amnesia, which has been characterized as a deficit in the ability to form new episodic memories (Cermak, 1985; Hayman, Macdonald, & Tulving, 1993; Kinsbourne, 1987). Further evidence that these two forms of memory are mediated by separate brain systems is provided by functional neuroimaging studies of healthy adults (Nyberg, Cabeza, & Tulving, 1996; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994).

Far less evidence in favor of this distinction has been reported for autobiographical memory. Patients with retrograde amnesia (i.e., amnesia for material learned prior to the onset of brain disease) often have impairment of both episodic and semantic autobiographical memory; brain damage in these patients is usually widespread and seldom respects distinctions of interest to psychologists. Several cases, however, have been reported in which episodic or semantic autobiographical memory is selectively impaired (Conway & Fthenaki, 2000; Kapur, 1999; Wheeler & McMillan, 2001). As reviewed in more detail below, functional neuroimaging studies of healthy adults have also distinguished episodic and semantic autobiographical memory (Conway, Pleydell-Pearce, & Whitecross, 2001; Conway et al., 1999; Fink et al., 1996; Maguire, 2001; Maguire & Mummery, 1999). The lack of evidence for the separation of episodic from semantic memory for real-life autobiographical memory relative to laboratory materials is in part attributable to the lack of methods for the reliable separation of these two memory systems within autobiographical memory.

4. The autobiographical interview

Methods for eliciting autobiographical memory, such as the cue-word method (Crovitz & Schiffman, 1974), often make no attempt at separating episodic and semantic autobiographical memory; they are rather concerned with the distribution of memories across time (Rubin & Schulkind, 1997). The most commonly used clinical test of autobiographical memory, the Autobiographical Memory Interview (AMI; Kopelman, Wilson, & Baddeley, 1989; Kopelman, Wilson, & Baddeley, 1990), assesses semantic autobiographical memory through a structured interview concerning autobiographical facts (e.g., where one lived during childhood). Episodic autobiographical memory is probed through free recall of events and scored according to a 0–1–2–3 system for specificity and richness of episodic recall. Because these two tests are not matched for psychometric characteristics, it can be difficult to draw firm conclusions about differential preservation or impairment of episodic and semantic autobiographical memory with this instrument (Kapur, 1999).

In normal everyday autobiographical recall, episodic and semantic autobiographical processes operate in tandem. Memory for any event, no matter how specific, is embedded in a semantic context that links events in a larger time frame. The rather unnatural act of separating these two forms of autobiographical memory can be accomplished with the remember/know technique (Conway, Collins, Gathercole, & Anderson, 1996). We have found, however, that application of this self-report technique to some healthy older adults and, in particular, to patients with brain disease often proves difficult. Alternatively, participants’ conscious state of recollection can be inferred by ratings of memory characteristics (e.g., imagery, thoughts and feelings, and contextual details) that correspond to veridical past experiences (Johnson, Foley, Suengas, & Raye, 1988).

Our Autobiographical Interview (Levine et al., 2002), transfers this burden of self-report from the participant to the experimenter. In this test, participants provide extemporaneous descriptions of autobiographical events from five life periods, with the only constraint being that the event must be personal and specific in time and place. The interview is audiotaped, transcribed, and scored according to a system by which episodic and semantic aspects of the protocol are quantified as dependent variables. This system (influenced by Johnson’s reality monitoring framework; Johnson et al., 1988; Johnson & Raye, 1981) assumes that details reflecting specific happenings, perceptual information, or mental states reflect episodic recollection (operationalized as “internal” details); factual information that is not specific to a particular time and place is classified as semantic (“external” details).

Previous dissociations between aspects of autobiographical memory have been restricted to cases or small groups with gross impairment or the use of different tests (as in the subtests of the AMI). In the Autobiographical Interview episodic and semantic contributions to autobiographical memory are extracted from within a single autobiographical memory, producing indices of separable memory components more amenable to quantification and comparison in group studies. These indices are measured at two levels of cueing (free recall and specific probe) to examine the influence of retrieval support.

5. Normal aging

Cognitive aging research indicates age-related deficits for episodic information, such as temporally specific
contextual details (e.g., McIntyre & Craik, 1987; Spencer & Raz, 1995; Zacks, Hasher, & Li, 2000), whereas semantic information, such as general knowledge and understanding of narrative meaning, is preserved or even facilitated in older adults (e.g., Adams, Smith, Nyquist, & Perlmutter, 1997). The effect of this age-related semantic bias was described by James (1890; quoted in Linton, 1975): “With each passing year, the days and the weeks smooth themselves out in recollection to countless units, and the years grow hollow and collapse.”

