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Episodic Memory formation: A review of complex Hippocampus input pathways

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Input pathways to the Hippocampus for Episodic Memory formation: a systematic review

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Abstract

Memories of everyday experiences involve the encoding of a rich and dynamic representation of the present objects and their contextual features. Traditionally, the resulting mnemonic trace is referred to as episodic memory, *i.e.* the "what", "where" and "when" of a lived episode. The journey for such memory trace encoding begins with the perceptual data of an experienced episode handled in sensory brain regions. The information is then streamed to cortical areas located in the ventral Medio Temporal Lobe, which produce multi-modal representations concerning either the objects (in the Perirhinal cortex) or the spatial and contextual features (in the parahippocampal region) of the episode. Then, this high-level data is gated through the Entorhinal Cortex and forwarded to the Hippocampal Formation, where all the pieces get bound together. Eventually, the resulting encoded neural pattern is relayed back to the Neocortex for a stable consolidation. This review will detail these different stages and provide a systematic overview of the major cortical streams towards the Hippocampus relevant for episodic memory encoding.

Keywords *episodic memory, Hippocampus, memory consolidation, Entorhinal cortex, mental representations, Neocortex, one-shot memory, computational neuroscience, neural networks, neuroanatomy*

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1 Introduction

1.1 What Episodic Memory (E.M.) is and its place in the human memory system

Learning incredibly quickly and building a huge mass of exploitable knowledge are two defining features of the brain. Memory is a mental process through which we can refer to our past experiences, make choices in the present and plan the future.

To begin with, memory is inherently divided into short (STM) and long-term (LTM) based on duration. While the former processes last from few hundreds of milliseconds (sensorial memory) to a few minutes (working memory), the latter can potentially endure a lifetime. More in details, long-term memories can be further distinguished into declarative and non-declarative depending on whether their recall is explicit or implicit, with the latter comprehending those where the retrieval is possible only through sub-conscious behaviours (e.g. procedural memory and conditioning) (Lynn Nadel 1995; Larry R. Squire and Dede 2015; Larry R. Squire and Zola 1996; L. R. Squire and Zola-Morgan 1991).

In the declarative group we find the memory systems whose content can be continuously recalled with a (seemingly) conscious act. The most prominent of this kind is Episodic Memory, which is in charge of storing the episodes we experience during the day as a sequence of events within a specific spatio-temporal framework. Further, the group of declarative systems also includes Autobiographical Memory, more sensitive to content regarding the self and the personal history Conway 1996, as well as Semantic Memory, which concerns abstract concepts and their meanings, believed to arise partially from the generalization over several experienced episodes. According to these declarative systems, a function of memory might be the creation of a coherent internal representation of the persona, gluing together stacks of autobiographic facts and notions about ourselves, forming the basis for high-level cognitive states and phenomena like consciousness and self-awareness (Tulving 1983).

At the core of these cognitive performances lies the incredible **episodic memory** ability of remembering an event after as little as a single exposure, resulting in the encoding of an experience in the brain under the form of a permanent episodic memory trace (Clayton and Dickinson 1998; Tulving 1999). In humans, this is traduced in the capacity of remembering an extraordinary amount of information from the past (T. F. Brady et al. 2008; Timothy F. Brady, Konkle, and Alvarez 2011; Konkle et al. 2010). From a functional perspective, the primary consequence of this one-shot learning ability is the opportunity to overcome the usual lengthy trial-and-error schema, providing a fast as well as durable means of acquiring new knowledge about the world. This invaluable property comes in handy in plenty of occasions when a repetition of an event is unlikely but the retention might be of vital importance, for instance during the eye-witnessing of an accident. Nonetheless, it is also well documented how memories are not permanently static, but instead are re-elaborated and transformed over time and as more experiences are recorded (S. F. C. Bartlett, Frederic C. Bartlett, and Frederic Charles Bartlett 1995; Brewer 2000; L. Nadel et al. 2012; Semon 1921; Semon 1923). However, not everything that happens during the day is meant to be kept forever. Instead, only what is able to trigger a certain arousal or emotional involvement will be tagged as potentially worth Pessoa 2010; for instance, a daily bus ride in a non-specified day of October

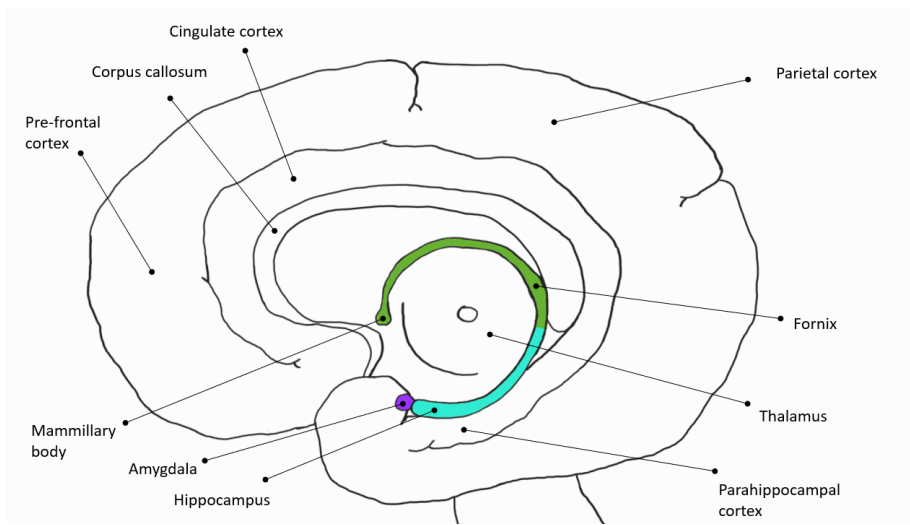


Figure 1: **Position of the Hippocampus** - schematic sagittal section of the human brain, the Hippocampus (cyan) is the structural continuation of the Fornix (green) and lays on top of the Parahippocampal cortex.

stands no chance against the first birthday of your daughter in gaining a place in long term memory.

Finally, understanding the dynamics of the processing and consolidation of experiences have been an endeavour tackled by psychologists and neuroscientists for decades. So far, we have managed to have an idea of the plethora of areas **and network** involved and several computational models have been proposed and fitted to the observations made by cognitive and neuropsychological studies **In this present review we will focus on the input involved in the episodic memory formation and not consider the networks involved in consolidation and retrieval.**

1.2 The network pathway for episodic memory encoding

From a more theoretical perspective, the structure of an episodic memory is regarded to encode the *what*, *where* and *when* something happened (Tulving 1983; Clayton and Dickinson 1998; Sugar and M.-B. Moser 2019), namely a conjunction of a content/object(s) and its spatio-temporal context. It is possible to trace the relevance of this pragmatic formulation in the organization of the information flow converging to the Hippocampus, probably the most important structure during the stages of memory formation. In the present review, the focus will be placed solely on the convergence of its cortical input streams.

