Forms of memory: Investigating the computational basis of semantic-episodic memory interactions
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1.1 Memory systems

1.1.1 Types of memory

Human memory is a fascinating phenomenon. It is what defines us at a fundamental level since it provides the basis for various high-level cognitive activities. First of all, memory enables us to grow as individuals and evolve as a species, since without memory of the past there would be no capacity for learning. Memory is also what makes the perception of time possible, since without memory there would be no before or after. Thanks to memory we are able to accumulate experience and information, and ultimately to extract a general concept from a particular context. Without memory, there would be no language. Finally, memory is what makes planning possible and gives us the ability to formulate and achieve long-term goals.

Human memory is not a unitary phenomenon, and over the years it has become increasingly clear that different types of memory exist. Tentative taxonomies of memory have been proposed based on neuro-anatomical divisions of the underlying neuronal systems associated with specific memory functions (Squire & Zola-Morgan, 1988; Squire, 1992); however, it is still not entirely clear how these differences translate to behaviour and brain activity. This thesis deals with long-term types of memory (i.e. declarative memory) and aims at investigating the dynamical interactions of semantic and episodic memory in behaviour.

1.1.2 Semantic and episodic memory

Endel Tulving, one of the first researchers to focus on the relationship between semantic and episodic memories, described episodic memory as "a system that receives and stores information about temporally dated episodes or events, and temporal-spatial relations among them" (Tulving, 1984, p.223). In contrast, "Semantic memory is the memory necessary for the use of language. It’s a mental thesaurus, organized knowledge a person possesses about words and other verbal symbols, their meaning and referents, about relationships among them, about rules, formulas, and algorithms for the manipulations of these symbols, concepts, and relations" (Tulving, 1972, p.386).

Human declarative memory is widely believed to consist of two distinct systems (Greve, Rossom & Donaldson, 2007; Tulving, 1972), episodic and semantic memory:
The episodic system enables us to remember the past and to time travel into the future. Information is assumed to be stored contextually, temporally and self-centered.

The semantic system is associated with rules, facts and in general with the knowledge of the world, including abstract representations of objects, people, historical events and word meanings.

An important distinction between episodic and semantic memory systems can be found in the mechanism implementing information retrieval. The process of retrieving an episodic memory (trace) is an activity associated with a sense of self-experience and linked to a spatial and/or temporal context. In contrast, retrieval from semantic memory is quite independent of self-experiences and contextual aspects (but not completely, see SAM-REM theory for example).

Tulving noted a key difference between semantic and episodic memory systems, inasmuch as the retrieval of episodic information is typically deliberate, often requires conscious effort, and is informally called “remembering” or “recalling”, while that of semantic information is usually automatic, and is often referred to as “knowing” (Tulving, 1984).

In his study, Tulving focused on the distinction between the autobiographical memory of personal events, and the memory that taps into our storage of culturally shared general knowledge about the world and facts, detached from any autobiographical reference. Also, “The relation between remembering and knowing is one of embeddedness: episodic remembering always implies semantic knowing, whereas knowing does not imply remembering.” An observation which captures the idea that multiple memory systems are organized in a structured and hierarchical fashion; so that the processing of episodic memories always requires, to some extent, the contribution of semantic memory whereas the processing of semantic memories can, apparently, be carried out without the contribution of episodic memory. It is important to note, at this point, that the position of this thesis regarding the hierarchical organization of semantic and episodic memory systems is radically different from the one proposed by Tulving. In fact, I will assume that the semantic system evolves from the episodic system during development and that the interactions between these two systems can take place at various levels of the hierarchical organization.
Differences between semantic and episodic memory have already been investigated quite extensively in fields such as cognitive psychology and cognitive neuroscience. However, there is still an ongoing debate on the controversial issue of defining a theory of human memory that captures, on the one hand, a modular description with functionally distinct components and, on the other hand, the ability to integrate information across multiple dimensions.