Few studies have examined this pattern within autobiographical memory (for exception, see Holland & Rabbitt, 1990). We recently administered the Autobiographical Interview to groups \( N = 18 \) of younger and older adults (Levine et al., 2002). Consistent with the earlier laboratory research, we found that younger adults produced more episodic details than did older adults in autobiographical recall, whereas production of semantic details was unimpaired or enhanced in older adults (see Fig. 1). This effect held when memories were matched for age. Piolino, Desgranges, Benali, and Eustache (2002) came to a similar conclusion in an aging study where episodic and semantic aspects of autobiographical memory were probed using separate interviews (as in the AMI). Retrieval support (e.g., recognition) has been known to reduce age differences in laboratory studies (Craik, 1983; Craik & McDowd, 1987). We found that retrieval support (in the form of cueing by the examiner) elevated all scores in both groups, but did not alter the pattern of group differences.

Why do older adults produce less specific autobiographical memories than do younger adults? One explanation is that older adults favor a more integrative approach to the past that stresses social roles and

Well, I only have one sister left now. She’s 95 years old and so I’m very close to my youngest sister’s family but she died four years ago. And I’m very close to all the kids, the grandchildren, the great-grandchildren. And I’ve always had Friday night dinners with that branch of the family since my husband and I are no longer together. So after my sister died my brother-in-law kept up the family dinners on Friday and so all his children, grandchildren and now great-grandchildren turn up, and that’s always a big do, the family. And it’s something I look forward to very, very much. And the winter when he goes away for six months, then two of his daughters take over. So we keep this thing going on the Friday night. I am closer to them actually than I am to my own branch of the family because I only have one married son. They have two children and they don’t do it Friday nights. So I see them when I see them. But this is an ongoing thing that is very precious to me.

An Italian restaurant. It was on the second floor of this restaurant and it was busy. I was at this little table. It was half the size of this table and this was a good date. The guy I was with was 6’4” and he was a big guy and he just looked really huge for the table. And I remember that looking kind of eye with a bit impatient with the service and I remember talking to him about Italian food and contemplating pasta or pizza and I ordered pizza. He ordered pizza as well. I think his had eggplant on it and I don’t like eggplant. I don’t remember what mine had on it though. I remember I didn’t eat the whole thing, taking home a doggy bag. I think I just had water. He had an espresso as well. He was wearing a blue polo shirt and I was wearing a gray long sleeved t-shirt, blue jeans, black shoes. He was wearing blue jeans and black shoes. I remember the waiters were wearing like white aprons, white shirts with a tie. We were going to order wine but we didn’t.

Fig. 1. Contrasting older and younger adults’ recollections from the previous year. Note the older adult’s emphasis on integrative semantic details (top) and the younger adult’s emphasis on the factual description (bottom).
generativity (Carstensen, 1995; Labouvie-Vief & Blan
chard-Fields, 1982). This argument suggests that stories long on detail and short on integration lack relevance for older adults. If they appear impaired on a test of episodic memory, it may be because the test does not measure their strengths. Accordingly, when underlining meanings, personal thoughts or feelings, qualitative inter
est, or gist information are assessed, older adults' narratives are rated higher than those of younger adults (Adams et al., 1997; Hashtroudi, Johnson, & Chro
siak, 1990; Holland & Rabbitt, 1990; James, Burke, Austin, & Hulme, 1998).

On the other hand, episodic details may be more difficult to retrieve than personal semantic information that is represented above episodic details in hierarchical models of autobiographical knowledge (Barsalou, 1998; Conway, 2001; Conway & Pleydell-Pearce, 2000). The lack of effect for retrieval support in our study suggests that older adults’ semantic bias may not simply be a matter of choice. It may instead reflect a loss of “res
olving power” within autobiographical memory, caus
ing retrieval search operations to terminate at the level of non-specific semantic representations (Craik & Gra
dy, 2002) due to age-related changes in prefrontal cor
tical function (Moscovitch & Winocur, 1992; Raz, Gunning-Dixon, Head, Dupuis, & Acker, 1998; West, 1996; although the contribution of changes in other re
gions cannot be ruled out, Greenwood, 2000). Evidence described below suggests that these changes may be lo
calized to dorsolateral prefrontal cortex.

It is likely that task demands interact with social and neurobiological characteristics of the rememberer in autobiographical information processing. Younger adults excel at tasks where reconstruction of episodic details is necessary (e.g., eyewitness testimony; Cohen & Faulkner, 1989; Coxon & Valentine, 1997; Yarmey, 1996), whereas older adults' style is better matched to tasks stressing social interchange (Cohen, 2000).

6. Frontal brain damage effects on autobiographical episodic recollection

As we did not directly measure prefrontal cortical function in our sample of older adults, we cannot say for certain that their pattern is attributable prefrontal cortical changes. Evidence in favor of a role for the prefrontal cortex in episodic recollection is derived from the case study literature on retrograde amnesia and the group study literature on focal lesion effects. As shown below, the prefrontal contribution is not unitary; it may be fractionated according to task de
mands.

