An historical perspective on Endel Tulving's episodic-semantic distinction

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Abstract

The distinction between episodic and semantic memory, proposed by Endel Tulving in 1972, remains a key concept in contemporary Cognitive Neuroscience. Here we review how this distinction evolved in Tulving`s writings over the years. Crucially, from 1972 onward, he argued that the two forms of memory were inter-dependent and that their interaction was an essential feature of normal episodic memory function. Moreover, later elaborations of the theory clearly proposed that these interactions formed the basis of normal declarative memory functioning. A later but crucial aspect of Tulving's contribution was his stress on the importance of subjective experience, which, according to him, "should be the ultimate object of interest, the central aspect of remembering that is to be explained and understood". We relate these and his numerous other ideas to current perspectives about the organization and function of human memory.

Keywords: Episodic memory, Semantic Memory, Ecphory, Chronesthesia, Autonoesis.

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'The term "memory" itself has become just an umbrella term covering all the different kinds, and one-time dreams of psychologists of coming up with a comprehensive "theory of memory" have become as irrelevant as psychological theories about umbrellas' (Tulving, 2007).

Endel Tulving first formally proposed the distinction between episodic and semantic memory in a book chapter dating from 1972 (Tulving, 1972). The distinction became extremely influential in memory research, both in experimental psychology and cognitive neuroscience, and is still of central importance today. Here we review how this distinction evolved over the years in Tulving's writings, including his celebrated book from 1983, "Elements of Episodic Memory". We focus on the development of Tulving's ideas and their impact on contemporaneous and subsequent research, rather than providing a comprehensive review of the episodic/semantic distinction. For a recent review of current perspectives on this topic, see Renoult, Irish, Moscovitch, & Rugg (2019).

1. 1972 Conception

In his 1972 book chapter, Tulving noted the *"looseness" and "ambiguity*" of the concept of memory and the importance of developing taxonomies of cognitive processes. He referred to semantic memory as a new conception of memory, first described by Quillian (1966), and then elaborated by Kintsch (1972), Collins and Quillian (1972) and Rumelhart, Lindsay and Norman (1972) in presentations at a conference on "organizational processes in memory", organized by Tulving in Pittsburgh in 1971. Tulving later explained that he wrote his 1972

chapter *"in reaction"* (Tulving, 1984a) to these presentations (later published in the same volume as that in which Tulving's chapter appeared), that left him in *"deep puzzlement"* about this new emerging field of semantic memory, that he thought had more to do with the *"understanding of language"* and *"much less relevance for remembering events"* or for the *"acquisition and recall of word lists"* (Tulving, 1983, page 20; see also Tulving, 1987a).

In the 1972 chapter, Tulving contrasted semantic memory with another kind of memory that he termed "episodic memory". He referred to these two kinds of memory as *"stores*" or *"systems*", but presented this distinction as a *"pre-theoretical position"* that did not imply that they were necessarily functionally distinct in any deep sense. Thus, this first conceptualization did not make a strong claim for two separate memory systems. Only in subsequent writings (e.g., Tulving, 1983, 1984a) did he make the assumption that the two systems were functionally distinct, in the sense that *"one system can operate independently of the other*" and that they were *"governed at least partially by different principles"* (Tulving, 1983, page 66). Tulving (1983) was aware that this functional distinction would likely court controversy. However, he expressed optimism about *"the possibility of distinguishing between the two systems on neuroanatomical and neurophysiological grounds"* and thus on their structural independence (Tulving, 1983, page 66; see also Tulving, 1986 and section 2.5), and cited studies of the effects of brain lesions in support of his position (Cermak, 1981; Mair, Warrington, & Weiskrantz, 1979; Squire, 1982; Victor, Adams, & Collins, 1971).

In the 1972 chapter, Tulving recognized that the distinction between semantic and episodic memory was not without precedent, similar distinctions having long been proposed in the philosophical literature (e.g., Bergson, 1911; Furlong, 1951; Russell, 1921). He noted however that *"the philosophical categories of memory have not had any influence on psychological*

research" (Tulving, 1972; while recognising Reiff & Scheerer, 1959 as an exception to this rule). A more nuanced position was adopted in his 1983 book, in which prior psychological writings describing similar distinctions are also cited (e.g., Bruner, 1969; Claparede, 1911). Of importance, both in the original 1972 chapter and subsequently Tulving argued that the two systems interact and are *"partially overlapping"* (Tulving, 1972) or, as stated later, that they are *"closely interdependent and interact with one another virtually all the time"*, (Tulving, 1983, page 65)

Definition of Episodic Memory. In the 1972 chapter episodic memory was defined as a memory *"system"* that *"receives and stores information about temporally dated episodes or events, and temporal-spatial relations among these events"* (Tulving, 1972). Although he recognized that the temporal contiguity between items was an important factor in the encoding of associative information in episodic memory, he argued that contiguity was not necessary for such encoding, hence his use of the more general term temporal-spatial *"relations"* in his definition. The paper also included the much simpler definition of episodic as memories for *"personally experienced unique events"* (Tulving, 1972).

Commentary: The basic notion of episodic memory as memory for unique events has changed little up to the present day (e.g., Moscovitch, Cabeza, Winocur, & Nadel, 2016; Rugg, Johnson, & Uncapher, 2015; Schacter & Madore, 2016). However, as we will see, this early definition was qualified and expanded over the years in Tulving's writings, and some important elements were added (notably, in respect of the important role of phenomenal experience or 'autonoetic consciousness', see section 2.2).

Definition of Semantic Memory. In the 1972 chapter semantic memory was defined as "*the memory necessary for the use of language. It is a mental thesaurus, organized knowledge a person possesses about words and other verbal symbols, their meaning and referents, about relations about them, and about rules, formulas, and algorithms for the manipulation of these symbols, concepts and relations"* (Tulving, 1972). Semantic memory thus had the capacity for *"inferential reasoning and generalization"* (Tulving, 1972), contrary to episodic memory, a capacity that was considered as its most important property by Quillian (1966). Moreover, semantic memory was held to contain no record of how its content was acquired, and thus learning in semantic memory was considered an unknown parameter (contrary to episodic memory): *"since input conditions responsible for the existing semantic structure are usually not known (…), the experimenter simply cannot be concerned with correspondences and discrepancies between input and output"* (Tulving, 1972). Indeed, studying established semantic concepts would not allow one to make inferences on how these concepts were initially learned. Finally, it was also proposed that, as both semantic and episodic memory contain *"mnemonic information for verbal materials"* (Tulving, 1972), they would frequently interact.

Commentary: In contrast to episodic memory, the concept of semantic memory has evolved considerably over the years, compared to this initial definition. In Tulving's original view, as in the literature of the time, semantic memory was tightly linked to language comprehension. His later definitions were more flexible and proposed that, although language plays a more important role in representing information in semantic than in episodic memory, not all semantic knowledge is acquired though language (Tulving, 1983, page 41, see also Tulving,

2005). This latter conceptualization is more resonant with current perspectives proposing that the ability to assign meaning to percepts does not necessarily depend on language (e.g., Binder & Desai, 2011; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017; Martin, 2007, 2016). Further, the notion that semantic memory does *"not register perceptible properties of inputs, but rather cognitive referents"* (Tulving, 1972), stands in contrast to current perspectives in which semantic memory is "embodied" or "grounded" in perception and action, and emerges out of interactions between modality-specific and amodal information (e.g., Binder & Desai, 2011; Lambon Ralph, et al., 2017; Martin, 2016; Matheson & Barsalou, 2018).