The starting point occurs at the level of the neocortex. Here, all the relevant information about the objects, space and time are collected and unified into a single entity that might be called a “scene” and gated to the Hippocampus, which acts like an hub collecting all the salient aspects of an episode. What is manipulated is perceptual data, processed by cortical areas like the temporo-occipital regions (for non-spatial features), whose output is routed towards the Perirhinal cortex, and the posterior-parietal (for spatial features) regions, whose output is sent to the

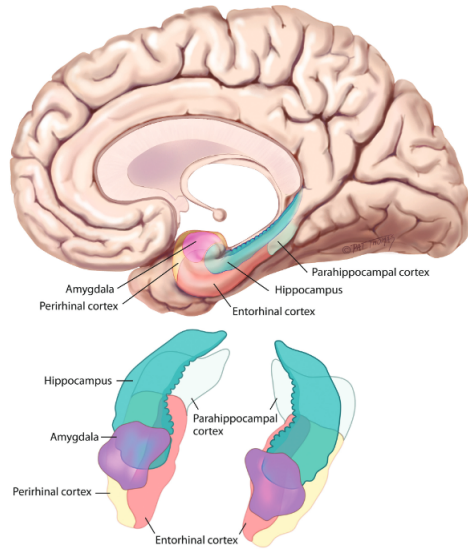


Figure 2: **Overview of the Medial Temporal Lobe** - sagittal section of the human brain, the Hippocampus (cyan) is the structural continuation of the Fornix and lays on top of the Parahippocampal, Perirhinal and Entorhinal cortex (light green, yellow and red respectively) - *From Raslau et al. 2014.*

Parahippocampal cortex, in the lower bound of the temporal lobe, as shown in figure ?? and 2. Once there, around the Rhinal Sulci all the information is passed to the Entorhinal Cortex (EC) and then inside the Hippocampal system, where the actual encoding takes place. Here, the stream firstly undergoes pattern separation in the Dentate Gyrus (DG), then a structural binding of the features in the auto-associative network CA3 (section 3 of the Cornu Ammonis CA, the “body” of the Hippocampus) and eventually arrives in CA1 and in the Subiculum, which project to higher cortical areas as well as upstream regions through feedback connections. Further, it is worth mentioning that several other circuits play a pivotal role in determining what is relevant, for instance the Amygdala and the Orbito-Frontal Cortex, responsible for determining the emotional valence of the perceptual information, and their relationship with CA1 (Pessoa 2010; Dong et al. 2009; Ishikawa and Nakamura 2003).

1.3 Aim of the present Review

The literature on Episodic Memory is vast and extended, alongside the one on Hippocampal processing. Nevertheless, the mechanisms underlying the formation and management of the memory traces are still poorly understood (Baddeley, Aggleton, and Conway 2002; Tulving 1999; Tulving 2002; Sugar and M.-B. Moser 2019; Burgess, Eleanor A Maguire, and O’Keefe 2002). Current computational models only able to capture and reproduce by simulation a fraction of the aspects exhibited by real biological substrates. On the other hand, electrophysiological, neurobiological, and behavioural research keep providing a large amount of data and recordings of new details of neurobiological dynamics involved in memory formation. A good

point from which to start disentangling the complexity of the system at hand is having an idea of its structure, in terms of architecture and components.

In this review, the objective is to illustrate the variety of input pathways leading to the encoding of an episodic trace in terms of content and spatio-temporal features realized within the Hippocampus, providing an overview of the information stream from the sensory processing regions to the inner areas of the Cornu Ammonis. In the first part, we describe how the acquisition and processing of perceptual features take place. We first address the object-related information pathway, describing the intricate connectivity and functional properties of the Perirhinal Cortex (PRC), in 2. Secondly, we consider the pathway for the spatial attributes, with the presentation of the central role of the Para-hippocampal Cortex (PHC) and the neuronal circuits in which it is involved, in 3. Thirdly, we introduce the importance of Entorhinal Cortex (EC), illustrating its centrality in intermediating between the neocortical associative areas, like the two aforementioned, and the Hippocampal formation, in 4. Finally, we shift the focus towards the Hippocampus, with a schematic overview of its internal connectivity and a brief description of a prominent computational model, in 5.

1.4 Abbreviations

ACC: *Anterior Cingulate Cortex*; AiP: *Anterior intra Parietal Cortex*; BLA: *Baso-Lateral Amygdala*; CA: *Cornu Ammonis*; DG: *Dentate Gyrus*; EC: *Entorhinal Cortex*; GN: *Geniculate Nuclei (Thalamus)*; HP: *Hippocampus*; IT: *Infero-Temporal cortex*; LA: *Lateral Amygdala*; LEC: *Lateral-Entorhinal Cortex*; LiP: *Lateral intra-Parietal cortex*; MEC: *Medial-Entorhinal cortex*; MPFC: *Medial-Pre-Frontal Cortex*; MT: *Medio-Temporal cortex*; MTL: *Medio-Temporal lobe*; OFC: *Orbito-Frontal Cortex*; OPFC: *Orbito-Pre-Frontal Cortex*; PB: *Peristriate Belt*; PCC: *Posterior Cingulate Cortex*; PFC: *Pre-Frontal Cortex*; PHC: *Para-Hippocampal Cortex*; PiC: *Piriform Cortex*; Pi: *Para-Insular cortex*; PP: *Perforant Path*; PPA: *Para-Hippocampal Place Area*; PPC: *Posterior-Parietal Cortex*, PRC: *Peri-Rhinal Cortex*; RSC: *Retro-Splenial Cortex*; Sb: *Subiculum*; STG: *Superior Temporal Gyrus*; TE[§]: *Temporal*; TEO⁴: *Temporo-Occipital*; TF⁴; TH⁴; Tpt: *Temporo-parietal area*; VMPFC: *ventro-Medial-Pre-Frontal Cortex*; VTPC *Ventral Temporo-Parietal Cortex*

2 Information about the objects: Perirhinal Cortex

The development of an object representation in the context of episodic memory is a process involving the collaboration of several systems across the whole cortex. The starting point is the acquisition of sensory stimuli from the external world, which are captured by specialized receptors and neuronal circuits, the senses. They measure the changes of specific physical quantities in the stimuli and convert their excitation into appropriate spike trains (Purves 2012; Butler n.d.). Then, the information is delivered to different areas in the cortex for a fine-grained perceptual processing. All these areas are internally structured in a hierarchical fashion, so that the early stages have the duty of dealing with the low-level aspects of the inputs, while the

[§] Ambiguous, there is an active debate over the actual origin of the acronym, see Weiner 2018

latest ones will deal with more abstract features. The prototypical example is the visual ventral system, which departs from the innermost region of the occipital lobe, V1, sensitive to primitive geometrical elements, and then develops ventrally through regions V2 and V4, where more convoluted shapes are detected, arriving eventually in the inferior-temporal cortex IT, in which a context-invariant image of the stimulus is formed. These processing patterns are repeated similarly in other senses, for instance the auditory system (Bornkessel-Schlesewsky et al. 2015; Perry and Fahlah 2014). Once unimodal high-level feature representations are reached, they are combined together to form more sophisticated multi-model characterization of the object.

Nevertheless, to achieve a more complete object representation, other ingredients than perceptions are required, such as the emotional connotation and the inference of the object's properties. The chief circuit dedicated to emotions is the Limbic System, a set of cortical and sub-cortical areas encompassing the Corpus Callosum and classically associated with motivation, reward and first-order emotional processing.

2.1 Perirhinal cortex - Neuroanatomy

Once a high-level characterization of a particular feature is achieved, it is combined together with other unimodal representations from other areas to form more complex multi-modal mental picture of the object. When the reference is the object identity, without spatial intendment, these multi-modal aggregation processes are often directed towards a specific area located in the medio-temporal region: the Perirhinal cortex, which encompass Broadman areas 35 and 36. By virtue of the quality of its afferent inputs, the Perirhinal cortex works as a place of convergence of the information concerning the representation of the identity of an object, ranging from concrete features like size and shape to more abstract aspects like emotional valence and semantic notions.