Patients with retrograde amnesia affecting recollection often have prefrontal cortical damage, although posterior (particularly temporal lobe) damage is also implicated (Kapur, 1999). We reported a case of dense isolated retrograde amnesia (i.e., amnesia for events predating the injury with normal performance on tests of anterograde memory) associated with focal damage in the right ventrolateral prefrontal cortex and underlying white matter (Levine et al., 1998). Although both episodic and semantic memory were impaired in the early phases of this patient’s recovery, he retained implicit and procedural knowledge (including some autobiographical knowledge) acquired before his injury and eventually re-learned his autobiography such that his pre-injury autobiographical knowledge was difficult to distinguish from controls. This knowledge, however, was not accompanied by a phenomenological sense of re-experiencing. The prefrontal lesion likely affected frontotemporal communication through transection of the frontal projections of the right uncinate fasciculus, a large white matter pathway previously hypothesized to mediate retrieval of personal episodic autobiographical memories (Markowitsch, 1995).1

As discussed in more detail below, neural represen
tation of autobiographical memory is distributed. Ac
cordingly, retrograde amnesia for autobiographical information can occur following damage to other re
gions, such as the medial temporal lobes (Nadel & Moscovitch, 1997) and occipital lobes (Rubin & Greenberg, 1998). It can be seen in the absence of focal brain damage, although the interpretation of these cases is controversial (Kapur, 2000; Kopelman, 2000). Our case study indicates that the right ventrolateral pre
frontal cortex is one among many candidate regions important to the retrieval of autobiographical episodic memory. This region has been associated with on-line maintenance of information held in working memory and with specification of retrieval search parameters (Fletcher & Henson, 2001; Petrides, Alivisatos, & Evans, 1995).

In accord with the general lack of research on real-life autobiographical memory relative to studies of materials learned in the laboratory, most group study evidence in support of the episodic/semantic distinction in patients with frontal lobe damage is derived from laboratory tasks (Schacter, 1987; Wheeler et al., 1997). Studies of autobiographical memory in patients with frontal brain disease have involved patients with combined frontal

1 This patient had a severe traumatic brain injury (he was struck by a car while riding his bicycle and was in a coma for several weeks). It is therefore impossible to rule out other damage as contributing to his neurobehavioral outcome. The right ventrolateral frontal focus, however, was the most prominent area of damage using the most sensitive structural neuroimaging protocols available. This finding was corroborated by a separate H 215O positron emission tomography (PET) study showing right frontal polar hypoperfusion during performance of a cued-recall task relative to both healthy controls and other patients with severe traumatic brain injury (who did not have retrograde amnesia) (Levine et al., 1998).
and non-frontal pathology due to dementia or Korsakoff's syndrome (Greene, Hodges, & Baddeley, 1995; Kopelman, 1989, 1991; Sagar, Sullivan, & Corkin, 1991; Thomas-Anterion, Jacquin, & Laurent, 2000). Very few studies have directly examined the effects of discrete frontal lesions on autobiographical memory (for exceptions, see Baddeley & Wilson, 1986; Della Sala, Laiacona, Spinnler, & Trivelli, 1993; Kopelman, Stanhope, & Kingsley, 1999). While these studies have consistently documented frontal lobe brain damage effects on strategic retrieval operations, the measures used (usually the AMI) may not be sufficient to test episodic/semantic dissociations within autobiographical memory (see above). Furthermore, as is often the case with focal lesion research, patients with different etiologies and lesion locations are combined within a single group, preventing conclusions regarding intra-frontal specificity of lesion effects.

Autobiographical Interview data from two in-progress studies in our laboratory suggest that prefrontal cortical damage can affect indices of episodic and semantic autobiographical memory, and that these effects may be specific to lesion location within the prefrontal cortex (McKinnon et al., 2002; Svoboda et al., 2002). This research has focused on two groups of patients: frontotemporal dementia (FTD) and focal frontal lesions due to vascular events or low-grade tumours. FTD is a pre-senile form of dementia that selectively affects the frontal and temporal cortices (Neary et al., 1998). It is distinguished from other forms of dementia by the appearance of personality change, social comportment deficits, and impaired self-regulation early in the course of the disease (Miller, Darby, Benson, Cummings, & Miller, 1997). Patients with focal frontal lesions may have similar deficits, particularly when damage affects the ventral portion of the prefrontal cortex (Eslinger & Damasio, 1985; Stuss & Benson, 1986), an area that is vulnerable to tissue loss in FTD (Rosen et al., 2002).