Tulving's (1972) observation that inputs to semantic memory are generally unknown still appears to be valid. Episodic memory is typically studied, at least in the laboratory, by investigating correspondences between inputs (i.e., study items) and outputs (i.e., memory for the items). In semantic memory experiments, however, we typically have little experimental control over the acquisition of semantic and conceptual knowledge, only over their expression. An exception to this situation are studies that investigated learning of new concepts in children and adults (e.g., Murphy, 2002). Whereas early investigations suggested that very extensive study was necessary to link new concepts to existing conceptual structures (Dagenbach, Horst, & Carr, 1990), more recent findings suggest that fast semantic learning is possible, even to the extent of a single (Borovsky, Elman, & Kutas, 2012; Borovsky, Kutas, & Elman, 2010; S. Chen, Wang, & Yang, 2014; Ding, Chen, Wang, & Yang, 2017; Zhang, Chen, Wang, Yang, & Yang, 2017) or only a few trials (e.g., Coutanche & Thompson-Schill, 2015), something that Tulving himself envisaged in his later work (e.g., Tulving & Markowitsch, 1998; Tulving, 2005).

Distinctions between Episodic and Semantic memory. According to the 1972 chapter, episodic memory has an *"autobiographical reference*", whereas semantic memory is *"detached from autobiographical reference"* (Tulving, 1972; see section 2.2 for further discussion on episodic and autobiographical memory). Perceptual characteristics of stimuli are stored in episodic memory (and thus episodic memory would be a *"more or less faithful record of personal experience"* whereas semantic memory encodes *"cognitive referents of input signals*" (Tulving, 1972), rather than perceptual information. Tulving (1972) went on to argue that semantic memory was much more related to learning in the classroom than episodic memory is, *"as classroom learning has little to do with students' remembering personally experienced events"* (Tulving, 1972). It was further proposed that an act of retrieval can modify the content of episodic memory, but not that of semantic memory. That is, retrieval from either semantic or episodic memory constitutes an episode that could potentially be "re-encoded" in episodic memory. Finally, semantic memory was held to be less prone to forgetting than episodic memory.

Commentary: Some of the criteria and properties differentiating the two systems described in Tulving's 1972 chapter are still accepted today, even as they have evolved over the years (see section 2). The autobiographical reference of episodic memory is uncontroversial, and episodic memories are still typically defined as referring to personally experienced events. Much research has been conducted in recent years on such topics as memory reconsolidation, updating, and integration, resonating with Tulving's (1972) idea that retrieval can produce modification and re-encoding of episodic memories (Antony, Ferreira, Norman, & Wimber, 2017; Hupbach, Gomez, Hardt, & Nadel, 2007; Loftus, 1975; Schlichting & Preston, 2015;

Schooler, Foster, & Loftus, 1988; Scully, Napper, & Hupbach, 2017). Additionally, while in the 1972 chapter, Tulving assumed that semantic memory was less vulnerable to loss of information, interference and forgetting than episodic memory (Tulving, 1972), later elaborations went further and explicitly proposed that information in episodic memory (based on a single learning event) was more fragile than typically highly overlearned semantic information (Tulving, 1983, page 45). The idea that episodic memories are vulnerable to rapid forgetting also resonates with current views (Barry & Maguire, 2019; Conway, 2009; Yassa & Reagh, 2013), although it is unclear how one could overcome the confounding effects of such factors as differential study exposures and retrieval opportunities when attempting to compare forgetting rates for episodic and semantic information. Additionally, semantic learning is typically considered to be slower than hippocampally-mediated episodic learning (e.g., McClelland, McNaughton, & Oreilly, 1995; Norman, 2010).

2. Re-conceptualization of the 1972 model

As noted previously, over the years Tulving modified, elaborated and ultimately largely re-conceptualized the constructs of semantic and episodic memory. In this section, we describe what we consider the most significant of these developments.

2.1. Developments related to both systems

Episodic and Semantic memory are propositional (declarative)

In the 1983 book, Tulving proposed that both semantic and episodic memory are *"propositional"*, meaning that their contents can be represented and expressed consciously,

have a truth value, and can be acquired from a single learning experience, in contrast to the functional properties of procedural memory (see also Cohen & Squire, 1980; M. A. Wheeler, Stuss, & Tulving, 1997). An important development in Tulving's thinking came with his realization that performance on standard tests of long-term memory does not exclusively depend upon episodic memory (Tulving, 1983; see also Mandler, 1980; Weiskrantz & Warrington, 1975 for similar ideas originating around the same time).

Standard recognition and recall tasks are not process-pure

In the 1972 chapter, laboratory tasks in which participants are asked to recall or recognize word lists were considered quintessential episodic memory tasks. Tulving (1972) proposed that in such tasks (which he later referred to as evaluating peoples' memory for "*miniature events*"; Tulving 1983, page 144), "*the occurrence of a verbal item in a given list, at a particular time, and in specified temporal relation to other items in the list is an autobiographical episode having no necessary extra-episode denotative reference"* (Tulving, 1972). Although he recognized that, if familiar words are used as the experimental materials, episodic memory might be encoding the outcome of semantic processing, he assumed that such processing was not a necessary precursor to episodic encoding. An exception to this assumption appears in a paragraph on guessing responses in memory experiments, where the possibility is noted that *"the subject retrieves information from his semantic memory in an episodic memory experiment"* (Tulving, 1972). By this view, therefore, and seemingly at odds with the assertion that list learning depends exclusively on episodic memory, it is possible that participants rely on semantic rather than episodic memory when performing an episodic memory task. This point is elaborated and extended in the 1983 book (Tulving, 1983) and in subsequent writings

(e.g., Wheeler et al., 1997). To quote from the book: *"most experienced and remembered events have factual contents whose characteristics are greatly influenced by semantic memory; performance on semantic tasks, on the other hand, may be influenced by episodic information*" (Tulving, 1983, page 55). One important consequence of episodes having semantic content is that it might sometimes be possible to use one system to answer questions putatively addressed to the other system (Tulving, 1983, page 64). Nonetheless, Tulving continued to argue that one can classify a task as episodic if successful performance is not possible without access to information about a specific episode (here, he cites *"conventional recall and recognition tasks*";). In later writings, Tulving (and his colleagues) elaborated this position further and argued that *"in terms of memory systems, all tasks are multiply determined*" (Tulving, 2002b; see also Tulving, 1991; Wheeler et al., 1997).