Afferences to the PRC

Several studies with macaque monkeys have allowed drawing a picture of the afferent pathways projecting to the PRC; among them, the research of W. A. Suzuki and D. G. Amaral used a retrograde tracing technique to investigate the neuroanatomy of this area (W. L. Suzuki and David G. Amaral 1994). Their results showed that a great deal of the afferent inputs comes from high-level unimodal visual areas and especially inferior temporal areas TE and TEO up to 62%, which include regions of the inferior and medial temporal cortex surrounding the PRC region, confirming the great importance of vision in the formation of mental representations. Interestingly, the configuration of the connections from inferior temporal regions to the medial areas and some amygdaloid nuclei are the results of some sort of pruning or refinement during development (Webster, L. G. Ungerleider, and J. Bachevalier 1991). Further, a quarter of the cortical projections originate in polymodal areas such as regions TH and TF of the Parahippocampal cortex, which are shown to be involved in the integration of auditory data; besides, these connections from PHC are considered to be *feedforward*, placing the PRC at an higher position in the associative hierarchy (Lavenex, Wendy A. Suzuki, and David G. Amaral 2002). Part of the remaining inputs are spared between some frontal areas, like the PFC (E. Hwang, Willis, and Burwell 2018) and the OFC for 2%, dedicated mainly to emotions and reward

(Rempel-Clower 2007); the Insular cortex for 2%, involved in multisensory binding of visual, proprioceptive, interoceptive and acoustic stimuli as well as elaboration of taste perception (Bushara, Grafman, and Hallett 2001; Bushara, Hanakawa, et al. 2003; Pritchard, Macaluso, and Eslinger 1999); the dorsal bank of the Superior Temporal Sulcus for 6%, devoted to poly-sensory integration of information from the visual, acoustic and somesthetic systems (e.g. touch, pain and heat) (Baylis, E. T. Rolls, and Leonard 1987; Bruce, Desimone, and Gross 1981; Hollins 2010), and some minor contribution from the Cingulate and Retro-splenial cortices (1%). Another strong afference comes from the anterior part of Superior Temporal Gyrus (STG), which is dedicated to acoustic processing but it is also partially sensitive to visual stimuli, at least rostrally (Baylis, E. T. Rolls, and Leonard 1987; Mesgarani et al. 2014). In addition, olfactory information has been shown to be involved, as projections from the Piriform cortex have been seen targeting the Broadman area 35, the ventral part of the PRC (Furtak et al. 2007). Additionally, another study using antero and retro-tracing methods has demonstrated the extensive connectivity between the temporal polar portion of the PRC and the deep layers of the amygdaloid complex, which is known to be responsible for emotional processing and arousal (Pessoa 2010; Stefanacci, W. A. Suzuki, and D. G. Amaral 1996; Whalen 1998). From the inner MTL, a consistent contribution from EC has been observed, mainly targeting region 35, which is considered to be a retro-active response to the feedforward projections from the PRC. Furthermore, a direct input from the Hippocampal structures (CA1 and the Subiculum) is also present, although modest, targeting area 36; however, these connections have to be interpreted as medium-range feedbacks to the stream coming from EC, CA3 and DG (Aggleton 2012; Furtak et al. 2007). In this fashion, it seems the PRC covers an important position with respect to the Limbic System, in which several areas have been shown to project to the Rhinal region, as it has been just illustrated. As such, the PRC is able to enrich the object representations with an effective personal and emotional valence, in addition to the plenty of information streamed from the sensory and poly-modal areas. Figure 3 provides a schematic overview of the main connections of the rhinal region.

Efferences from the PRC

Eventually, the same authors Suzuki and Amaral conducted another study with an analogue methodology, but this time aiming to uncover the efferences from the PRC. Their results showed the presence of several feedback connections back to the input areas, especially the higher visual regions like TE and TEO. However, these back-projections turned out to be frequently asymmetric, meaning that some cortical areas receive substantially less afferent connections from the PRC than they projected to it. This is for instance the case of the Insular cortex (Lavenex, Wendy A. Suzuki, and David G. Amaral 2002). Other relevant efferences are those targeting the posterior thalamus, especially the lateral and medial geniculate, and the peri-sylvian region, connections that are thought to modulate various association processes, as described in a tracing study with cats (Menno P. Witter and Groenewegen 1986). Regarding the Amygdala, the afferences coming from the PRC are solid and more or less symmetric, but heterogeneously partitioned over the amygdaloid nuclei (Stefanacci, W. A. Suzuki, and D. G. Amaral 1996). The major output pathway involves the lateral EC (LEC). It is in fact the gateway region that will introduce the high-level information about the object to the Hippocampal structures,

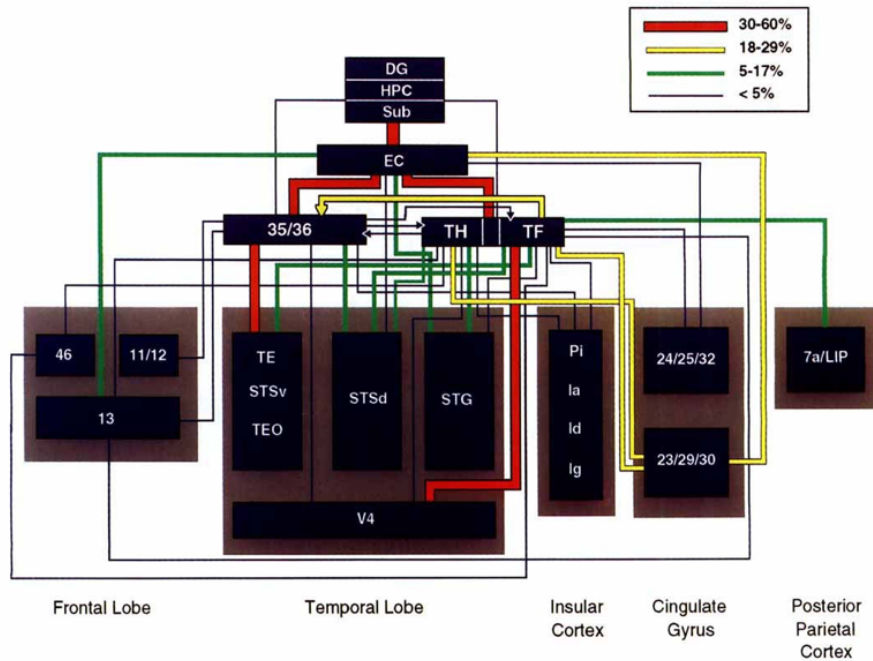


Figure 3: **Connectivity of the rhinal cortex** - 35/36 (Perirhinal cortex) and TH/TF (Para-hippocampal cortex) - Legend: *Dentate Gyrus*, *HPC Hippocampus*, *Sub Subiculum*, *EC Entorhinal Cortex*, *STSV ventral Superior Temporal Sulcus*, *STSD dorsal Superior Temporal Sulcus*, *STG Superior Temporal Gyrus*, *LIP Lateral Intra-Parietal area*, *Pi Para-insular cortex* - From *W. A. Suzuki and D. G. Amaral 1994*.

where the memory is properly formed. On the other hand, the direct projections towards the Hippocampus are rare and, as mentioned before, mostly concerns CA1 and SB as feedback connections (Furtak et al. 2007).

Eventually, from the picture of this connectivity profile what emerges is the responsibility of the PRC to define the content of an experienced episode, the *what* aspect, in terms of its perceptual features, through the sensory areas, and personal connotations, from the Limbic areas. The resulting enriched mental representation is then channeled to the Entorhinal-Hippocampal network, where it will be merged with the contextual information and recorded in a memory trace.

Below, is illustrated a schematic overview of the connectivity presented so far (4).