As seen in Fig. 2, age- and education-matched control subjects show a preference for internal (episodic) details in the Autobiographical Interview protocols, whereas patients with FTD show the opposite pattern. This effect, which can be seen as an exaggeration of the age-related effect reported above, suggests that patients with FTD have a specific deficit in recollection, and that non-episodic (semantic) autobiographical knowledge is not impaired and perhaps even facilitated in these patients, possibly as a compensatory process. Moreover, certain patients in our FTD sample have dense retrograde episodic amnesia as measured by our test; their recall of specific details from personal past events is practically nil, even though they can elaborate on personal factual information without difficulty. (see also Piolino et al., 2003).

Results from our focal lesion patients support and extend these observations. Patients with ventral prefrontal damage were significantly impaired relative to controls on internal, but not external details (see Fig. 2). Patients with dorsolateral prefrontal damage produced a different pattern. Internal detail production was indistinguishable from controls, but external detail production was significantly elevated (see Fig. 2). In some cases, the examiner had to interrupt patients as their protocol length exceeded time limits. External detail production was not limited to semantic information (as it was in older adults and in patients with FTD); it also included extraneous episodic details about separate events. The dorsolateral prefrontal cortex is associated with monitoring memory retrieval output (Fletcher & Henson, 2001; Stuss et al., 1994). FTD patients also have dorsolateral pathology and produce elevated external details. It should be noted that although our patients may show recall or source monitoring problems, none showed frank confabulations (as is case for most focal frontal lesion patients in the chronic phase of recovery).

Our findings from focal lesion and frontotemporal dementia patients are contrasted to those from patients with focal medial temporal lobe, diencephalic, or Alzheimer pathology who show loss of access to stored memories along a temporal gradient (Greene et al., 1995; Kopelman, 1993). Using an earlier version of the Autobiographical Interview, Moscovitch, Yashchysyn, Ziegler, and Nadel (1999) documented a flat gradient in medial temporal lobe amnesic patients. The current version has been administered to amnesic patients H.M. (Steinvorth & Corkin, 2002) and K.C. (Rosenbaum, McKinnon, Levine, & Moscovitch, submitted), both of whom show dense retrograde amnesia with a flat gradient (for conflicting results using a similar scoring method, but different testing procedures, see Bayley, Hopkins, & Squire, 2003).

![Fig. 2. Mean number of details recalled (per memory, averaged across five life periods) in patients with frontotemporal dementia (FTD), focal dorsal frontal lesions, focal ventral frontal lesions, and age- and education-matched controls. Internal details include event details, perceptual details, and recollected thoughts and feelings from the time of the event. Internal details are interpreted as reflecting a conscious state of episodic re-experiencing. External details include statements of personal and public facts (the largest category), details from other events, and metacognitive statements. They reflect non-episodic (most semantic) processes. *: significantly different from controls, p < .05.](image-url)
The patients with focal dorsolateral prefrontal damage do not appear to have a deficit in episodic recollection as is the case with the medial temporal lobe amnesics. Their findings rather indicate interference within memory that results in mnemonic disorganization. In these cases, retrieval support had the paradoxical effect of increasing external detail production due to inefficient use of the cues, whereas the same support manipulation brought the performance of ventral prefrontal patients to the level of controls (Svoboda et al., 2002). The paradoxical effect observed for dorsolateral prefrontal patients was also observed for older adults (Levine et al., 2002), corresponding to recent suggestions age-related cognitive changes are due to dorsolateral (and not ventral) prefrontal dysfunction (MacPherson, Phillips, & Della Sala, 2002; Phillips, MacPherson, & Della Sala, 2002). These findings illustrate the complexities of cueing effects in patients with compromised frontal function. Because memory deficits can be reduced or eliminated with retrieval support in prefrontal patients and older adults (Craik, 1983; Craik & McDowd, 1987; Stuss et al., 1994), retrieval support effects are often taken as evidence of prefrontal dysfunction. These effects, however, depend on the type of retrieval support and how the participant engages with it. Our data suggest that patients with dorsolateral prefrontal dysfunction may engage with retrieval support as implemented in the Autobiographical Interview maladaptively. A more specific retrieval support manipulation, such as recognition, may have more beneficial effects.

7. Functional neuromanatomy of everyday autobiographical memory

The Autobiographical Interview data presented above are consistent with prior research indicating that episodic and semantic autobiographical memory can be dissociated both behaviorally and probably anatomically. Whereas brain lesion studies define regions necessary for a given function, functional neuroimaging studies indicate regions activated in association with that function, even if they are not crucial.

In the behavioral studies reported above, we separate episodic from semantic autobiographical memory at the time of protocol scoring. In our functional neuroimaging research this distinction is made by design at the stages of encoding and selection of autobiographical material. This is accomplished by training participants to recognize unique events in their everyday lives and to document their experiences on audiotape such that a feeling of re-experiencing would be evoked when exposed to that recording at a later date.