Commentary: The notion that memory tests are not "process pure" is widely held and has formed the basis of several important theoretical developments (Jacoby, 1991; McCabe, Roediger, & Karpicke, 2011). The notion is exemplified by "dual process" models of recognition memory (Atkinson & Juola, 1973; Johnston, Dark, & Jacoby, 1985; Mandler, 1980; see Yonelinas, 2002 for a review), in which it is proposed that even a memory judgment as seemingly simple as determining whether a test item is "old" or "new" can be supported by two functionally and neurally dissociable memory signals. The development of memory tests such as the autobiographical interview, inspired by Tulving, also illustrates the point that semantic and episodic elements are naturally mixed in narrative recall of personal events, and must be separated post-hoc via specialized scoring protocols (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002).

2.2. Re-conceptualization of episodic memory

Episodic memory is constructive

The 1972 book chapter proposed that *"episodic memory is a more or less faithful record of a person's experiences"* (Tulving, 1972). A more nuanced perspective was offered in later elaborations of the theory, for instance the proposal that the temporal organization of events in episodic memory can be *"easily changed or lost"* (Tulving, 1983, page 38), and that, *"although a good deal of remembering is more or less veridical, a good deal of it is not"* (Tulving, 1983, page 187). The process of ecphory described in the book also entails a constructive perspective on memory retrieval (see section below on ecphory).

Commentary: These latter perspectives are a better match than the original one to contemporary conceptions of episodic memory that put an important focus on its constructive nature (Addis, 2018; Barry & Maguire, 2019; Cheng, Werning, & Suddendorf, 2016; Conway, 2009; Irish, 2019; Schacter & Addis, 2007; Yassa & Reagh, 2013). For instance, some authors note that episodic memories are *"summarized and generic" rather* than *"a literal record"* of experiences (Conway, 2009), that they typically reflect *"only the gist of an episode"* (Cheng, et al., 2016) and that episodic memory and imagination rely on the same neurocognitive processes (Addis, 2018; Irish, 2019).

Ecphory is a component of the process of retrieval

In his 1983 book, Tulving introduced the concept of ecphory (adapted from Semon, 1904; see also Tulving & Madigan, 1970; Tulving; 1976; 1982) as an *"obligatory"*, automatic and pre-

conscious aspect of retrieval, by which a stored memory trace interacts with a retrieval cue (Tulving, 1983). Accordingly, engrams (stored memory "traces") are manifest only when they interact with an appropriate retrieval cue. In the process of *"synergistic ecphory"* a retrieval cue activates the engram, leading in term to the emergence in consciousness of a memory of the original event. Tulving argued that synergistic ecphory is a *"constructive"* process that *"uses components from episodic memory (the engram) as well as semantic memory (the cue)"* and results in the conscious experience of remembering, such that the rememberer attributes the *"ecphorized event*" to the past (Tulving, 1983, page 180). In the context of the semantic-episodic distinction, ecphory can thus be considered as an example of an interaction between the two systems. Accordingly, ecphoric information is *"an amalgam of episodic and semantic information"* (Tulving, 1985b). The constructive nature of the process of ecphory is illustrated by the fact that the experienced ecphoric information need not exactly correspond to information represented in the engram, as it will depend on other factors also, such as the nature of the retrieval cue and the cognitive state of the rememberer (Tulving, 1983, page 187).

Commentary: The concept of synergistic ecphory resonates well with contemporary ideas about "pattern completion", the process by which information belonging to a specific episode can be retrieved from episodic memory when cued with a partial or degraded version of the original event (e.g., Liu, Gould, Coulson, Ward, & Howard, 2016; Rolls, 2013). As alluded to above, the concept is also consistent with contemporary views emphasizing the reconstructive aspects of memory. Of interest, Semon's (1904) terminology has been recently incarnated in the notion of 'engram cells' – cells comprising neural assemblies in widely

distributed brain regions that are co-activated when a specific event is experienced, and whose reactivation (either in response to a retrieval cue or an experimental intervention such as optogenetic stimulation) results in retrieval of the event (Rao-Ruiz, Yu, Kushner, & Josselyn, 2019; Tonegawa, Liu, Ramirez, & Redondo, 2015).

Subjective awareness of remembering is a crucial aspect of episodic recall

The 1983 book points to the importance of the *"subjective awareness of remembering*" or *"recollective experience"* (Tulving, 1983, page 10) as a fundamental aspect of episodic memory. Indeed, the primary referent of episodic memory is held not to be a chronological ordering of events (an "objective" time-line), but rather a sense of traveling along a subjective time-line into the past (Tulving, 1983, page 42), later to be termed "mental time travel" (Tulving 1985b; 2002b), a perspective similar to that of James' (1890). Recollection was also considered to have a distinct *"affective tone"* (Tulving, 1983, page 48), analogous to James' "warmth and intimacy" (James, 1890), that would not be present in the actualization of knowledge from semantic memory (see also Tulving, 1987). Tulving was at pains to stress the importance of these aspects of mnemonic experience, which "*should be the ultimate object of interest, the central aspect of remembering that is to be explained and understood"* (Tulving, 1983, page 184).

Further development of Tulving's ideas about the centrality of mnemonic experience came in 1985 with the introduction of the concept of *autonoetic* awareness (self-knowing), held to provide *"the characteristic phenomenal flavor of the experience of remembering"* (Tulving, 1985b). Autonoetic awareness refers to the ability to 'transport' oneself through subjective time that is, to engage in mental time travel. A synonymous term "autonoesis" was

introduced later (Tulving, 2001b, 2005). This form of awareness was contrasted with the *noetic* (knowing) awareness associated with semantic memory, and to the *anoetic* awareness (non-knowing) associated with procedural memory.

According to this 1985 perspective, anoetic awareness (characteristic of procedural memory) is bound to the present. Even though organisms having only this type of awareness may be aware of their current surroundings and internal states, they would not be able to project themselves in time. Noetic awareness (associated with semantic memory), by contrast, allows an organism to represent objects, concepts and events even in their absence, although this awareness is also rooted in the present. Accordingly, the ability to *"mentally travel in space"* (rather than time) was proposed as a property of semantic memory (Tulving, 2005). Finally, autonoetic awareness (held to be a capacity unique to humans) allows the rememberer to mentally travel through time, both to remember past events and to "pre-experience" future events. This form of awareness was held to be both a *"necessary"* feature of episodic memory (as organisms "cannot remember without awareness", Tulving, 1985b; see also Tulving, 2002b) and its most distinctive aspect (Tulving, 1995, Wheeler, Stuss, & Tulving, 1997). Of importance, it was proposed that autonoetic awareness *"includes but transcends"* noetic awareness (Tulving, 2002a; see also section 2.4: Semantic processing always precedes episodic encoding). In the view of Wheeler, Stuss, & Tulving (1997), autonoetic awareness is not only oriented towards the past and the future, but also concerns the *"ability to be aware of the self's present"*, something the authors related to William James' *"stream of consciousness"* (James, 1890), and to provide a sense of continuity to our personal experiences. Tulving (1985b) went on to propose the now well-known "Remember-Know" paradigm to experimentally differentiate autonoetic and noetic awareness during memory

retrieval (and thus retrieval from episodic and semantic memory, respectively; see also Gardiner, 2001).