2.2 Functions

In the big picture outlined in the introduction, one of the chief roles of the PRC is to collect and process uni and polymodal perceptual information about objects from the higher sensory areas as well as other attributes like the emotional valence from the limbic system, eventually forming a complex non-spatial representation with a

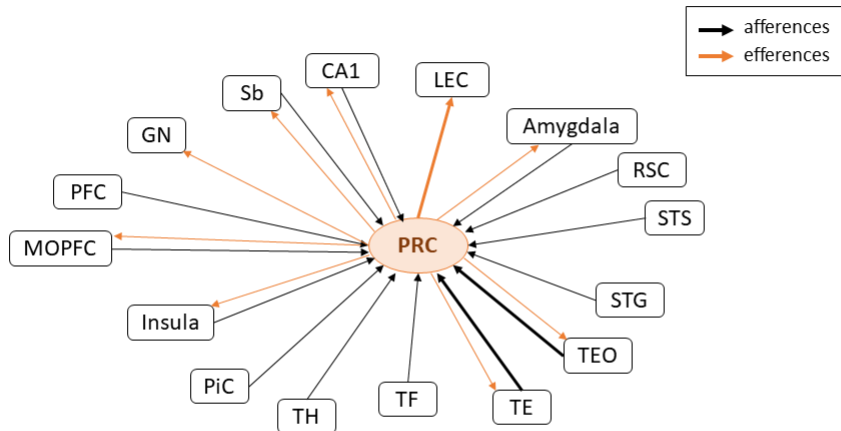


Figure 4: **Main connections to and from the PRC** - the strongest weights are in bold - Legend: CA1 *Cornu Ammonis 1*, LEC *lateral Entorhinal Cortex*, RSC *Retro-Splenial Cortex*, STS *Superior Temporal Sulcus*, STG *Superior Temporal Gyrus*, TEO TE TF TH *temporal regions*, PiC *Piriform Cortex*, MOPFC *medial Orbito-Pre-Frontal Cortex*, PFC *Pre-Frontal Cortex*, GN *Geniculate Nuclei*

possibly elevated degree of abstraction. In other words, it contributes to the *what* pathway of the episodic memory system, implemented by the consistent connectivity with the LEC, which channels non-spatial information to the internal Hippocampal formation. This systemic picture is backed up by several neuroanatomical studies, as previously illustrated, and by experiments with lesioned rats, in which it has been explicitly shown how the PRC and LEC regions prioritize non-spatial features instead of location-related ones (Burwell and David G. Amaral 1998; Deshmukh, Johnson, and Knierim 2012; Keene, Bladon, et al. 2016).

High-level object representation

The PRC is characterized by its object identification function, exemplified by the sensitivity to complex features combination in virtue of its high poly-modality, thus placing this area as a top-level stage of the Visual Ventral System (VVS) (Holdstock et al. 2009; Murray and Bussey 1999). This viewpoint has led T. J. Bussey, L. M. Saksida and E. A. Murray to propose their Perceptual Mnemonic/Feature Conjunction (PMFC) model, which considers the PRC as responsible for the creation of a high-dimensional object representation. The main prediction of this view is that lesions in this region would not lead to any perceptual impairment, but that complex discrimination tasks with elevated degree of ambiguity would become much

harder due to the unavailability of a multi-modal high-level representation and the constraint of relying on lower level (unimodal) information. This has been corroborated by a study with lesioned PRC monkeys, displaying the predicted weakened performances (Bussey, Saksida, and Murray 2003; Bussey, Saksida, and Murray 2005).

Involvement in memory tasks

There is considerable evidence linking the PRC to associative memory, i.e. pairing two elements together. In the inferior-temporal area TE and the Perirhinal area 36 (and similarly in 35), studies conducted with lesioned monkeys have identified neurons responsive to the co-presence of two stimuli but not them alone, therefore operating a unification into a single item (Fujimichi et al. 2010; Messinger et al. 2001; Naya et al. 2003). Similar results have also been obtained with neuroimaging on humans (Haskins et al. 2008). Eventually, these conclusions have been efficiently revised and substantiated by the review of K. S. Graham and colleagues (Graham, Barense, and A. C. H. Lee 2010).

The PRC is also part of the BIC model (*Binding of Item and Context*), proposed by Diana and colleagues (Diana, A. P. Yonelinas, and Charan Ranganath 2007; H. Eichenbaum, A. Yonelinas, and C. Ranganath 2007), which intends to capture the dynamics of the medial temporal lobe during memory retrieval by proposing that each component (PRN, PHC and HP) plays a role depending on the specificity of the recognition task and the available information. Within their framework, the PRC is thought to rely on item *familiarity*, where the retrieval is based on the perceived strength of the encoded trace and does not produce a detailed memory representation, in opposition to *recollection* (used by PHC and HP), where specificity and contextual information play the main roles.

Emotional and semantic features

Another important aspect of the PRC is the integration of affective and abstract connotations, which includes both emotional valence and semantic meaning. On the one hand, in virtue of its connections with Limbic structures like Amygdala and the OFC, it is able to endow object representations with more motivational and emotional attributes. Support for this comes from studies of fear and reward conditioning (Kholodar-Smith, Boguszewski, and T. H. Brown 2008; Lindquist, Jarrard, and Thomas H. Brown 2004; Liu and Richmond 2000) and the observation that the Amygdala significantly modulates visual recognition processing (Perugini et al. 2012) especially when reward is involved (Murray 2007). On the other hand, its elevated poly-modality and its availability of enriched object representation put the PRC in the suitable conditions for encoding semantic meanings (Taylor et al. 2006). Indeed, neuropsychological research with patients affected by dementia with impaired antero-medial temporal lobe have shown severe deficits in semantic tasks, for instance semantic object recognition (Becker and Overman 2002; Clarke and Tyler 2014; Davies et al. 2004; Patterson, Nestor, and Rogers 2007), and also showed the importance of the PRC in fine-grained discrimination tasks (Moss et al. 2005). Eventually, all these properties have led researchers to the definition of a more extended network of structures, the so-called Anterior Temporal system (AT), in which the PRC occupies the central node (Howard Eichenbaum, Otto, and N. J. Cohen 1994; Charan Ranganath and Ritchey 2012). Some other areas belonging to this network are the amygdala, the lateral OFC and the temporo-polar cortex. Together,

these regions account for the behaviours of the PRC in motivational, emotional and social processing, but also in recognition of familiar objects by taking advantage of the dense connectivity of the PRC with the sensory areas (Farovik et al. 2011; LaBar and Cabeza 2006; Meunier, Jocelyne Bachevalier, and Mishkin 1997; Olson, Plotzker, and Ezzyat 2007).

Finally, what can be concluded regarding the PRC is that it represents one of the highest stages involved in the object representation. The information it is capable to transmit through its afferences is remarkably rich and multi-dimensional; an indispensable step for the realization of a solid episodic memory trace.

3 Information about the location : Parahippocampal cortex

Beside representing the object identity, it is of great interest to evaluate its spatial features. The hierarchical sensory processing outlined before is similarly applicable here. Again, the visual system represents the primary player, in particular the dorsal stream developing from V2 to V3, and the Medio-Temporal cortex MT towards the Parietal cortex (Born and Bradley 2005; Rauschecker 2018). The information obtained concerns the location of the object in the visual field, its position, speed and other spatial aspects. Moreover, other senses contribute to reach these *where* assessments; for instance, the auditory system provides support for the localization by exploiting the time difference of the arrival of the sound's wave to the ears as well as the information concerning the body movement (Shamma 2001; Bizley and King 2008).

3.1 Parahippocampal cortex - Neuroanatomy

The Parahippocampal gyrus is an extended cortical region located in the temporal lobe and covers a pivotal role inside the Limbic system. Nevertheless, our current area of interest is restricted to a limited portion of it located in the posterior Parahippocampal cortex, at the boundary with the Rhinal sulcus. Within this region, two functionally and cytoarchitecturally distinct partitions have been identified: TH, smaller and in medial position, and TF, larger and laterally located (Von Bonin and Bailey 1947). These two areas exhibit strong coupling.