1.1.3 Lesion data and the multiple memory systems approach

In the early 19th century, French philosopher Maine de Biran was one of the first to assert that human memory is subserved by multiple underlying systems. Yet, the empirical evidence to support the multiple memory systems view was provided more than a hundred years later. The first scientist to suggest that different neurological systems underlie long-term memory phenomena was Eduard Claparède (1951). Based on his observations of amnesiacs, he determined that patients were able to recall “passive associations or idea reflexes”, which he called marginal memories, even when they had great difficulty recalling events from their own past. These he called egocentric memories. Later, Nielson (1958) built upon these findings to differentiate further between temporal amnesia, involving a loss of personal experiences, and categorical amnesia, involving a loss of acquired facts (Crovitz, cited by Herrmann, 1982). In 1989, Tulving described in detail the case study of a patient called K.C. In a motorcycle accident K.C. experienced severe brain damage to the frontal regions. As a result of this damage, he suffered a total loss of his own episodic memory. Interestingly, his semantic memory system seemed to work fine. Another well-known case discovered by a neurosurgeon named William Scoville reported an opposite dissociation. In an attempt to cure a patient called H.M. of his epileptic seizures, the surgeon had sectioned parts of both the left and right side of the patient’s hippocampus. This resulted in the patient completely losing the ability to store new information. “Surgery had interfered with the process of storing or retrieving new memories but had not touched previously stored memories” (Corkin, 2002). The famous cases of the amnesic patients H.M or K.C. proved that even if some parts of the memory system are damaged, others continue to function normally. Additional proof that the two systems are dissociable comes from younger patient data, which show that children with early-onset amnesia have intact semantic but impaired
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Episodic memory, whereas the opposite pattern occurs in developmental amnesia (Greve et al., 2007). Furthermore, neuropsychological evidence also suggests that episodic memory and semantic memory are supported by functionally and anatomically distinct brain systems.

1.1.4 Dissociating the neural correlates of long-term memory.

When the ability to form new autobiographical memories is lost while the old memories are intact, we may deduce that the episodic memory system is damaged whereas the semantic memory system is unharmed. We may consider this empirical pattern as supporting evidence of a dual process approach to memory. In other words, change occurs that affects one process but not the other. A limitation of data from lesion studies, however, is that it only provides information about the specific damaged region that is involved in the task performance. Moreover, evidence that different tasks are sub-served by different brain regions does not immediately imply functionally different systems. Willingham and Goedert (2001) clarify this example with an analogy: "One could draw an analogy to a computer hard drive: If two Microsoft Word documents occupy different parts of a computer’s hard drive, does that indicate that there is a fundamental difference between them? No, because the representation format and the processes (i.e., software) needed to interpret the two files are the same, despite their different “anatomic loci”." By the same token, Microsoft Word and Microsoft Excel documents would be considered different, even if they occupied neighbouring or even interleaved portions of the hard drive, because they use different formats and different processes are required to interpret them.

The same logic is applicable to memory. Anatomic separability is not enough. There must be a difference between the representations at a cognitive level of description to draw the conclusion that they are truly different and correspond to separate memory systems. It is becoming increasingly clear that complex cognitive activities like memory processing rely on the integrity of extended networks of brain regions rather than on the exclusive workings of individual regions.

The reliance on dissociations in the episodic-semantic distinction is therefore problematic. Hintzman (1984a) pointed out that when one variable shows different effects on two tasks, this is viewed as dissociation. However, in the case of variables that
have one effect on semantic memory and a different effect on the episodic one, there is no way to predict how the dissociation will occur. This way every dissociating result will count as evidence for the proposed distinction. Dissociation says nothing about causation. As for the results of tests conducted on patients suffering from brain damage, David Horner pointed out that “among the experiments that have demonstrated dissociation of episodic and semantic memory, many of the results can be explained without invoking the existence of separate memory systems” (Horner, 1990). This is because many semantic memory tasks, like word recognition, require the subject to recall well-learned information, a type of information preceding brain damage that has been repeated often, is well consolidated and over-learned.

### 1.1.5 A processing view of human memory

As already noted by Tulving in 1972, the classic theoretical approach to the study of memory has often relied on the categorization of empirical phenomena on the basis of some specific dimension, which is assumed to imply a qualitative difference in the underlying memory systems. Very often the existence of a contrast is deduced from the informational content of memories, and over the years a number of dichotomies have been used to describe differences in memory, like semantic-episodic, declarative-procedural, perceptual-conceptual and explicit-implicit.