Commentary: Current research in autobiographical memory often relies heavily on subjective reports, such as ratings of vividness, visual perspective or sense of reliving of memories for past experiences (e.g., Rubin, Deffler, & Umanath, 2019; Siedlecki, 2015; St Jacques, Szpunar, & Schacter, 2017). Obviously, these phenomenologically-derived measures cannot have clear equivalents in non-human animals (or in young children, see *Episodic memory emerges later in development than semantic memory* in section 2.4), precluding the comparative study of these aspects of memory function (but see Tulving, 2005 for the description of the "spoon test", a test of autonoesis that he proposed could be used in non-human animals). The ability of some non-human animals to engage in memory-guided behavior that fulfills the classic "what? when? where?" criteria for the operation of episodic memory (Clayton, Bussey, & Dickinson, 2003; Clayton & Dickinson, 1998), along with evidence that the neural circuits supporting episodic memory seem to be largely conserved through evolution, at least in mammals and birds (Allen & Fortin, 2013), calls into question Tulving's assertion of the uniqueness of episodic memory to humans. Tulving's later writings recognized these findings and that *"interesting analogues of episodic memory exist in non-human animals"* (Tulving, 2001a), but argued that they did not demonstrate that these episodic (or *"episodic-like")* forms of memory included autonoesis (Tulving, 2001a, 2005). Interestingly, subjective and objective measures of episodic memory can be dissociated in humans, for instance in the case of lateral parietal lesions that do not affect the accuracy of memory judgments but lead to a reduction in associated confidence ratings (Hower, Wixted, Berryhill, & Olson, 2014; Simons,

Peers, Mazuz, Berryhill, & Olson, 2010; see also Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007; Davidson, et al., 2008). Such findings suggest that the subjective experience of recollection that typically accompanies successful episodic retrieval depends on neural regions distinct from those that support retrieval itself (see also Bastin, et al., 2019 and the role of attribution systems that would translate content reactivation into a subjective experience). More generally, subjective and objective measures of episodic memory can sometimes be dissociated experimentally, for instance in healthy aging, with some studies reporting reduced objective but preserved subjective recollection relative to young adults (Duarte, Henson, & Graham, 2008; Duarte, Ranganath, Trujillo, & Knight, 2006; Folville, et al., 2019; Mark & Rugg, 1998).

Episodic memory and subjective time: *Autonoetic awareness versus Chronesthesia*

In the 1983 book, Tulving noted that semantic memory is *"actualized*" in the present moment (page 48) whereas episodic memory is oriented towards the past. In contrast, in 1985 and in subsequent writings, Tulving proposed that episodic memory is associated with autonoetic awareness (see above) and allows humans to re-experience the past and to pre-experience the future, providing an important evolutionary advantage (Tulving, 2005). Tulving proposed a related concept, chronesthesia, that first appears in the 1985 paper as synonymous with the sense of subjective time (see alsoTulving, 2002a). Here, he cited an article by Bouman and Grünbaum (1929), although this was not cited in later publications. The article, in German, is entitled *"Eine Störung der Chronognosie"* (*a disturbance of chronognosia)* and reports a clinical case study of a patient suffering from *"disorientation in time"* following an *"influenza psychosis"*. The patient is said to understand time as a concept but to be unable to accurately

situate in time events that happened after his illness, and thus suffers from an impairment in the representation of subjective time (the case is reminiscent of that of the celebrated patient KC, see Rosenbaum, et al., 2005; Tulving, 1985b; Tulving, Schacter, McLachlan, & Moscovitch, 1988a). In later writings, Tulving distinguished chronesthesia (the sense of subjective time that makes mental time travel possible) from *chronognosia,* defined as semantic knowledge about physical time (Tulving, 2002a; Tulving & Kim, 2007). He recognized that chronesthesia was closely related to autonoetic awareness (its *"predecessor",* Tulving, 2002a; or a *"a specifically time-oriented facet"* of it, Tulving & Kim, 2007), both being forms of consciousness that imply awareness of self in time, the difference being about an "*emphasis"* on self in the former case and on subjective time in the latter (Tulving, 2002a). Tulving noted that this distinction was subtle and speculative, and the rest of the chapter did not discuss further how autonoetic awareness and chronesthesia might be dissociated (Tulving, 2002). Furthermore, it was proposed that both autonoesis and chronesthesia should be impaired in amnesic patients. The concept of chronesthesia was not mentioned in later discussions of future-oriented thought (e.g., Szpunar & Tulving, 2011), when autonoetic awareness was given the central role.

Commentary: In line with Tulving's later ideas (see below), recent evidence suggests that semantic memory contributes significantly to past and future thought (Abraham, Schubotz, & von Cramon, 2008; Irish, Addis, Hodges, & Piguet, 2012; Irish & Piguet, 2013; Klein, 2013; Prebble, Addis, & Tippett, 2013; Race, Keane, & Verfaellie, 2013; Szpunar, Spreng, & Schacter, 2014; Wang, Yue, & Huang, 2016). For instance, due to his preserved semantic knowledge, it was reported that amnesic patient KC understood time as a concept, and could correctly order

events on a timeline (Craver, Kwan, Steindam, & Rosenbaum, 2014). This is not in disagreement with Tulving's perspective, who reported that patients without autonoetic awareness such as K.C. had *"no difficulty with the concept of chronological time"* (Tulving, 1985b; see also Tulving, 2001b) and went on to propose that *"semantic memory also allows an individual to construct possible future worlds"* (Tulving, 2005) through chronognosia, defined as semantic knowledge about physical time (Tulving, 2002a; see above). KC "*thus exhibits a dissociation between knowing time and experiencing time"* (Tulving, 2001b). As discussed in Tulving (2005), *"no kind of memory other than episodic has any special relation to time. Semantic memory allows the individual to know, at Time 2, something about what happened at an earlier time, Time 1, but it does not allow the individual to remember what happened. Semantic memory also allows an individual to construct possible future worlds, but since it is lacking autonoetic capability, it would not allow the individual to mentally travel into his own personal future".* Amnesic patients with medial temporal lesions have indeed been shown to be able to list relevant issues about the future but to provide impoverished descriptions when asked to elaborate about this factual knowledge (Race, et al., 2013). Interestingly, patients with semantic dementia (see section 2.2) also have difficulties constructing detailed novel future scenarios, despite relatively intact episodic memory (Irish et al., 2012; Irish & Piguet, 2013). Semantic memory thus seems to provide the "scaffolding" necessary to construct and simulate future events (Irish, et al., 2012), consistent with Tulving's idea that episodic memory *"operations depend on"* (Tulving, 2001b) and *"require"* (Tulving, 2002b) semantic memory.

Episodic or Autobiographical Memory?