Afferences to the PHC

Over the years, several studies have shed light on the connectivity of this area and the information pathways in which it is involved; in this regard a special mention goes to the research using retro-tracing conducted by W. A. Suzuki and D. G. Amaral, quoted above concerning the Perirhinal connectivity. Starting with the afferent streams, the first fact to be highlighted is the predominance of the visual processing areas as a source of stimulation; in fact, the regions belonging to the Peristriate belt (like V4) constitutes the single largest cortical input to both TH and TF. In addition, the caudal region of TE and the medial of TEO, two important high-order visual areas, have been shown to have meaningful projections to TH (Boussaoud, Robert Desimone, and Leslie G. Ungerleider 1991; Distler et al. 1993). Another third of the cortical afferences is brought by the Superior Temporal Gyrus (STG) displaying consistent connectivity with TH, especially the posterior auditory association

cortex (Tpt), and only moderate connectivity with TF (Tranel et al. 1988). Conversely, the dorsal bank of Superior Temporal Sulcus (STS) projections to TF are stronger (up to 16% of its inputs) than its projections to TH (around 8%) (Barnes and Deepak N. Pandya 1992; Seltzer and Deepak N. Pandya 1978). In addition, the Perirhinal regions, 35, and 36, have afferent connections to TH and TF, but their strength is considerably inferior to those going in the opposite direction and are considered to be *feedback* instead of *feedforward* (Lavenex, Wendy A. Suzuki, and David G. Amaral 2002). Moving towards the Parietal lobe, extensive investigations have confirmed its tight relationship between the PHC; in particular, the lateral intra-Parietal and the Posterior Parietal cortex are connected to TF (R. A. Andersen et al. 1990; Marek-Marsel Mesulam et al. 1977).

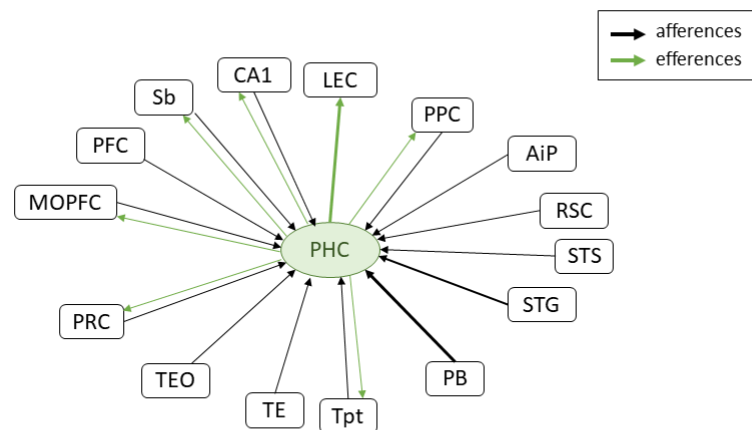


Figure 5: **Main connections to and from the Parahippocampal cortex** - the strongest weights are in bold; - Legend: CA1 *Cornu Ammonis 1*, LEC *lateral Entorhinal Cortex*, PPC *Posterior-Parietal Cortex*, AiP *Anterior intra Parietal Cortex*, RSC *Retro-Splenial Cortex*, STS *Superior Temporal Sulcus*, STG *Superior Temporal Gyrus*, PB *Peristriate Belt*, Tpt *Temporo-parietal area*, TEO *TE temporal regions*, PRC *Perirhinal Cortex*, MOPFC *medial Orbito-Pre-Frontal Cortex*, PFC *Pre-Frontal Cortex*, Sb *Subiculum*

A moderate input stream is also the one coming from the Frontal lobe, more specifically forming the dorso-lateral PFC and targeting both TH and TF (R. A. Andersen 1997; Selemon and Goldman-Rakic 1988). Another functionally important afferent pathway is constituted by sub-regions in two Hippocampal structures, the proximal CA1 and the distal Sb, with the hypothesized role of sending a feedback on

the spatio-temporal information that is being processed upstream (Aggleton 2012; Furtak et al. 2007; Charan Ranganath and Ritchey 2012). Lastly, one of the most relevant afferent stream to the PHC is represented by the Cingulate cortex, with the RSC being the primary source (Baleydier and Mauguiere 1980; Kobayashi and David G. Amaral 2007; Markowska et al. 1989; D. N. Pandya, Hoesen, and M.-M. Mesulam 1981). An explanation behind this latter close relationship between the PHC and the RSC is the involvement of these two regions in the Default-Mode Network, an important cerebral structure responsible for mind-wandering, self-reference, and resting state (Raichle 2015; Raichle et al. 2001).

Efferences from the PHC

The outputs from the Parahippocampal cortex partially overlap with the PRC, in that it also targets the OFC, a frontal hub receiving salient sensory and subcortical data (Cavada et al. 2000), the medial PFC (Carmichael and Price 1995), and EC, although unlike the PRC it aims at the medial part instead of the lateral and the feedback it receives from EC is significantly stronger (W. A. Suzuki and D. G. Amaral 1994). Besides, a relevant output is directed right at the areas 35 and 36 of the PRC and, as mentioned before, they are stronger than the afferent counterparts. Going further, other feedback connections were identified by using an anterograde tracing technique, like the projections to the Auditory Association cortex (Tpt), an area dedicated to sound processing and learning (Tranel et al. 1988). Another temporal region targeted by strong Parahippocampal output is the STG, as emerged in a retrograde tracing research in macaque monkey (Muñoz and Insausti 2005); withing the same study, also connections with the Parietal cortex have been individuated.

Taken together, the inputs converging to the PHC enable it to build up a representation of the contextual features of an episode like the spatio-temporal connotations, answering the *where* and partially the *when* something occurred. The downstream projections to the LEC further stream this information towards the next stage of memory encoding and those to the frontal and Perirhinal regions constitute mainly feedforward contributions, while the back-projections to the other source areas provide feedback. In figure 5, I presented an illustration of the overall PHC connectivity (5).

3.2 Functions

Primarily, the PHC is particularly relevant for early spatial processing and the recognition of familiar places, unlike the PRC described before. This contrast suggested a double dissociation, *i.e.* the attribution of two cognitive functions to two distinct areas by alternatively assessing the functional performance of one while the other is impaired. Eventually, this intuition has found good support in the literature both from cognitive studies (Davachi, J. P. Mitchell, and Wagner 2003; Davachi 2006; H. Eichenbaum, A. Yonelinas, and C. Ranganath 2007; Weis et al. 2004) and from lesioning studies in monkeys (Alvarado and Jocelyne Bachevalier 2005). From these, the common findings link the posterior PHC to the encoding and recollection of contextual information, and the PRC to item recognition and more generally to the object-related features instead of spatiality. In this regard, the BIC model mentioned previously in 2.2 configures the PHC as capable of recollection-based retrieval relying on contextual information prompted by Hippocampal activation. Further,

the model makes the prediction that the PHC may be processing contextual data not only on spatiality, but also on semantics (Moshe Bar and Elissa Aminoff 2003).

Scene perception

As such, the prominent functions of the PHC have been prompted to be contextual memory and scene perception. During various neuroimaging fMRI investigations where participants witnessed different scenes (either passively or task-oriented), an increased activation of the PHC have been observed, especially in the so-called Para-hippocampal Place Area (PPA), an inferior-temporal division of the PHC particularly devoted to the encoding and recognition of complex scenes (Moshe Bar and Elissa Aminoff 2003; R. Epstein and Kanwisher 1998; R. Epstein, Harris, et al. 1999; Mullally and Eleanor A. Maguire 2011). However, other regions like the anterior PHC also respond to places, but they tend to be more inactive during recognition, suggesting that when the input cue is strong enough, the scene is perceived as familiar and the sole PPA is sufficient for its elaboration (Köhler, Crane, and Milner 2002; E. A. Maguire et al. 1998; Weis et al. 2004). Neuropsychological studies have further confirmed the primary role of these regions in contextual processing and the emergence of spatial agnosia. For instance, scene memory was compromised upon lobectomy of the Anterior Temporal lobe (with or without PPA) (Pigott and Milner 1993), while a loss of environmental familiarity occurred after damages at the medial temporo-occipital cortex, in a similar fashion of prosopagnosia to faces (Landis et al. 1986).