Even though such an approach is useful to arrive at a theoretical understanding of memory systems (Tulving 1972), it has become increasingly clear that different types of memory are governed by a single large-scale modular system. This means that a high degree of reciprocal influence between different memory systems (i.e. modules) exists and can emerge at different levels of description (i.e. behaviour or brain activity). Therefore, it may not always be appropriate to reduce human memory to a dichotomous system and, even more importantly, to draw a distinction between memory systems on the sole basis of task performance (McKoon, Ratcliff & Dell, 1986; Ratcliff, Hockley & McKoon, 1985; Ratcliff & McKoon, 1986). This thesis contends that semantic and episodic memories are the expressions of an integrated multi-dimensional system with specialized functional modules. This argument rests on two ideas. First, since memory is a modular system, it seems more appropriate to look at the differences between modules by focusing on the processing characteristics of each, similarly to what has
been recently proposed for the implicit-explicit types of memory (Henke, 2010). Second, since the functional organization of the whole system can vary continuously from total segregation, where each module works independently, to complete integration, where both modules work in concert, it seems logical to look at the interactions between modules in terms of information integration and segregation (Tononi, Edelman & Sporns, 1998).

Applying the concept of information integration to a modular memory system means that depending on both the internal and external conditions of the system (i.e. task-set, mood, stimulus feature, encoding conditions), either the uni-dimensional or multi-dimensional account of memory is better suited to explain a given behavioural pattern. The uni-dimensional explanation applies when both semantic and episodic memory modules support behavioural performance in concert. Information across these two dimensions is coherently integrated in a uni-dimensional memory representation underlying behaviour. The multi-dimensional explanation instead is relevant when each memory module works independently and information is not integrated across both dimensions; a multi-dimensional memory representation underlies behaviour.

1.2 A memory for events

1.2.1 Episodic memory

As in order to understand a Turing machine it is critical to know what is being written on the tape (content of information) and what operations are allowed to manipulate the symbols (processing operations), likewise, with a good level of approximation, the characteristics of the cognitive memory systems are consistent with the content of the memory traces and the operations permitted (i.e. encoding and retrieval). The episodic memory is optimized to rapidly bind together different pieces of information (features) in a single unified memory trace. Features encode various types of information, and in this thesis I will mainly focus on the distinction between content features (i.e. content or item information including semantic, phonological and orthographic information) and contextual features (i.e. properties that correspond to the "physical, spatial/temporal, environmental, physiological, and/or emotional states in which the item was experienced", Malmberg & Shiffrin, 2005, p.323).
Over the years, researchers have thoroughly studied the effects of various factors on behavioural memory performance, such as encoding strategy (e.g., Paivio, 1971), incidental context during encoding (Smith & Vela, 2001), levels of processing (e.g., Craik & Tulving, 1975), contiguity (e.g., Kahana, 1996), materials (e.g., Nelson, 1979) and testing conditions (e.g., Gillund & Shiffrin, 1984). This interest generated a wealth of empirical data and led to the development of several comprehensive classes of models of episodic memory (e.g., ACT* by Anderson 1983a; CHARM, by Eich, 1982; MINERVA, by Hintzman & Ludlam, 1980, Hintzman, 1984b; SAM, by Raaijmakers & Shiffrin, 1980, 1981; REM by Shiffrin & Steyvers, 1997; TODAM, by Murdock, 1982, 1993). In the remaining part of this section I will describe in detail some of the effects, associated with episodic memory processing, which characterized the episodic dimension of memory performance in the experiments of Chapters 2, 3 and 4 and underpin the theoretical considerations of Chapter 5.

1.2.2 Encoding Specificity

Tulving believed that episodic memory differs from semantic memory in the way memory is encoded. Episodic memories are filled with contextual features, such as emotions and location, because they are an integral part of this type of memory. It is not just the words presented to the subject under specific environmental conditions that are stored in the episodic memory, but rather the entire event. Episodic memories contain rich contextual information from the study episodes during which they were formed. In contrast, the semantic memory system is less sensitive to contextual influences during retrieval because these contextual factors were not stored in the semantic memory trace. Since the episodic memory system is highly sensitive to context, both encoding and retrieval of events occur in relation to their temporal and spatial dimensions.

Thompson and Tulving originally formulated this concept in 1970 as the principle of encoding specificity. Later research showed that when a list of words was presented with sound in the background (instrumental music or white noise), the subject performed better in the recall test 48 hr. later and retained more words if the acoustic background was maintained rather than changed or removed. If learning occurred in quiet background conditions, recall performance was the same regardless of silence, music, or white noise in the background (Smith, 1985). Previous studies by
Godden and Baddeley (1975) produced similar results by showing that divers recalled words better when the recall condition matched the original learning environment, either underwater or on land. Apart from these external contextual differences, internal contexts like emotions or mood also influence our memory. Our memory for event information is better if we are in the same mood as when we encoded the information (Blaney, 1986). Similarly, another study demonstrated that if people learned the test materials while they were either intoxicated or sober, their subsequent recall performance was better if they were in the same psychological state. Participants who studied the test materials when intoxicated performed better at test when they were intoxicated (Goodwin et al., 1969).