From his first writings, Tulving defined episodic memory in term of its *"autobiographical reference"*, in contrast with semantic memory and its *"cognitive reference*" (Tulving, 1972). The examples used by Tulving to illustrate what episodic memory was were mostly examples of autobiographical memories (*"Last year, while on summer vacation, I met a retired sea captain who knew more jokes than any other person I have ever met";* Tulving, 1972), and also some examples of laboratory experiments *("One of the words I am sure I saw in the first list I studied was legend"*; Tulving, 1972). Tulving (1983) later noted that he favored the phrase episodic memory for *"the relative brevity of the term"* as compared to *"autobiographical memory"* that suffers from *"its connotations of a literary account of one's life"* (Tulving, 1983, page 28).

When describing typical laboratory studies of episodic memory, in which participants have to remember *"miniature events"* (Tulving, 1983, page 144) such as a word's occurrence in a list, Tulving considered such an occurrence to be *"an autobiographical episode"* (Tulving, 1972). Thus, in these writings and later (e.g., Tulving, 1995, table 54.1, where "autobiographical" is listed as another term for episodic memory) no conceptual distinction is made between laboratory studies of episodic memory and studies of autobiographical memory in terms of their relation to the general concept of episodic memory. Tulving discussed this and related issues in his 1983 book and concluded that laboratory studies are a valid way to examine episodic memory: *"I know no compelling reasons why the general principles that apply to remembering of mini-events in the laboratory should be greatly different from those governing the remembering of real-like experiences"* (Tulving, 1983, page 146).

Tulving later made reference to Cermak and colleagues (Cermak, 1986; Cermak & O'Connor, 1983) in support of the idea that the semantic-episodic distinction applies to autobiographical memory, drawing a distinction between autobiographical episodes and personal semantic memories (Tulving et al., 1988), the latter being partly preserved in amnesic patient KC, as well as in some other amnesic patients described in the literature at the time (such as patient S.S. in Cermak & O'Connor, 1983). However, no conceptual distinction is drawn between non-personal semantic memories and autobiographical knowledge, or between episodic memories and autobiographical episodes.

Commentary: The fields of (laboratory-based) episodic memory and autobiographical memory have developed in parallel over the last three decades. Principles of memory derived from the laboratory have proven useful in the study of "real life" memory in areas as diverse as eye-witness testimony (e.g., Wixted, Mickes, Clark, Gronlund, & Roediger, 2015), classroom learning (e.g., Karpicke & Blunt, 2011) and singular public events (e.g., Talarico & Rubin, 2003). Moreover, most investigators recognize the large overlap in the neural circuits underpinning recollection, as this is operationalized in the laboratory and autobiographical memory retrieval (Moscovitch, et al., 2016; supplemental Figure 4a versus 4b; Rugg & Vilberg, 2013; Svoboda, McKinnon, & Levine, 2006), even though some differences have been described (Cabeza, et al., 2004; X. Y. Chen, Gilmore, Nelson, & McDermott, 2017; Gilboa, 2004; McDermott, Szpunar, & Christ, 2009). It should be noted, however, that it is difficult to match autobiographical memory and laboratory-based tasks in term of processing demands, such as stimulus elaboration (while participants in autobiographical memory experiments may take 5-10 seconds to re-experience a memory, processing times are typically much

shorter in lab-based experimental designs; Conway et al., 2002; Svoboda et al., 2006) or remoteness of study episodes (in lab-based tests, stimuli are typically experienced only a short time before the test, whereas autobiographical retrieval can reach back over decades).

2.3. Re-conceptualizations of semantic memory

Although Tulving elaborated and re-conceptualized the constructs of both episodic and semantic memory and their relation over the years, he had a clear focus on episodic memory, which he fully recognized. As he noted for example in the first chapter of "Elements of Episodic memory": *"The kind of memory that is involved in remembering past events is called episodic memory. This is what this book is about"* (Tulving, 1983, page 1). Nonetheless, we note below two examples of reconceptualizations of semantic memory, both of which resonate with contemporary perspectives.

Semantic memory is knowledge of the world

In contrast to his earlier conceptualizations (see section 1) that strongly associated semantic memory with language (Tulving, 1972), Tulving proposed in his 1983 book that semantic memory would be better referred to as general *"knowledge of the world"* (see also Tulving, 1985b; 1987b; 1995; 2005) to avoid association with the linguistic definition of semantics and too tight an association with language. As Tulving notes, *"we know many things about the world that are neither meaningful, nor readily expressed in words or other symbols"* (Tulving, 1983, page 28).

Commentary: As noted above (see section 1), this latter conceptualization of semantic memory is in keeping with current perspectives that propose that the ability to assign meaning to percepts does not necessarily depend on language (e.g., Binder & Desai, 2011; Lambon Ralph, et al., 2017; Martin, 2007, 2016). Interestingly, most of the examples of tasks tapping semantic memory in the 1983 book still involved language, and certain tasks such as naming or lexical decision tasks would not be classified as semantic *stricto sensu* as of today, as they do not require participants to process meaning (reviewed in Renoult, 2016). Nonetheless, the point was clearly made that this broader consideration of semantic memory as knowledge of the world opens the floodgates to a wide variety of tasks that can be construed as depending on semantic memory (e.g., sentence verification, naming of category instances, production of opposites, concrete-abstract decision, feature-dimension decisions (such as judgements on real world size or indoors/outdoors classification), etc.) whereas episodic memory is typically evaluated with tests of recall and recognition.

Semantic memory is culturally shared

In 1983, Tulving highlighted the culturally shared nature of semantic memory, which was considered to be *"independent of a person's identity"* (page 9), and thus reflective of *"the responses made by other members of the language community in the same situation"* (page 25; see also Tulving, 1987b). Similarly, in the precis of 'Elements of Episodic memory', Tulving noted that the veridicality of semantic memory is defined by *"social agreement"* (Tulving, 1984).

Commentary: The idea that the content of semantic memory is largely shared between members of a culture is consistent with current perspectives, and inter-individual variations in semantic knowledge have been somewhat neglected (but see Hampton, 1979; K. E. Johnson & Mervis, 1997; McCloskey & Glucksberg, 1978). However, this definition of semantic memory is inconsistent with the idea mentioned above that the semantic-episodic distinction applies to autobiographical memory, exemplified in the distinction between autobiographical episodes and personal semantic memories (Tulving et al., 1988), as personal semantics are presumably specific to an individual. That being said, whereas early descriptions assumed that personal semantics should be considered as expressions of semantic memory, more recent data suggest that this view may be an oversimplification (Grilli & Verfaellie, 2014; Renoult, Davidson, Palombo, Moscovitch, & Levine, 2012).

2.4. Re-conceptualization of the relationship between episodic and semantic memory

Context dependency does not necessarily dissociate episodic and semantic memory

In his 1983 book, Tulving noted that, in contra-distinction to semantic memory, episodic memory is often considered to be context-dependent (e.g., Ehrlich, 1979; Kintsch, 1980), as defined by "*the tendency for the processing of a unit of information (e.g., its encoding, or retrieval) to be influenced by other units of information that are present at the time of processing"* (Tulving, 1983, page 44). However, he expressed doubts about the usefulness of this distinction and noted that *"knowledge of the world may be as context-dependent as is our knowledge of the past"* (Tulving, 1983, page 45). Tulving supported this view by citing

research published at the time that demonstrated context effects in semantic processing. This included studies reporting that how the meaning of a word is processed (and how a specific meaning is selected) depends on its presentation context (Schvaneveldt, Meyer, & Becker, 1976), as well as studies reporting analogous priming effects for semantic and episodic memory (Mckoon & Ratcliff, 1979). Moreover, Tulving rejected the idea that, in his words, *"whenever a word is seen, heard, spoken, written (…) the same underlying representation is either fully or partially activated"* (Tulving, 1983, page 241), and proposed instead that semantic representations could be *"recorded in many different forms, and that there is no necessary and direct connection between and among separate representations of one and the same lexical unit"* (Tulving, 1983, page 241).