In our functional magnetic resonance imaging (fMRI) study of everyday autobiographical memory (Levine et al., in press), participants collected approximately 120 of these personal episodic recordings over a 5-month period. Importantly, they did not listen to the recordings after they made them. At the time of scanning, we selected recordings at random from this pool with the only constraint being that the average age-of-memory was matched across participants at 5 months. Brain activation in relation to these recordings was contrasted to that evoked by three conditions designed to control for various aspects of semantic memory: general semantic (readings from a book about the history of Toronto), personal semantic (personal factual information, such as one's route to work), and other episodic (other participants' transcribed personal episodic recordings). Ratings taken at the time of scanning after each recording confirmed that feelings of re-experiencing were significantly higher in the personal episodic than in the other three conditions.

By comparing regions of brain activation with these three control conditions, we were able to identify a pattern of brain activation both sensitive and specific to autobiographical episodic recollection. This pattern comprised regions identified above as important in patient studies as well as regions implicated in processes that support episodic memory (even if they are not critical to episodic memory). Posterior activations supporting inspection of imageable representations and retrieval of spatial context (posterior cingulate, retrosplenial, and medial parietal cortex; Burgess, Maguire, Spiers, & O’Keefe, 2001), and interpretation of others’ movements, goals, and intentions (temporoparietal junction; Frith & Frith, 1999) were observed.

As expected with the monitoring operations involved in processing the autobiographical narrative stream, bilateral high dorsolateral/superior medial prefrontal activations were present. In combination with the proliferation of non-episodic details reported above in patients with high dorsolateral damage, this finding suggests that these regions are involved in mnemonic control operations, but are not necessary for episodic recollection. Ventrolateral prefrontal cortex was also activated in relation to the personal episodic condition, although it was greater in the left hemisphere, whereas patient M.L.’s ventrolateral prefrontal lesion was right-lateralized (Levine et al., 1998). Left anteriormedial prefrontal activation extended from the anterior cingulate forward to the frontal pole. This focus of activation is consistent with previous research on introspective self-related information processing (Christoff & Gabrieli, 2000; Craik et al., 1999; Frith & Frith, 1999; Kelley et al., 2002; Stuss & Levine, 2002).

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2 Greater specificity of these effects may appear when lateralization of damage is taken into consideration. At the time of this writing, we do not have sufficient data to analyze lateralization effects.
The pattern described above was observed when the personal episodic condition was contrasted to all three control conditions. Although each of the control conditions was associated with a unique neural pattern, their shared distinction from the personal episodic condition corresponds with the distinctness of the phenomenological state induced by the personal episodic recordings, even when the control condition involved self-reflection (as in the personal semantic condition). In other words, the identified pattern is specific not just to autobiographical memory, but rather to episodic autobiographical recollection. Similar patterns have been reported in other functional neuroimaging studies of autobiographical memory (Andreasen et al., 1995; Andreasen et al., 1999; Conway et al., 2001; Conway et al., 1999; Fink et al., 1996; Maguire & Mummery, 1999; Nyberg, Forkstam, Petersson, Cabeza, & Ingvar, 2002), but these studies used events identified by the participants (either during the scan or in a pre-scan interview) with varying degrees of control over event selection, verification, and prior rehearsal and re-encoding.

8. Summary

There is more than one kind of autobiographical memory. A main thrust of our behavioral and functional neuroimaging research is the distinction between episodic and semantic autobiographical memory. Although there is abundant evidence for the dissociation of episodic from semantic memory from experimental studies of stimuli encountered in the laboratory, this is harder to achieve within autobiographical memory, which is specific to the individual, difficult to bring under experimental control, and is mediated by episodic and semantic processes operating in parallel. The Autobiographical Interview is a promising tool for the separation and quantification of these two forms of autobiographical memory. Our data suggest that episodic autobiographical memory can be selectively affected by aging and frontal brain disease. Damage to ventral prefrontal regions associated with self-regulation and connected to the medial temporal lobes is related to reduction in episodic specificity, presumably reflecting a state of consciousness partially stripped of the benefits of mental time travel and relatively constrained to the here and now. Damage to dorsolateral prefrontal regions affects the mnemonic operations involved in selection and control of autobiographical memories. It may clutter the mnemonic landscape, but may not affect episodic autobiographical recollection per se.

These data are complemented by functional neuroimaging studies of autobiographical memory. The pattern of prefrontal activations evoked by recollection of verified, randomly selected everyday events in our investigation of autobiographical memory was broadly consistent with the patient data. This pattern included left anteromedial prefrontal activity that has been reported in other studies emphasizing self-related information processing. Additional lateral temporal, temporoparietal, and retrosplenial/posterior cingulate activations suggested that these regions also support everyday autobiographical episodic memory. These findings were consistent in comparison to three types of semantic memory, including personal semantic memory.