Overall these findings show that the retrieval of episodic information is better when the conditions under which information was encoded and retrieved are the same.

1.2.3 Repetition priming

A well-known effect in the memory literature is long-term repetition priming, which means that processing certain information (e.g., a word) a first time makes it easier to re-process that same information a second time. In a typical repetition-priming paradigm, participants are given a list of words to memorize, and after an interval they are tested on their implicit memory of those items. Implicit memory tasks, such as the perceptual identification, lexical decision and word-fragment completion tasks, measure the participants’ memory of previously studied materials without their knowledge (Neath & Surprenant, 2003). For example in the experiment by Tulving, Schacter and Stark (1982), participants first received a list of low-frequency words (e.g. ARCHDUKE) to study and then, one hour later, a word-fragment completion task in which they had to complete word-fragments of previously studied words (e.g., AR_ _ _ _ KE) and also new words (e.g., _AR_VA_ _). Results showed that participants performed better on fragments of previously studied words than on fragments of new words. When they were tested again seven days later, this effect remained practically unchanged.

Whereas there is a wide consensus on the long-term repetition priming of whole words, other forms of repetition priming, such as letter or morpheme (i.e. the smallest meaningful units in a language) priming, are more controversial. These forms of priming introduce critical questions regarding the representational format of memory traces.
and, more importantly, provide empirical evidence for the debate on multi-dimensional theories of memory. In order to appreciate the theoretical importance of this finding, however, it is important to introduce the subject of semantic memory. I will, therefore, come back to the issue of morphological priming in section 4 of this chapter, where I will discuss interactions between semantic and episodic memory in relation to the issue of memory dimensionality.

1.3 Memory for knowledge

1.3.1 Semantic memory

The general knowledge a person possesses about the world that is not linked to an individual's personal experience is called semantic memory. Literally translated, “memory for meaning”. Semantic memory is quite different from episodic memory inasmuch as the contextual information encoded at the time of learning is no longer encoded or has been lost in some way. An example of semantic memory would be a discussion between two people in which the first person mentions owning a bicycle. Rather than visualizing a specific episodic memory of a bicycle, the other person can access the semantic definition of a bicycle and immediately understand what the first person is talking about. Unlike episodic memories, all the information is free from context and only an abstract form of information is stored for use in new situations. Without semantic memory, every time you saw a pencil on a desk you would have to determine its function.

An important characteristic of the semantic memory system is its configuration. Remembering one particular fact brings related facts closer to consciousness. This facilitation of related concepts is called “spreading activation”. Collins and Quillian (1969) discussed the structure of the semantic memory in terms of a network. Within this network each concept constitutes a node, and concept nodes are linked together by pathways of associations between concepts. This explains why related concepts become available when a particular concept is activated. For example, reading the word “boat” activates its mental representation as well as all the nodes connected to it, like “sea” or “water”. Another important feature of semantic memory is the accessibility of the information. Retrieving information from semantic memory is thought to be a fully automatic process that costs no effort. Retrieving episodic information, on the other
hand, is believed to be a process that does require effort and is not automatic. As seen in the previous example about spreading activation, whenever a word is activated it is the meaning of this word that becomes immediately accessible, rather than a specific event related to the word.

The configuration of semantic memory appears to be much more structured and free from error in comparison with episodic memory. Information stored in the episodic system is more prone to error due to the loose structure it possesses, and it is easier to lose the information because it applies to only one specific event (fewer links binding together features into single traces). In semantic memory instead, the information is often learned in a better way and is less vulnerable to forgetting because it is embedded in rich cognitive structures (more links binding the elements). Nevertheless, semantic memory retrieval is not entirely free of error either.

Semantic memory is generally thought of as a system where information is stored in a context-free, abstract and rule-like format. Features encoded in the memory traces, therefore, are thought to reflect higher-order properties that are independent of specific instances, but rather reflect statistical regularities over multiple instantiations. Given the complexity of the empirical findings and of the semantic memory system, significantly fewer general models have been proposed (e.g., the spreading activation model of Collins and Loftus, 1975; ACT*, by Anderson, 1983a; McClelland, 2000).