Commentary: Episodic memory is still often defined in terms of its context-sensitivity, a property that semantic memory is held to lack (see Wheeler & Ploran, 2009). Note however that context can have multiple meanings (Baddeley, 1982). It can refer to the context of initial acquisition, which typically is not considered to be included in a semantic memory representation (e.g., where/when one initially learned what autonoesis meant), while such contextual information is a defining feature of episodic recollection. Context-sensitivity can also refer to the fact that retrieved content can differ depending on the retrieval cues "*that are present at the time of processing"* (Tulving, 1983, page 44). From this perspective, semantic memory is indeed context-dependent, as noted by Tulving. The meaning attributed to a particular stimulus event is clearly affected by the context of its presentation (such as the context provided by single words or sentence clauses preceding a target word, e.g., Bentin, McCarthy, & Wood, 1985; Kutas & Hillyard, 1984; Meyer & Schvaneveldt, 1971), as well as by

current emotional state (e.g., Chwilla, Virgillito, & Vissers, 2011; Havas, Glenberg, & Rinck, 2007). Moreover, semantic control mechanisms, which bias meaning selection, are a crucial component of semantic memory (reviewed in Jefferies, 2013; Lambon Ralph, et al., 2017).

Episodic and Semantic retrieval depend on different retrieval mechanisms

In his 1983 book Tulving proposed that access to semantic memory is automatic (such as accessing meaning when reading words), but that access to episodic memory tends to be deliberate and to require *"conscious effort"* . He further proposed that retrieval required that the rememberer was in *"retrieval mode"*, a cognitive state that enables internal and external events to be processed as retrieval cues (Tulving, 1983; page 46). Tulving recognized that little was known (at the time) about retrieval mode*, "other than it constitutes a necessary condition for retrieval"* (Tulving, 1983, page 169), and that the rememberer *has "no awareness of retrieval mode"* (Tulving, 1983, page 170). He further noted later in precis of "Elements of episodic memory" that *"all retrieval is cued"* and that *"an important problem lies in the identification of invisible cues"* (Tulving, 1984).

Commentary: Research on semantic memory has confirmed that words and other conceptual stimuli can activate their meanings automatically, in the sense that "semantic activation" is unaffected by intention to access meaning (see Neely, 1991; Neely & Kahan, 2001 for reviews). Recent research has demonstrated that episodic memories can also be retrieved unintentionally, and that such involuntary memories (spontaneous recollections of the past that are seemingly not associated with a conscious search) are relatively common (e.g.,

Berntsen, 1996, 2009; Mace, 2004; Mace, Atkinson, Moeckel, & Torres, 2011). Note that this is not totally in contradiction with Tulving's views, in that he commented that *"the absence of goal-directed cognitive activity"* may be sufficient to *"place the episodic system into the 'retrieval mode'"* (Tulving, 1983; page 46). However, the definition of involuntary memories as being independent of consciously-mediated search partially contradicts Tulving's notion that access to episodic memory *"usually requires conscious effort"* (Tulving, 1983; page 46). As mentioned above, very little was known at the time about retrieval mode (Tulving, 1983). Since then, it has has been operationalised as a tonic state that is maintained during a retrieval task with neural correlates that can be revealed by contrasts between appropriately matched episodic and a non-episodic tasks (Rugg & Wilding, 2000, see also section 2.5 on the neural correlates of episodic memory).

Semantic processing always precedes episodic encoding

Tulving (1972) proposed that whereas episodic memory encoding might often be influenced by semantic processing, there are situations where this would not be the case (e.g. the sensory elements of an experience might be remembered without relying on the semantic system). In the 1983 book however he proposed that episodes almost invariably have semantic content, and thus that episodic memory encoding typically entails engagement of semantic memory (Tulving, 1983, pages 29 to 31). Nonetheless, Tulving at that time still considered that events could be encoded in episodic memory, *"even if the meaning of the occurrence is unknown"* (Tulving, 1983, page 37), a proposal consistent with what he later framed as the "parallel hypothesis" (see Tulving, 1987b). By contrast, comprehension of an event and relating its content to existing knowledge is a necessary precursor to semantic

encoding. Episodic memory encoding was thus held to be more direct (*"experiential"*, Tulving, 1983, page 41) than semantic memory. Tulving made the further point that while simple perceptual events could be encoded directly into episodic memory, more complex events, such as those extending over a significant period of time, necessitate interpretation by the semantic system if they are to be successfully encoded in episodic memory (Tulving, 1983, page 38).

Later elaborations of his theory, as articulated in what became the "SPI model" (for Serial Parallel Independent; Tulving, 1993a, 1995, 2001a, 2005; Tulving & Markowitsch, 1998), and initially referred to as the *"embeddedness hypothesis*" (Tulving, 1984b, 1985a, 1987b), proposed that all perceptual information passes through the semantic system before it is encoded in episodic memory (that is, the information is serially encoded). Information entering semantic memory is derived exclusively from "perceptual systems", and thus, contrary to Tulving's initial view (Tulving, 1972), perceptual information is not encoded in episodic memory until it has been *"interpreted*" by semantic memory (Tulving, 2001a). The output of the semantic memory system then serves as input to the episodic system, which *"computes the temporo-spatial contextual coordinates of the incoming information in relation to already existing episodic information, or to the self"* (Tulving, 1995). The SPI model stipulates that information in each system is then stored in parallel in different brain regions. During retrieval, the two systems are considered to operate independently of each other. Thus, Tulving and Markowitsch (1998) argued that, in cases of anterograde memory impairment, semantic and episodic memory might both be impaired, or semantic memory might be spared (as, they claim is the case in developmental amnesia; Elward & Vargha-Khadem, 2018; VarghaKhadem, et al., 1997, but see below). They were adamant, however, that the reverse could not occur, that is, impaired semantic memory in the face of spared

episodic memory. As noted below, this prediction seems not to have stood the test of time. Finally, Tulving and Markowitsch (1998) proposed that awareness associated with episodic and semantic memory is also embedded, such that remembering (episodic retrieval) always implies knowing (semantic retrieval), but not vice-versa (e.g., one could have general knowledge that the Sahara is hot, without having related episodic memories; see section 2.2). Therefore, episodic memory *"includes but goes beyond knowledge of the world"* (Tulving & Markowitsch, 1998).