Relations with the RSC

In addition, the RSC is highlighted to be a relevant region for spatial processing, although it differs from the MTL as it is involved in more self-referenced representations, supported by the presence of head-direction cells (Chen et al. 1994; R. A. Epstein 2008). Furthermore, a review of the neuropsychological literature concluded that damages at the RSC often lead to topographical amnesia, whose symptoms are heavy disorientation and deficits in spatial navigation (E. Maguire 2001). Another lesioning study in rats showed how the RSC might be involved in context-fear conditioning, which represents a good example of spatial self-centred non-declarative memory system (Keene and Bucci 2008).

Models of the PHC

Eventually, various studies have proposed different models for generalizing better the actual function of PHC and RSC. One of these proposals comes from E. M. Aminoff and colleagues. They suggested that the PHC and RSC belong to a broader network, comprising also the MPFC, devoted to process spatial and non-spatial context-associations, where a context has been operationalized as an environment surrounding a meaningful collection of objects, with possibly spatial relationship with each other (Aminoff, Gronau, and Bar 2007; E. M. Aminoff, Kveraga, and Moshe Bar 2013). Another model is the one of C. Ranganath and colleagues, in which they consider the PHC and RSC within a larger network, called Posterior Medial System, the mammillary bodies, anterior thalamic nuclei and pre/para-Subiculum. Some of the roles of this extended network cover spatial navigation, mainly through the PPA and RSC just described, and the elaboration of “situational models”, intended as mental representations that integrate and group together internal and external instances, spatial and non-spatial; indeed, this last function can be easily connected

with Episodic Memory (Diana, A. P. Yonelinas, and Charan Ranganath 2007; Charan Ranganath and Ritchey 2012; Zwaan and Radvansky 1998). Lastly, the involvement of the PHC in the Default Mode Network as part of the *MTL subsystem*, together with the PHC, RSC, LiP, VMPFC and HP. Functionally, the role of this sub-network is related to reasoning about the present and the future through episodic simulation and mnemonic scene construction, especially by providing contextual information (Andrews-Hanna et al. 2010; Daniel L Schacter and Addis 2007; Daniel L. Schacter, Addis, and Buckner 2007). Further, the Default Mode Network comprises also another subsystem, composed of frontal and temporo-parietal areas, devoted to process more self-referential content and oriented to meta-cognition and mind-reading (Ochsner et al. 2004; Vanderwal et al. 2008). More broadly, both subsystem interact and converge on two midline hubs, the MPFC and PCC (Buckner et al. 2009), endowing the Default Mode Network with the ability to picture an internal representation of oneself in salient events and his own mental states, besides aspects of social cognition and mental simulation. For these reasons, the PHC has been suggested to account also for the generation of autobiographical memories, which can be loosely seen as exceptionally self-referenced episodic memories (Svoboda, McKinnon, and Levine 2006).

4 The Entorhinal cortex bottleneck

After collecting information about the object and its spatial features in the Perirhinal and Post-rhinal cortices, the journey towards a unified experience representation encounters the Entorhinal cortex, covering the Broadman’s areas 28 and 34. It is commonly considered as the main intermediary between the Hippocampus and the Neocortex, and thus plays a primary role in the genesis of episodic memory and spatial processing in general. One of its principal function is to act as a gateway, channeling inputs from the Rhinal regions to the inner Hippocampal loop. At this stage spatial and object-related information still not merge together, but instead pass through two distinct Entorhinal regions, respectively medial and lateral.

4.1 MEC neuroanatomy

The medial entorhinal cortex (MEC) receives afferent connections from a variety of neo-cortical areas mainly devoted to spatial processing. The most prominent ones are the PHC, RSC and some visual-spatial regions in the parietal lobe, which bring highly-elaborated information. Besides, the dorso-caudal side also receives connections from the Hippocampus and specifically from the Pre and Para-Subiculum, generally considered as the last component of the Hippocampal circuit. The contributions from these last two parts concern the representation of spatial direction, confirmed by the abundance of head-direction cells and the experiments with lesioned rats (Canto et al. 2012; Fyhn et al. 2004). Regarding the efferences from the MEC, by means of the Perforant Path, the Hippocampus represents the main target, to which positional and directional information is delivered. Among the different neuronal population in the MEC, grid cells are undoubtedly the most investigated since their discovery (Hafting et al. 2005) and provide one third of the connection to Hippocampus, while the rest is largely composed of non-selective cells (50%),

head-direction cells, speed cells and boundary cells (Sasaki, S. Leutgeb, and Jill K Leutgeb 2015).

4.2 MEC functions

As already anticipated, the MEC is thought to play a primary role in gating spatial information from the Neocortex; however, an active contribution to spatial processing itself is also well documented.

Grid cells

Most notably, grid cells are specialized neurons possessing grid-like spatial fields and their firing rate is relative to the subject’s position in the environment (Giocomo, M.-B. Moser, and E. I. Moser 2011; Rowland et al. 2016), independently of locomotion (Killian, Jutras, and Buffalo 2012). Further, grid cells are known to be the precursors of Hippocampal place cells, which can be regarded to provide an upgraded and fine-tuned encoding of the subject’s location (Neher, Azizi, and Cheng 2017; Solstad, E. I. Moser, and Einevoll 2006). For instance, recordings from the dorsolateral-ventromedial axis of the MEC have exposed how grid cells in this region are involved in building an allocentric spatial representation, highly correlated with the downstream place cell’s activity (Fyhn et al. 2004). This and other studies have uncovered the relations between Entorhinal grid cells and Hippocampal place cells in CA1, showing how grid cells are helpful but not sufficient for orthogonal representations and the emergence of global remapping in the Place cells. Place cells are also able to operate in the absence of MEC inputs. Nonetheless, the exchange between the two regions is required for stabilizing their theta rhythms (4-8Hz). Theta rhythms have been extensively linked to spatial and episodic memory processing, especially during encoding of events sequences and recall when coupled with gamma waves (*theta-gamma coupling*) (Buzsáki 2015; Jezek et al. 2011; Oliva et al. 2016; Tort et al. 2009; Theodoni et al. 2018; Jensen and Lisman 2005). In particular, grid cells are necessary for processing temporality in CA1 as in phase precession (S. J. Mitchell and Ranck 1980; Schlesiger et al. 2015). This last property, exhibited in MEC and CA1 spatially-tuned cells, is defined as a progressive anticipation of the firing activation within the theta cycle, in other words the cells spike earlier. The computational advantages of such behaviour are yet to be validated, but some accredited hypothesis are the encoding of relevant information beyond spatial position, facilitation of a more efficient synaptic plasticity and the contribution in representing behavioural sequences (Jaramillo and Kempter 2017; Qasim, Fried, and Jacobs 2021; Reifenstein and Kempter 2020).