1.3.2 Associative priming

A well-known effect in the language domain is semantic or associative priming. Priming in this form refers to the fact that the processing of a semantically meaningful stimulus (i.e. the word cat, the number 4 or the equation 4+3=X) is facilitated when a semantically associated stimulus has been encountered previously (i.e. the word dog, the number 2 or the equation 1+5=X). The key idea is that a link of some sort exists in semantic memory among different representations. An intuitive way to visualize semantic memory is as a network of nodes where each node represents a semantic (context-free) representation (i.e. the concept of cat). Each node is then connected to other nodes via links that represent semantic associations and relationships. Priming in this view can be explained as the facilitatory effect arising from the activation spreading over semantic relationships linking related concepts. The insights provided by a
spreading activation theory of semantic memory spawned a host of computational models to account for semantic associative priming in both short-term and long-term paradigms. Particularly relevant for this thesis are the neural network models proposed by Masson (1995) and by Becker, Moscovitch, Behrmann and Joordens (1997), which will be discussed in greater detail in Chapter 5.

### 1.3.3 Morphological priming

In natural languages morphemes represent the smallest unit bearing a semantic meaning. In some natural languages (as in Dutch for example), morphemes can be found as self-standing objects (e.g. huis) or as compound objects (e.g. huisarts). The interesting aspect of these grammatical objects is that they provide a way to investigate the structure of semantic memory and, in particular, the type of representations stored therein.

The existence of morpheme priming has been validated numerous times. Murrell and Morton (1974) were the first to study repetition priming of morphemes. The main part of their experiment consisted in an identification task in which participants were asked to identify briefly presented words (e.g., mile). Prior to this task, participants had studied words falling into one of four conditions: the repeated condition (e.g., mile), the morphologically related condition (e.g., miles), the orthographically related condition (e.g., mild) and the unrelated condition (e.g., car). Participants performed significantly better when they had previously studied the same word or a morphologically related word compared to when they had previously studied a word that was orthographically related or unrelated. The morpheme priming effect, however, turned out to be significantly smaller than the word priming effect.

More recently, in their study of long-term repetition priming of morphemes, Rueckl and his colleagues used a procedure similar to that of Murrell and Morton in a fragment completion task (Rueckl, Mikolinski, Raveh, Miner & Mars, 1997). Before the test, participants had studied words that fell into one of the four conditions listed above: the repeated condition (e.g., hat), the morphologically related condition (e.g., hats), the orthographically related condition (e.g., hatch) and the unrelated condition (e.g., dog). They were then asked to complete word fragments (e.g., h_t) of target words (e.g., hat). It was found that participants managed to complete significantly more word fragments
when the target words were morphologically related to the words they had studied than if they were orthographically related or unrelated. Still, completions were considerably higher in the repeated condition than in the morphologically related condition.

Overall these results are suggestive of a semantic memory system where only meaningful units are represented such as words or morphemes. In contrast, purely perceptual units such as letters are not represented in the system since they do not possess a meaning of their own. In this view repetition priming effects are expected only for items that bear a representation in semantic memory, however see Schacter (1992) for an alternative view.

1.4 Interactions between memory systems

1.4.1 A hierarchy of memory systems

The question of how many systems underlie human behavioural memory performance has a long history in the cognitive psychology tradition, with early studies focusing on crossover dissociations as a means to identify true (non-removable) interactions between latent variables or processes (Loftus, 1978; Wagenmakers, Krypotos, Criss & Iverson, 2012). In the past forty years research on memory has seen, on the one hand, the development of mathematical models providing formal explanations of the observed behaviour (Anderson, Silverstein, Ritz & Jones, 1977; Ebbinghaus, 1885; Raaijmakers & Shiffrin, 2002) and, on the other hand, the development of more elaborate and clever behavioural paradigms to tease apart the effects of different non-observable processes underlying behaviour (Bamber, 1979; Jacoby & Kelley, 1992; Newell & Dunn, 2008). With the later advancement of neuro-imaging techniques, it has become increasingly clear that two (or more) separate but partially overlapping neuronal systems underlie behaviours that are commonly ascribed to either semantic or episodic memory. This has sparked a fierce debate over the correct interpretation of the available empirical data on memory, namely whether human memory at the level of behaviour works as a single unitary system or as the collection of multiple memory systems.