9. Implications for developmental studies of human memory

We have described neuropsychological and functional neuroimaging evidence that autobiographical recollection is an advanced mnemonic capacity mediated by higher cortical regions, including critical nodes in the prefrontal cortex. Some have argued that this capacity is unique to humans (Suddendorf & Corballis, 1997; Tulving, 2001). The remarkable feats of non-episodic (i.e., procedural and semantic) memory are often mistaken for episodic recollection. For example, scrub jays can represent content, location, and temporal information of food caches (Clayton, Griffiths, Emery, & Dickinson, 2001). As noted by Tulving (2001), these examples represent “fixed behavior prompted by fixed knowledge,” as opposed to the unprompted, flexible retrieval and use of information for personal gain (although they do qualify as episodic by the standard of the original definition; Tulving, 1972). As another example, an eminent neuroscientist recently told me of an episode in which his horse reacted emotionally to a location made significant by an event occurring there one year before. The horse’s behavior was clearly influenced by a single remote event. The critical questions: Did the horse ever spontaneously retrieve and use that information of its own accord for a specific future purpose? Was this information integrated into the temporal fabric of the horse’s life? Or was it simply experienced in the here-and-now, in response to a conditioned stimulus?

Similar arguments are often made in relation to the behavior of infant children and preschoolers. In lectures or informal discussions in which I remark that episodic recollection is not firmly established before age 4 years, I am invariably bombarded with examples of earlier long-term memory. There is no question that infants can acquire and represent knowledge, as most obviously shown in the development of language and motor skills. Children as young as 6–9 months of age can recall information about the location and sequence of events associated with a particular context, but only in the presence of the specific environment in which the information was recalled (Shields & Rovee-Collier, 1992). They can further demonstrate knowledge of single events (Meltzoff, 1988), even after a delay of two years.
(Myers, Clifton, & Clarkson, 1987; Perris, Myers, & Clifton, 1990). As a personal example, at the age of 18 months, my daughter could recall the prior location of her favorite ball (which routinely disappeared under furniture or behind objects) with a much higher reliability than could I. As uncomfortable as it makes me feel as a proud father, I am forced to ask the same questions of my 18-month-old daughter as I would ask of the horse. It is with even greater discomfort that I report that the answers are roughly the same for both.3

Developmental studies of both laboratory and real-life autobiographical mnemonic tasks and studies of retrospective memory in adults converge on the age of 4 years as a time of emergence of episodic recollection (e.g., Usher & Neisser, 1993). This capacity is distinct from on-line self-representation, as demonstrated by the ability of 18–24-month-old infants to detect a covertly placed mark or sticker on their head upon looking in a mirror (Amsterdam, 1972). When the mirror image is replaced with a video image of the child taken a few minutes ago, 4–5-year-olds demonstrate delayed self-recognition by reaching for the sticker, while few 2–3-year-olds do so (Povinelli, Landau, & Perilloux, 1996). This finding suggests that the younger children’s self-concept lacks the temporal dimension necessary for awareness that the self watching the video is the same self depicted in the video (Povinelli et al., 1999). Indeed, the younger children (but not the older ones) referred to their video image in the third person (Povinelli et al., 1996). This was recently rather eloquently demonstrated by my daughter at the age of 2 years, who, when shown video of her as an infant, demanded to see the “new Sadie.”

Perner and Ruffman (1995) argued that the awareness of knowledge (i.e., knowing that) emerges before awareness of how one came into possession of that knowledge (i.e., reflecting on the origin of that knowledge as part of one’s past). In one experiment, the child may or may not perceive the location of a hidden piece of candy (either by seeing it being hidden or being told of its location). The dependent variable in this experiment is not whether the child found the candy (i.e., knowing that the candy was in location A) but rather how they attributed their successful search (i.e., seeing, being told, or guessing). Performance on this and related tasks increases systematically from ages 3–6 (Perner & Ruffman, 1995). Similar to Johnson and colleagues’ Reality Monitoring Framework (Johnson et al., 1988; Johnson & Raye, 1981) from which we drew in developing our Autobiographical Interview, Perner and Ruffman (1995) emphasize the perceptual origins of knowledge as cues to attributing a past event to one’s own autobiography (see also Foley, Johnson, & Raye, 1983; Perner, 2001; Ratner & Foley, 1994). Studies of children’s autobiographical memory also emphasize the distinction between knowing that and a feeling of re-experiencing. Event knowledge can be retained by 2-year-old children for long time periods (Fivush & Hamond, 1990; Nelson, 1989). Yet before age 4 years (and further on in the pre-school years) this knowledge is fragmentary, cue-dependent, and inconsistent (Fivush & Hamond, 1990; Hudson & Fivush, 1991; White & Pillemer, 1979). While this event knowledge may persist, it does not ultimately become integrated into the self, probably because it precedes the development of the neurocognitive machinery necessary for temporally extended self awareness (Perner & Ruffman, 1995; Wheeler et al., 1997).