Object encoding

Another spatial property of MEC in its superficial layers is the positional encoding of objects. This ability is achieved by the so called “object-vector coding”, an allocentric representation of objects in space, independent of the animal’s location, a behaviour that resembles that of landmark cells in CA1 (Deshmukh and Knierim 2013; Høydal et al. 2019; Colgin 2015). Furthermore, the co-existence of two distinct circuits, both populated by grid cells, have been proposed within two of the layers of the MEC. The first one is composed of pyramidal neurons, devoted to intra-Entorhinal processing and supporting spatial computations like path integration. The second one is composed of stellate neurons, more oriented to support down-

stream Hippocampal activity, for instance by stabilizing phase precession (Sasaki, S. Leutgeb, and Jill K Leutgeb 2015). Besides encoding for egocentric and allocentric positions, feature-based processing has also been observed in MEC, specifically from non-grid cells in the superficial layers, which compose the two third of the neuronal population. In a study where MEC cells were recorded before and after modification of features in the environment, while grid cells maintained stable activity fields, non-grid cells underwent total remapping, suggesting their specificity in representing non-spatial characteristics (Diehl et al. 2017).

Taken together, these results provide a picture of the MEC, which goes beyond spatiality itself and in which the integration with feature-based processing creates already in MEC an almost multi-modal representation that will serve downstream computations for a more complete picture of the experience.

4.3 LEC neuroanatomy

The lateral Entorhinal cortex receives its main input stream from the PRC, which constitutes a high stage of the ventral pathway related to object features; other afferences come from the ACC and the MPFC (Deshmukh, Johnson, and Knierim 2012). Of particular relevance to the interactions between LEC and PER is the connectivity with the inhibitory network composed of the Anterior intra Parietal cortex (AiP) and the lateral Amygdala (LA), which targets the superficial and deep layers of LEC and PRC. Experiments using electrical stimulation have shown the importance of the influence of the emotional circuits in the transmission of the information from the Neocortex to the Hippocampus. Indeed, saliency, attention and expectation (encoded in AiP and LA) can modulate the sub-cortical Hippocampal loop (Curtis and Paré 2004; Kajiwara, Takashima, et al. 2003; Willems, Wadman, and Cappaert 2016).

4.4 LEC functions

The functions of the LEC concern mainly non-spatial processing. In this regard, lesions to this area impair context and place-object recognition memory, although non-associative recognition seems to be preserved (Wilson et al. 2013). This suggests a role of LEC in constructing a joint representation rather than simply selecting independent features. In addition, two distinct sub-populations of cells were identified as elaborating objects: one type firing when the animal was close to the objects, the other type firing at places where the objects were presented on previous trials, providing a readout of past experiences in the environment. The last cells generally did not respond to the object when it was present, suggesting that they responded to the object-trace (Tsao, M.-B. Moser, and E. I. Moser 2013). Together, these studies converge towards an idea that the LEC links object, location, and context for memory consolidation. Besides, it has been suggested that it might play an intermediary position between the Hippocampus and the ACC, a region documented to hold long-term memory for objects and their location (A. Weible et al. 2012; A. P. Weible et al. 2009). Moreover, an experiment with rats in which the connections between LEC and MPFC of opposite hemisphere were lesioned, demonstrated the importance of these interactions for the associative episodic-like memory (integration of the *what*, *where* and *when* of an experience), but not for the non-associative-like memory, for which the characteristics were taken singularly (Chao et al. 2016).

4.5 Double dissociations

The functional distinction between medial and lateral EC is a claim supported by several studies, suggesting a double dissociation is taking place. The main results have shown that MEC lesions provoke impairment of spatial processing, non-spatial object recognition and path integration, while LEC lesions preserve space navigation and path integration but do impair the detection of spatial and non-spatial changes, although the presence of spatial cells is weak (Deshmukh and Knierim 2011; Hargreaves et al. 2005). Nevertheless, the distinction might be blurrier, with the LEC dealing with joint spatial and non-spatial information and the MEC dealing tangentially with context. This suggests the existence of interactions between objects and space as early as the Entorhinal cortex; however, these observations are not intended to fundamentally challenge the assumed functions of the BIC model aforementioned (2.2) (Hunsaker et al. 2013; Van Cauter et al. 2013).

5 Hippocampus

The Hippocampus is a sub-cortical structure belonging to the “ancient brain”. Its two primary functions are spatial navigation and memory. It is located ventrally respect to the Para-hippocampal area and it develops around the body of the Fornix. Its main region develops as a horn-like shape, which gave it the name of Cornu Ammonis (CA), further subdivided into 4 sub-areas. The other two principal regions are the Dentate Gyrus and the Subiculum, which together with CA form a circular functional structure unfolding as DG – CA3 – CA1 - Sb (P. Andersen et al. 2006). In the brain, the Hippocampus is present in double copy, as well as the rest of the MTL, one for each hemisphere, which display some internal composition and functional dissimilarities; for instance, the left CA3 area is thought to represent space in a discrete way while the right CA3 area would represent space in a more continuous way (Hou, Yang, and Yuan 2013; Jordan 2020).

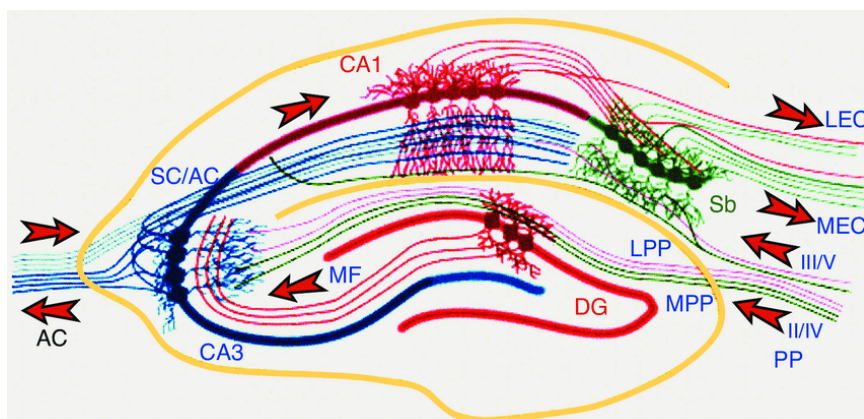


Figure 6: **representation of the Hippocampal network in rats** - Legend: CA3 Cornu Ammonis 3, CA1 Cornu Ammonis 1, EC Entorhinal Cortex, DG Dentate Gyrus, MF Mossy Fibers, SC Schaffer Collateral pathway, STS Superior Temporal Sulcus, STG Superior Temporal Gyrus, PB Peristriate Belt, Tpt Temporo-parietal area, AC Associational Commissural pathway, Sb Subiculum - From R. Kesner 2013

5.1 Hippocampus - input and output channels

The most prominent input stream to the Hippocampus comes from EC, a gate for the information coming from the MTL. From EC it departs the so-called Perforant Path (PP), a pack of connections that projects with various densities to all the Hippocampal sub-regions that owes its name to the fact that it perforates the Sb to arrive at the DG (Groen, Miettinen, and Kadish 2003). In addition, the upstream MEC and LEC generally targets different strata of their destination areas, and in particular layer II of EC aims at DG and CA3 meanwhile layer III aims at CA1 and Sb. Figure 7 depicts the principal Hippocampal afferences from the MTL.