Commentary: The proposition that new episodic memories cannot be acquired without semantic memory is difficult to reconcile with findings of relatively preserved new (anterograde) episodic memory learning in semantic dementia patients (Adlam, Patterson, & Hodges, 2009; Graham, Simons, Pratt, Patterson, & Hodges, 2000; Irish, et al., 2016; Simons, Graham, Galton, Patterson, & Hodges, 2001; Simons, et al., 2002), who suffer from a progressive deterioration of semantic and conceptual knowledge. In these studies, semantic dementia patients were reported to form episodic memories for events and stimuli that they failed to comprehend. However, as mentioned by Tulving (2001), the tests used in these studies do not necessarily rely on recollection (e.g., rich re-experiencing of episodic details or source memory), as tests of recognition memory (Adlam, Patterson, & Hodges, 2009; Graham et al., 2000; Simons et al., 2001) or visual memory (the Rey complex figure in Irish et al., 2016) can be supported by familiarity (i.e., a sense of prior exposure bereft of contextual details; but see Simons, et al., 2002 for evidence of preserved source memory in some semantic dementia patients). Moreover, as discussed by Adlam et al. (2009), until advanced stages of the disease (when episodic memory may be impaired too, e.g., Maguire, Kumaran, Hassabis,

& Kopelman, 2010), patients still have some preserved knowledge that could be used to facilitate episodic encoding, as well as preserved perceptual memory (cf. Tulving, 2001). Thus, the findings from semantic dementia are not totally incompatible with the SPI model, although they suggest that at least some forms of "episodic-like" learning are possible even when semantic processing is impaired.

Another assumption of the SPI perspective is that anterograde amnesia can impact episodic memory while sparing new semantic learning. Evidence for this claims rest mainly on reports of individuals with "developmental amnesia" following damage to the hippocampus early in life (see Elward & Vargha-Khadem, 2018 for review). These individuals perform poorly on laboratory tests of episodic memory while demonstrating normal performance on non-episodic tasks such as reading, spelling and comprehension. Whereas these features of developmental amnesia might point to normal semantic learning that is independent of episodic memory (something that has rarely if ever been reported in the adult amnesia literature; e.g., Bayley, O'Reilly, Curran, & Squire, 2008; but see Tulving, 1993b and Tulving et al., 1988 for descriptions of some semantic learning in patient KC), it has been noted that this dissociation may reflect the contribution to semantic learning of degraded, but not absent, episodic memory supported by a partially functioning hippocampus (e.g., Squire & Zola, 1998; Vargha-Khadem, et al., 2003). This interpretation of semantic learning in developmental amnesia, seemingly in contradiction to the SPI model, relies on the assumption that declarative memories initially depend on the hippocampus before being consolidated in the neocortex (McClelland, et al., 1995; Sekeres, Winocur, & Moscovitch, 2018; Squire, Genzel, Wixted, & Morris, 2015). For instance, according to the "trace transformation" hypothesis (Sekeres, et al., 2018; Winocur & Moscovitch, 2011), semantic knowledge emerges from episodic memory with time and experience (reviewed in Renoult, et al., 2019; Sekeres, et al.,

2018; Winocur & Moscovitch, 2011). The theory proposes that, in some cases, both the original *and* the semanticized version of a memory may co-exist and interact in response to current task demands, but that all declarative memories (including semantic memories) initially depend on the hippocampus. One possibility, suggested by Elward & Vargha-Khadem (2018) is that even though this initial reliance on the hippocampus may hold in adults, the memory systems of children with developmental amnesia may develop differently, optimizing semantic learning in the presence of early hippocampal damage. However, these patients are nonetheless slow to learn new semantic information when assessed in laboratory settings, and presumably depend on incremental cortical learning (Elward & Vargha-Khadem, 2018).

Episodic memory emerges later in development than semantic memory

In later writings, the topic of the development of episodic memory received significant attention in Tulving's work (e.g., Tulving, 2005; M. A. Wheeler, et al., 1997), although he did not directly contribute to research on this topic himself. Tulving proposed that the development of long-term memory systems began with an initial reliance on a *"stimulus driven"* procedural system, followed by development of semantic memory and, finally, episodic memory (M. A. Wheeler, et al., 1997). He related the development of semantic memory and noetic awareness to the Piagetian notion of object permanence, something that infants acquire around 8 months (Piaget, 1954), and to the ability of infants to perform deferred imitation from around 9 months (Meltzoff, 1988). He considered both of these capacities to rely on the existence of mental representations of objects in their absence. Tulving further proposed that, even though there may be evidence for memory of events relatively early during development (from around 1 to 2 years old), this was supported by

semantic as opposed to episodic memory. This early form of event memory is typically expressed non-verbally, or involves recall of words or short phrases identical to those initially studied (Bauer & Wewerka, 1995; Howe & Courage, 1993). Tulving also noted that young children typically do not perform well on tests of source memory before around the age of 5. That is, despite being able to remember the events that they studied, young children are poor at remembering the study context (Gopnik & Graf, 1988; Lindsay, Johnson, & Kwon, 1991; Wimmer, Hogrefe, & Perner, 1988). Similarly, Tulving (2005) observed that prior to around 5-6 years of age, few children understand the difference between Remembering and Knowing (C. N. Johnson & Wellman, 1980). He discussed research on the "mirror test" in infants (Gallup, 1970) and noted that the awareness of one's physical appearance and of *"the constancy of that appearance through time and space"* that infants display around 18 months is a necessary precursor to autonoetic awareness (M. A. Wheeler, et al., 1997). In other words, autonoetic awareness, defined as the ability "*to become aware"* of one's *"existence in subjectively experienced time*", must *"include but transcend self-awareness"* (Tulving, 2001b). Autonoetic awareness itself emerges on rarely before around 4 years of age (as described in Tulving, 2005; see also Tulving, 2002) and then progressively matures.

Commentary: The observation that episodic memory develops later than semantic memory, and only in association with the development of a sense of self in time (Fivush, 2011; Howe & Courage, 1993, 1997; Nelson & Fivush, 2004), is uncontroversial and largely consistent with the literature on autobiographical memory development that typically operationalizes episodic memory in term of phenomenological aspects of recollection (Fivush, 2011). Consistent with Tulving's writings, infants may be able to show memory for specific events,

for instance memories for sequences of actions demonstrated through deferred imitation (Bauer, 2007), but this ability depends on semantic rather than episodic memory (Newcombe, Lloyd, & Ratliff, 2007). In other words, such memories may depend on knowledge and understanding of the action sequence, rather than on the specific context of its acquisition. Some authors have argued that generalization of what is learned (such as understanding that the word cat applies to different exemplars) is more important from an adaptive point of view than remembering the specific circumstances in which the information was learned, and thus should develop earlier (Keresztes, Ngo, Lindenberger, Werkle-Bergner, & Newcombe, 2018; Newcombe, et al., 2007). The capacity to remember events experienced from a first person perspective of oneself mentally travelling through time (relying on autonoetic awareness) has been held to emerge later, around the end of preschool years (Atance & O'Neill, 2005; Fivush, 2011), consistent with Tulving's estimation of emergence around 4 years old. Moreover, this ability develops progressively, with more autobiographical features and references to spatial and temporal contexts being reported by children as they develop (Bauer, 2007; Nelson & Fivush, 2004; Newcombe, et al., 2007; Ngo, Horner, Newcombe, & Olson, 2019). These findings are arguably consistent with recent observations that the development of episodic memory correlates with the maturation of hippocampal subfields (Canada, Ngo, Newcombe, Geng, & Riggins, 2018; Keresztes, et al., 2018; Lee, Ekstrom, & Ghetti, 2014).