In this thesis I will look at the expression of human memory during behavioural performance and discuss whether the data is best accounted for by postulating two dimensions along which memories are organized and processed (i.e. semantic and
episodic dimensions). For the present context human memory is defined as a modular and integrated system where different specialized modules participate of the same general structure. These memory modules are dedicated processors for a specific type of information (i.e. semantic or episodic) that are integrated in the same global memory network. As mentioned previously, the segregation vs. integration criterion (Tononi et al., 1998) allows us to distinguish conceptually between two opposing forces (or tendencies): segregation, where each memory module works in isolation, and integration, where both memory modules work in concert. In this theoretical perspective, the issue of dissociating between memory systems can be framed correctly both in terms of structural and functional differences. This thesis will concentrate on the relation between functional organization and behavioural performance, and will therefore not discuss further the relation between the structural organization of brain networks implementing memory systems and their functional expression during behavioural performance.

1.4.2 Mapping function to behaviour

The question of how many dimensions underlie behavioural memory performance is quite problematic since it impinges on whether it is possible to establish a mathematical correspondence between behaviour and the underlying memory systems. The goal of this thesis is to investigate in behaviour if this correspondence dissociates over memory systems, in other words whether it is possible to parcel out the interaction between memory systems during behavioural performance in terms of modularity. In relation to the lesion data and the role of structural differences for dissociating memory systems, this thesis assumes that multiple functional organizations can emerge from the same large-scale structural system. Therefore the focus will be on dissociating different functional organizations of semantic and episodic memory systems. A one-dimensional configuration means information integration across both dimensions, whereas a multi-dimensional configuration implies segregation of information over both dimensions.

On a global level modular memory, intended as the collection of semantic and episodic memory modules, can be described as a multi-dimensional dynamical system with two focal points or attractors. This view is akin to the description in physics of how
gravity affects a system composed of two planets orbiting around each other (i.e. earth and moon). When evaluating the dynamics of such a system, how the system responds and adapts in response to external perturbations, one must evaluate, on the one hand, the global dynamics of the system; how the system behaves when seen as a single unified entity. On the other hand, one must also evaluate the internal dynamics of each of the systems participating in the global one; that is how each of the internal systems changes its dynamics due to global perturbations. In this example, the internal systems correspond to the two planets and their reciprocal influence due to the effect of gravity. The crucial aspect of this definition is that the global dynamics of the system as a whole influence and, at the same time, are influenced by the internal dynamics of each of its constituents; in other words, the effect exerted by each planet on the other planet is a crucial component in understanding the global behaviour of the whole system (orbit of the two planets). Conversely, to fully understand the dynamics governing each of the internal components, one must be able to relate the global functioning of the system to the functioning of each of its components. Local and global dynamics are mutually informative and provide insights on the hierarchical organization of its constituents.

In relation to memory, the proposed analogy is that semantic and episodic memory modules constitute the focal points of a multi-dimensional memory system where each module presents some degree of inter-dependence with the other. The varying degrees of inter-dependence are the result of the underlying neural machineries implementing each module, which are overlapping parts of the same extended large-scale network. The aim of this thesis is to investigate in behaviour the computational basis of the interactions between semantic and episodic memory systems in order to gain insights regarding their functional organization.

In the following section, I will review some key empirical findings that provide a first characterization of the mutual interactions between semantic and episodic memory.

1.4.3 The levels of processing effect

A first prime example of an interaction between semantic and episodic memory systems is the level of processing effect (Craik & Lockhart, 1972). Previous research has shown now across a number of tasks that events and words that were encoded (studied)
during semantic-based tasks were better recognized in a later test phase than events and words which were encoded during non-semantic episodic tasks (Greve et al., 2007; Menon, Boyette-Anderson, Schatzberg & Reiss, 2002). This effect is a clear example of a hierarchical interaction between memory systems with, in this case, the processing of semantic information providing an advantage for later episodic memory performance.

1.4.4 Extra-list cued recall

Another task suited to capturing interactions between semantic and episodic memory is the extralist cued recall task. This task consists of two stages, namely a study phase and a test phase. During the study phase, the participants study a list of words, in either an intentional learning setting (i.e., the participants are instructed to study the list items for an unspecified memory test) or an incidental learning setting (i.e., the participants are required to process the items on the list, without being aware that their memory will be tested later on). Once the study phase ends, the study items become unavailable and the test phase either commences immediately or is preceded by a distractor task (e.g., doing mental arithmetic, studying a second list of words or moving from one room to another). During the test phase, the participants receive a list of cues, which are semantically associated with the initial words in a one-to-one manner (e.g., if the word FIRE is on the study list, then the test list might contain an item such as WATER - ____). Afterwards they have to recall the items from the initial list (in our example, the correct response to the cue WATER - ____ would be FIRE, making FIRE the target). Importantly, the test cues are always new items, which did not appear on the study list (thus, "extralist" cues).