It would be illuminating to apply the Autobiographical Interview to preschoolers. Given the above findings, one might predict that they would show recall of internal details relative to school-age children and that individual differences in autobiographical recall would correspond to differences in development of self-awareness capacities. This deficit, however, would have different origins than in the patients, where recall was tested for events that presumably benefited from fully developed encoding and retention mechanisms. Preschoolers’ responses to cueing may assist in localizing effects to the encoding or retrieval stages.

Retrospective generation of memories across the lifespan by adults in response to cue words have produced estimates of the offset of childhood amnesia (and onset of autobiographical memory) ranging from 2 to 7 years (Dudycha & Dudycha, 1941; Wetzler & Sweeney, 1986). This large range may relate to inconsistencies in memory definition, confounding episodic with semantic aspects of autobiographical memory or failing to consider issues of richness and specificity. In order to study the subjective experience of early childhood recollections, Bruce, Dolan, and Phillips-Grant (2000) used the remember/know distinction (Gardiner, 1988; Tulving, 1985). Participants produced and dated two types of early memories: those that they could remember happening, and those that they knew happened (for example from photographs) but could not remember. Cumulative frequency distributions of each type of memory relative to age were plotted. The 50th percentile was treated as a threshold marking the offset of childhood amnesia. This threshold occurred at age 3.20 for the “know” distribution and age 6.07 for the “remember”

3 Different uses of the terms “episodic” and “autobiographical” can create confusion. Some developmental theorists (e.g., Povinelli, Landry, Theall, Clark, & Castille, 1999) reserve the term “autobiographical” for memories that are accompanied by self-awareness, and “episodic” for simple recall of events specific in time and place (i.e., the Tulving, 1972 definition). In this paper, “autobiographical memory” is used as an umbrella term for the dissociable components of episodic and semantic autobiographical memory. In spite of terminology differences, the underlying notion of self-aware (autonoetic) autobiographical recollection as an evolutionarily and ontogenetically advanced conscious capacity is consistent.
distribution, mapping onto the differentiation between semantic and episodic aspects of autobiographical memory, respectively. The arithmetic mean of these, 4.64, was considered average age at which childhood amnesia is eclipsed by the retrievability of personal memories (Bruce et al., 2000), corresponding to the evidence above that younger children’s experiences of events lack a subjective quality.

Howe and Courage (1993, 1997) argue that the knowledge structure of the self enhances the organization of memory in general beginning at age 2 years, with increasing storage of autobiographical memories as this knowledge structure develops. They believe that recall of personally experienced events does not reflect a psychological or neurological discontinuity (i.e., a separate neurocognitive system); it rather reflects continuous development of human information processing systems established in infancy. This model is consistent with the findings described above in its emphasis on the self as central to autobiographical memory development, as illustrated in the following statement: “Prior to the first appearance of me, events that the infant experienced could not have been encoded with reference to the self: They were not personally experienced, and there was no autobiographical framework.” (Howe & Courage, 1997, italics in original). The lower limit of age 2 years corresponding corresponds with the more basic form self-awareness as measured by the mirror test, not to the more advanced and later-developing temporally extended self-awareness (Povinelli et al., 1996, 1999). While these models may differ in their conceptualization of the developmental course of these forms of self-awareness, the important point for our purposes is their mutual emphasis on the self.

Social interaction theory, on the other hand, places a greater emphasis on environmental influences—namely the style of parent–child interaction regarding past events (Fivush & Reese, 1992; Hudson, 1990; Nelson, 1993). These interactions can facilitate children’s formulation of their own memories as narratives, with individual differences in this capacity related to the degree of elaboration in parent–child discourse (Hudson, 1990). Although this theory is often placed in opposition to Howe and Courage’s self-knowledge theory (Howe & Courage, 1997), they are not mutually exclusive. As illustrated by Harley and Reese (1999) both self-knowledge and social interaction contribute to the development of autobiographical memory. A neural substrate for reciprocity between these two mechanisms is proposed below.

This brief and by no means exhaustive review of childhood memory strongly suggests that continuous, stable autobiographical recollection begins to emerge around age 4 years (see the volume by Moore & Lemon, 2001 for comprehensive review). Howe and Courage (1993) argue the offset of infantile amnesia is “located” in cognitive advances (“software”) rather than neurobiological (“hardware”) changes. Under the assumption that the mind is a function of the brain, however, these software upgrades must have neural correlates. An explosion of neuroscience research occurring in the past decade has greatly facilitated the understanding of these mechanisms.