2.5. Neural correlates of Episodic Memory

The episodic-semantic distinction was originally framed at the functional level (Tulving, 1972), and only later was it explicitly proposed that the two systems should be differentiable at the structural (neural) level also (Tulving, 1983; 1986). Subsequently, Tulving and colleagues

helped pioneer the application of functional neuroimaging to the study of such memory dissociations. Wheeler, Stuss and Tulving (1997) reviewed the available neuropsychological and functional neuroimaging evidence and concluded that the prefrontal cortex played a crucial role in episodic memory and, especially, in autonoetic awareness. Tulving, Kapur, Craik, Moscovitch, and Houle (1994) proposed that left prefrontal regions played a key role in episodic encoding, whereas right prefrontal regions supported the maintenance of episodic retrieval mode (see section 2.4). These ideas were formalized in the *Hemispheric Encoding/Retrieval Asymmetry* (HERA) model (Habib, Nyberg, & Tulving, 2003; Lepage, Ghaffar, Nyberg, & Tulving, 2000; Nyberg, et al., 1996; Nyberg & Tulving, 1996; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). Because episodic encoding was held to necessitate semantic retrieval (see section 2.4*)*, the model implied that left prefrontal regions also played an important role in semantic retrieval (Tulving, et al., 1994).

Wheeler, Stuss and Tulving (1997) proposed that while prefrontal regions support autonoetic awareness, memory *"contents"* were represented in posterior cortical regions. These posterior regions would be *"permeated"* by autonoetic awareness during ecphory (Wheeler et al., 1997). Levine et al. (1998) reported evidence from a brain lesioned patient that supported a role for frontal cortex - especially in the right hemisphere - in autonoetic awareness, but specifically noted that the uncinate fascicle, the white matter tract linking temporal and frontal regions, might in fact be the crucial structure underlying recollective experience. More recently, Nyberg, Kim, Habib, Levine & Tulving (2010) argued it was left parietal and frontal regions that were involved in mental time travel and the sense of subjective time (although a reviewer noted that this study included only 5 participants). Consistent with current perspectives, Tulving recognized the important role of the hippocampus in ''*enabling the operations of episodic memory"* (Tulving & Markowitsch,

1998). Moreover, based on a meta-analysis of PET studies, Lepage, Habib and Tulving (1998) proposed the HIPER (Hippocampal Encoding/Retrieval) model, according to which the anterior hippocampus is more involved in encoding and the posterior hippocampus in retrieval. In addition to examining episodic retrieval with PET and fMRI, Tulving and his colleagues also contributed to the investigation of episodic memory using event related potentials (ERPs; e.g., Duzel, et al., 1999; Duzel, et al., 2001; Duzel, Yonelinas, Mangun, Heinze, & Tulving, 1997; A. S. N. Kim, Vallesi, Picton, & Tulving, 2009).

Commentary:

Early neuroimaging studies of memory were constrained by the need to use PET methodology, which provides no easy way to separate item- and state-related neural activity or to study the neural correlates of successful versus unsuccessful encoding and retrieval. Partly for these reasons, the early observations of Tulving and colleagues have not all stood the test of time. For instance, in the case of HERA, while left prefrontal regions are considered to play an important role in semantic control (e.g., Jefferies, 2013; Lambon Ralph, et al., 2017), right prefrontal cortex appear to be implicated in post-retrieval monitoring rather than, or in addition to, the maintenance of a retrieval mode (e.g., Fletcher & Henson, 2001; Rugg, 2004). It should be noted, however, that a key prediction arising from the notion of retrieval mode – that episodic retrieval should be associated with evidence for neural activity that is sustained across successive retrieval attempts – motivated fMRI studies employing hybrid block- and trial-wise designs to separately identify item- and state-related retrieval-related neural activity (Donaldson, Petersen, Ollinger, & Buckner, 2001; Velanova, et al., 2003; Woodruff, Uncapher, & Rugg, 2006; see Duzel, 2000 for an analoguous ERP study). Notably,

Velanova et al. (2003) reported that, relative to an easy retrieval test (recognition of words presented on multiple study occasions), a more difficult test (recognition of once-studied words) was associated with sustained activity in a widely distributed set of regions that included right lateral PFC. It is also noteworthy that while the HERA framework has largely been subsumed by more detailed models of retrieval processing, direct evidence in support of the framework (at least, for young adults) was provided by findings from two transcranial magnetic stimulation (TMS) studies (Rossi, et al., 2001; Sandrini, Cappa, Rossi, Rossini, & Miniussi, 2003).

Arguably, the HIPER model has fared better. While criticized at the time (Schacter & Wagner, 1999), the question of the longitudinal specialization of the hippocampus remains an important topic of contemporary investigation (e.g., Brunec, et al., 2018; Poppenk, Evensmoen, Moscovitch, & Nadel, 2013), and an updated version of HIPER has recently been advanced (HERNET; Kim, 2015). Perhaps more important than any single empirical contribution, though, Tulving deserves credit for his role in illustrating the potential and utility of non-invasive functional neuroimaging methods in the study of human memory.

Conclusion

We have reviewed Endel Tulving's writings on the semantic-episodic distinction, from his first book chapter in 1972 to the various later elaborations of his theory. Numerous aspects of the theory evolved over the years, but it is striking how many of the ideas and concepts developed by Tulving permeate contemporary cognitive neuroscience models of memory. Of importance, although Tulving's contribution to declarative memory research is sometimes summarized in terms of a rigid distinction between semantic and episodic memory, it is clear

that from his earliest publications (Tulving, 1972) he recognized that the two forms of memory are highly interactive, and likely share functional properties and neural underpinnings. Moreover, one of the most important aspects of the theory is the idea that these interactions lie at the heart of adaptive declarative memory function. As he expressed it in 1985, *"both the general nature and specific characteristics of recollective experience (the phenomenal experience of remembering a past event) are determined jointly by episodic and semantic information"* (Tulving, 1985).

Tulving's view that it is not necessary to assume *"that the distinction between knowing and remembering is always sharp"* (Tulving, 2005) and that the distinction may be "*subtle"* (M. A. Wheeler, et al., 1997) is consistent with current perspectives that semantic and episodic memory are closely intertwined, yet maintain a degree of distinctiveness (for a recent review, see Renoult, et al., 2019). Given the extensive overlap in their neural substrates, an important question for future research will be to understand the neurocognitive mechanism of mental time travel and other phenomenological aspects of remembering, the features of episodic memory Tulving considered to be its most important characteristic (Tulving, 1983, 1985b, 2005; M. A. Wheeler, et al., 1997).

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