An important diagnostic aspect of this task in relation to semantic-episodic memory interactions is that there appear to be two main strategies that the participants can use in order to solve the task. One course of action involves retrieving the initial words through free recall and matching them to the cues (i.e., an "episodic" strategy). Another course of action relies on generating semantic associates for each cue, based on free association, and testing the associates for recognition (i.e., a "semantic" strategy). Furthermore, the performance of the participants, as measured by the percentage of correct responses, has been found to depend on a number of factors that influence either episodic memory or semantic memory. For instance, task performance is affected by
presentation rate, level of processing, frequency, concreteness and imageability (Nelson, Schreiber & McEvoy, 1992), variables which have an impact more on episodic than on semantic memory. Conversely, performance is also influenced by the number of semantic associates of the cue and of the target, as well as the interrelations between the cue, the target and their associates (Nelson, Bennett, Gee, Schreiber & McKinney, 1993), factors which are tied more to semantic rather than episodic memory.

1.4.5 Implicit long-term memory

For almost a decade now, studies of subliminal perception have been conducted to investigate the extent to which conscious access of information can be excluded from long-term memory, both during the encoding and the retrieval of information. Over the years, it has become clear that subliminal presentations provide a way to tap into implicit forms of memory. Previous research has shown the existence of short-term subliminal priming in both semantic and episodic based tasks (Balota, 1983; Bodner & Masson, 1997; Van Den Bussche, Van Den Noortgate & Reynvoet, 2009; Van Den Bussche & Reynvoet, 2007; Carr & Dagenbach, 1990; Dehaene et al., 2001; Dehaene, Changeux, Naccache, Sackur & Sergent, 2006; Draine & Greenwald, 1998; Kiefer & Martens, 2010; Forster & Davis, 1984, 1987; Forster, 1998; Marcel, 1983; Masson & Bodner, 2003; Masson & Isaak, 1999); however much less is known regarding subliminal long-term memory. In the second chapter of this thesis, I investigated with a series of experiments if words which have been processed during encoding semantically and subliminally would lead to a long-term repetition priming effect in a later perceptual identification task. This question is crucial to understanding the interactions between semantic and episodic memory, since it provides a way to test whether there is an automatic component in the interaction between semantic and episodic memory. In absence of controlled (conscious) processing, does encoding lead to the storage of information in long-term memory?

1.4.6 Dimensionality of human memory

The question of the dimensionality of human memory is an old one, and it has been a fundamental question in memory research for more than 30 years. With the advancement of modern cognitive science, the question has been tackled at various
levels of analysis ranging from behaviour to brain activity. It is acknowledged by now that two different systems support semantic and episodic memory performance, and a loose distinction is often suggested on the basis of neuroimaging findings and brain lesion data. Overall these results indicate that different neuronal networks implement the memory functions that at the level of behaviour are generally ascribed to either semantic or episodic memory. In the third chapter of this thesis I will investigate how two competing hypotheses on the dimensionality of memory can be tested and quantified in behaviour, namely whether memory performance is best accounted for by a uni-dimensional or a multi-dimensional explanation. The concept of dimensionality is a theoretical construct invoked in the present context to provide a unifying conceptual framework that relates patterns of behavioural performance with hypotheses regarding the functional organization of the memory modules. The functional configuration of the memory modules is defined along a continuum ranging from integration (one-dimensional) to segregation (multi-dimensional).

A first approach to answer the question of memory dimensionality could be measuring memory performance in two laboratory tasks commonly associated with different types of memory, such as lexical decision and recognition for example, and then comparing behaviour across these two tasks within an appropriate analytical framework. Previous studies have shown that depending on the experimental design, it is not always possible to draw comparisons between conditions and/or tasks. The problem is that a clear separation of semantic and episodic memory on the basis of pure task performance is not always possible (McKoon et al., 1986). Hence, a more principled approach involves the definition of a theory of the memory system involved and a description of how this relates to the processing components estimated in behavioural tasks (Ratcliff et al., 1985).

Over the last years some approaches have been developed to disentangle the contributions of different dimensions underlying memory performance (Bamber, 1979; Jacoby, Toth & Yonelinas, 1993; Newell & Dunn, 2008; Prince, Brown & Heathcote, 2012a, see also Yonelinas, 2002). In the third chapter of this thesis, I will focus in particular on the approach of state-trace analysis, initially introduced by Bamber in 1979 as a non-parametric way to test the dimensionality of a given set of observations. Over the last years this analytical framework has been successfully applied in a number of experiments to distinguish whether observed performance is best explained by one or
two underlying dimensions (Loftus, Oberg & Dillon, 2004; McCarley & Grant, 2008; Newell, Dunn & Kalish, 2010; Prince et al., 2012a).