The research reviewed above shows that autobiographical recollection is mediated by a distributed system with critical nodes in the frontal lobes. This research prompts the hypothesis that developmental brain changes supporting autobiographical recollection may involve the frontal lobes (particularly anteromedial frontal regions) as well as frontal interconnectivity. What is the evidence for this hypothesis?

**10. Co-incidence of prefrontal systems maturation and the onset of autobiographical recollection**

One consistent finding in studies of human brain development is that the proportion of gray to white matter declines with age (Jernigan, Trauner, Hesselink, & Tallal, 1991; Sowell et al., 2003) reflecting regressive activity within gray matter (e.g., synaptic pruning; Cowan, Fawcett, O’Leary, & Stanfield, 1984) and progressive activity (e.g., increased myelination and axonal growth) within white matter (Yakovlev & Lecours, 1967). Studies including pre-school-aged brains have shown cortical gray matter volume increases until age 4, then declines, whereas white matter volume rises steadily, stabilizing at 20 years (Pfefferbaum et al., 1994).

Cortical thinning is not uniform over cerebral cortex; it is greatest over parietal and frontal regions (Jernigan et al., 1991; Sowell et al., 2003; Sowell et al., 1999). Regressive cortical and progressive subcortical changes occur late in the prefrontal cortex relative to early sensory cortices supporting visual and auditory functions that mature in infancy (Huttenlocher & Dabholkar, 1997). A study of post-mortem brains noted that polar prefrontal cortex thickness (among other prefrontal cortical regions) peaks at around age 4 (Rabinowicz, 1979). Functional neuroimaging findings described earlier emphasize the anteromedial prefrontal cortex (extending to the frontal pole) in the processing of self-related information and autobiographical recollection. The functional neuroimaging data in particular point to the interactivity of this region with other prefrontal, posterior, and subcortical regions.

The regressive cortical gray matter and progressive white matter changes may increase signal-to-noise in prefrontal systems interconnectivity and mediate the development of circuits shaped by environmental stimulation and input from other cortical areas; synapses that are not incorporated into these circuits disappear...
(Changeux & Danchin, 1976; Huttenlocher & Dabholkar, 1997). The resulting increase in intracerebral information transfer efficiency may support a neural substrate for the rapid integration of sensory and self-related information necessary for the emergence of autobiographical recollection. (For the ontogeny of cortico-cortical information transfer as measured by EEG coherence, see Thatcher, 1997.) The mechanism by which environmental stimulation sculpts prefrontal circuits may explain individual differences in the development of autobiographical memory as a function of parent–child interactions (Nelson, 1993; for a review of neural plasticity in development, see Robertson, 1999, Chap. 8). On the other end of the aging spectrum, age-related prefrontal gray matter tissue loss (Raz et al., 1997) reduces the efficiency of this system.

I acknowledge that developmental brain changes are many and complex, supporting performance on a variety of tasks. White matter changes continue into the adult years (Yakovlev & Lecours, 1967), likely mediating the development of social behavior and self-regulation through adolescence and early adulthood. There is also evidence that gray matter changes in children and adults are non-linear (Giedd et al., 1999; Sowell et al., 2003). Nonetheless, given the importance of interconnected prefrontal function to autobiographical recollection and the co-incidence of prefrontal systems maturation with the onset of autobiographical recollection, further direct investigation of this correspondence is warranted.

11. Conclusions

Autobiographical recollection reflects an advanced state of consciousness that allows humans to escape the confines of the here and now and perceive the self as continuous across time (Tulving, 2002). This capacity is probably necessary for human survival and related to self-regulation and life quality. Because it is inherently subjective, autobiographical recollection is difficult to quantify. Moreover, at least in naturalistic observation, it is inextricably bound with non-episodic aspects of autobiographical memory, such as personal semantics. Research on autobiographical memory requires novel instruments, such as the remember/know technique (Gardiner, 1988; Tulving, 1985), the Autobiographical Interview (Levine et al., 2002), and prospective collection of autobiographical material (Levine et al., in press) that can be used to dissociate these and other aspects of autobiographical memory, including the contribution of emotion.

We have presented patient and functional neuroimaging evidence that autobiographical recollection is mediated by a distributed cortical and subcortical system, with nodes in the prefrontal cortex. Much work remains in refining lesion–behavior relationships and understanding the function of this system in healthy adults, yet initial data suggest that anterior, medial, polar, and ventral prefrontal regions are important in the temporal transposition of experience from the here and now to the past and future.

Developmental studies at both ends of the age spectrum add a possibility of modeling normal changes in brain and behavior that is not available in lesion or functional neuroimaging studies of adults. Future research will likely reveal that the complexity of these brain–behavior relations is far greater than portrayed in this paper. This research is necessary, however, to fully understand the remarkable achievement of time travel in the human mind.

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