1.4.7 Hierarchical representations in semantic memory

Another fundamental question for understanding interactions between semantic and episodic memory is how information is represented in memory traces. In other words whether the representations are hierarchically structured within and between them, possibly due to the functional organization of the episodic and semantic memory modules. In the fourth chapter, I will present results from an experiment where I looked at the structure of semantic memory representations by distinguishing aspects of perceptual processing (i.e. processing a letter string with no semantic content, for example cot) from aspects of conceptual processing (i.e. processing of a stimulus with semantic meaning, for example cat).

Previous studies of semantic priming have shown across a number of tasks that the repetitions of both words and letters lead to a faster and more accurate processing of the same stimulus on any subsequent encounter, an effect generally called repetition priming effect (RPE). The observed priming effects for words and letters, however, have been found to differ on a number of properties such as for example retention interval (i.e. time it takes for the RPE to disappear) and magnitude (i.e. size of the RPE effect). The general insight followed here is that differences between priming effects for words and letters are representative of differences in the representational components of memory, namely differences between content features (i.e. semantic meaning) and perceptual features (i.e. orthography). Following this rationale, the first experiment of the fourth chapter will address the question of whether semantic memory representations consist exclusively of phonological, syntactical and semantic representations, or instead they also include higher-order properties such as morphological structure; in other words whether semantic memories possess a representational component for morphology. To answer this question, I will investigate the existence of morphological information in semantic memory by testing whether the repetition of morphological information in a typical semantic-based task such as lexical decision leads to a repetition priming effect.
1.4.8 Frequency effects for words and letters

A second fundamental aspect related to the representational structure of semantic memory is the nature of normative frequency. Normative frequency generally refers to an estimate of how many times a given linguistic unit (i.e. a word or letter) is encountered in a standard piece of natural text (i.e. newspaper). It is known that at some level of representation normative frequency is stored in semantic memory, however it is not clear yet how this property is collocated in a unified memory system involving a semantic and an episodic module. Under the assumption that letters are not represented in semantic memory, it becomes a non-trivial issue to assess whether normative frequency for letters is a property of episodic memory and whether it can interact with normative word frequency for words.

To be more precise, the core question of the argument is at which level of the cognitive architecture frequency effects are seated (i.e. is normative frequency a perceptual or a conceptual property?). One way to answer this question is by looking at how the frequency of occurrence for a word (supposedly a property of the semantic system) relates to the frequency of occurrence of letters (supposedly a property of the episodic system). In other words, by manipulating normative frequency for both words and letters it is possible to obtain a first impression of whether word and frequency effects are indeed different effects and, if so, how they interact with each other (additive or modulatory effects). Focus of the second experiment of the fourth chapter will be the manipulation of normative word and letter frequency in the Dutch language in order to measure within lexical decision different effects on semantic processing.

Taken together, the results of the experiments described in the fourth chapter provide important insights regarding the functional organization of semantic memory representations. These results will be crucial for the theoretical considerations proposed in Chapter 5 where I will discuss the functional organization of memory systems in light of current global models of memory.

1.5 Overview of the thesis

The overarching goal of this thesis is to investigate the hierarchical organization of semantic and episodic memory during their interactions in behaviour. The remaining part of this thesis is structured in 4 main chapters as follows. Chapter 2 presents the
results of a series of experiments aimed at testing the hypothesis that the storage of information in long-term memory is necessarily dependent on the focus of attentional resources. Chapter 3 comprises of two main sections. The first section provides a short but detailed introduction (a sort of toolkit) of state-trace analysis along with its most recent developments in the framework of Bayesian statistics and some illustrative simulations. The second section presents the results from a state-trace experiment I conducted to examine the processing components underlying semantic and episodic memory interactions. Chapter 4 presents results from two behavioural studies aimed at investigating the functional organization of semantic memory. Both experiments were carried out in Dutch with the first looking at the existence of morphological priming and the second one at the effects of normative frequencies over word and letter priming. Chapter 5 provides a review of the current global models of memory and discusses how the results presented in this thesis can be explained within a unified formal framework. Lastly, Chapter 6 presents a short recap along with some final considerations.