Besides EC, several other structures send information directly downstream. The PCC and other Parietal areas have been correlated with spontaneous activity and successful item recollection (Vincent et al. 2006). The MPFC and medial OFC turn out to be important pieces in autobiographical memory and self-referential processing, besides belonging to the Default Mode Network (Cabeza et al. 2004; Cavada et al. 2000; Eleanor A. Maguire and Mummery 1999; Zhou et al. 2008) The PHC represents a direct gateway for the Neocortex, as documented by Diffusion Tensor imaging (Powell et al. 2004; M. P. Witter et al. 2000) and neurological studies (Talamini et al. 2005). The Fornix, a structure of white matter belonging to the Limbic system, is generally considered as the main relay of Hippocampal connections. Its activity has been extensively linked to memory performances both in animal models (Douet and Chang 2015; Gaffan 1994) and humans patients affected by neurodegenerative diseases, such as Alzheimer’s disease. In addition, in psychiatric disorders, such as schizophrenia, where studies using diffusion-tensor-imaging showed marked abnormal Fornix connectivity (Kubicki et al. 2005; Kuroki et al. 2006). Further, CA1 and the subicular area exchange projections with the baso-lateral Amygdala, with which share convergent excitatory and inhibitory inputs to the medial OPFC (R. P. Kesner et al. 1996; Baldwin, Sadeghian, and Kelley 2002). Ventral CA1 has also been shown to connect with hypothalamic periventricular area, which is implicated in autonomic and somatic responses, like digestion, reproduction and defense (Dong et al. 2009). Interestingly, the posterior cortical nuclei of the amygdaloid complex, a region that in rats receives pheromonal information from the olfactory bulb, also projects to the hypothalamus as well as to CA1 and proximal Sb, suggesting another pathway through which Amygdala’s activity may affect memory formation (Kemppainen, Jolkkonen, and Pitkänen 2002; Petrovich, Canteras, and Swanson 2001).

5.2 Hippocampus - internal connectivity

Focusing on the internal connectivity of the hippocampal formation, the general direction is circular although several backward streams are present. The starting area is the Dentate Gyrus, whose granule cells heavily projects to the pyramidal neurons in CA3 through the so-called mossy fibers (Lim et al. 1997). Although not so well known, backward connectivity to multiple strata of DG has been observed (David G. Amaral, Scharfman, and Lavenex 2007; Blaabjerg and Zimmer 2007). In addition, CA3 is well known for its substantial recurrent structure that confers self-association properties. Next, CA3 innervate CA1 via Schaeffer’s collaterals, which target both interneurons and pyramidal cells. On the other hand, ascending retro-projections from CA1 are weak or absent, although inhibitory feedback from CA1 to other Hippocampal sub-regions was observed from a small subset of GABAergic

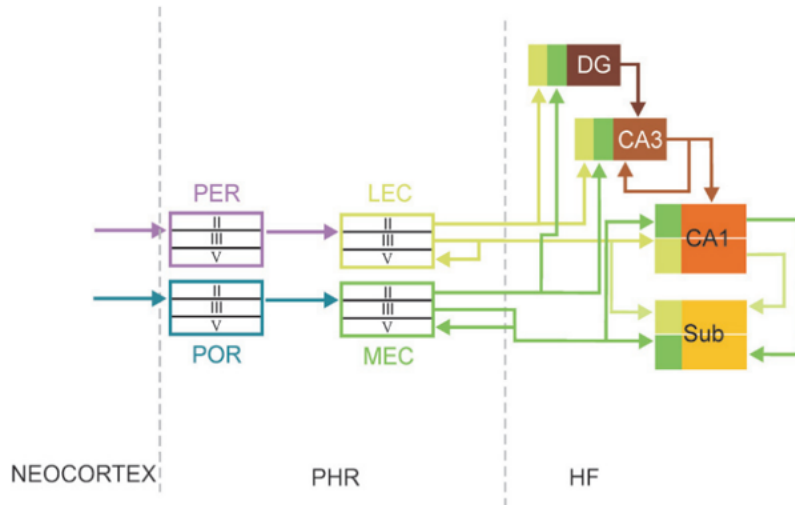


Figure 7: **Projections from the Rhinal Sulci to the hippocampal formation** - where: DG *Dentate Gyrus*, CA3 *Cornu Ammonis 3*, CA1 *Cornu Ammonis 1*, Sub *Subiculum*, LEC *Lateral Entorhinal Cortex*, MEC *Medial Entorhinal Cortex*, PER *Perirhinal Region [Cortex]*, POR *Post-Rhinal Region*, PHR *Para-Hippocampal Region [Cortex]*, HF *Hippocampal Formation* - from Menno P. Witter 2010.

neurons (Cappaert, Wadman, and Menno P. Witter 2007; Kajiwara, Wouterlood, et al. 2008; Megías et al. 2001). Recurrent connectivity in this area has been documented, but it is modest compared to that in CA3. Thereafter, projections from CA1 to Sb are robust and generally target opposite parts: proximal to distal and vice-versa. From SB, the feedback to CA1 is weak and not sufficiently detected, while its main destination, together with parts of the CA1 outputs, is layer V of the Entorhinal Cortex as well as back-projections also directly to the Perirhinal and Para-hippocampal Cortices, mainly from the Pre and Para-subiculum (Mulders, West, and Slomianka 1997). Figure 7 shows the internal Hippocampal connectivity as well as the principal afferences from the medio-temporal cortex and EC. For a quality in-depth illustration of the connectivity structure, we highly recommend the review “Connectivity of the Hippocampus” (Menno P. Witter 2010).

5.3 A computational model of Hippocampal dynamics

Among the models that have been developed to describe the neuroanatomical pathways involved in Episodic memory (REFs??) we have chosen to focus on the one developed by Edmund Rolls, who applied a computational approach to the understanding of Hippocampal functioning (Edmund T. Rolls 2010). He proposed a theoretical model explaining a variety of features at play. The motivation behind the description of this theoretical model is to propose an integration of the neuroanatomical connection provided in the previous paragraph. According to Edmund Roll’s model, the entrance is EC, as described before, gating high-quality information about the experience coming from the Neocortex. The next passage is DG, whose granule cells projects to pyramidal CA3 neurons with a rather low ratio, around 50:1.

Further, the DG is well known to exhibit active neurogenesis also in adult brains (Cameron and McKay 2001; McDonald and Wojtowicz 2005) a phenomenon that, coupled with the seemingly random connectivity with downstream CA3 neurons and competitive learning, allows an effective orthogonalization of the Neocortical inputs and makes the DG earn the role of “pattern separator” (Jill K. Leutgeb and E. I. Moser 2007; Jill K. Leutgeb, S. Leutgeb, et al. 2007; Santoro 2013). The effect of this input separation is pivotal for maximizing the downstream storage capacity and improve the ability to discriminate different experiences. Then, in the next step, there is the first formation of a trace linking together aspects of the episode that have been separated until then, encoding spatial and object-related information. CA3 is usually pictured as a continuous attractor network, whose dynamics heavily rely on its large number of recurrent connections, around 10’000 per cell (Cerasti and Treves 2013; Miles et al. 2014). In practice, after the imposition of a specific neural firing pattern, initially retained as a short-term memory, it is consolidated through long-term potentiation (LTP). The following stage is represented by CA1, receiving streams from the Schaffer collaterals and the Perforant Path. Some of the computational functions of this area have been proposed as recording memory traces and facilitating retrieval. For these properties, the features that could support it are: associatively scalable connections from CA3, minimizing information loss; propagation and expansion of input patterns over a large number of cells, aided by the larger size of CA1; and the abstraction and chunking of sequential patterns through competitive learning, which would facilitate retrieval in the sense that fewer cells would be needed to represent temporal patterns.

6 Conclusion

The formation of an episodic memory trace is the results of the activity of a large number of regions.

6.1 A schematic model

Figure 8 above illustrates the emerged connectivity delineated in this review. Information about objects and people flows from the higher stages of the ventral sensory areas and generally converges in the PRC (35 and 36 Broadman areas), where it gets combined with top-down data coming from the Frontal lobe and emotional valence from the Amygdala, as showed in figure above in orange. These inputs enable the PRC to produce an enriched representation of the objects in an episode, the episodic *what*, as it is pictured by the PMFC model in 2.2. Similarly, spatial information travel from the sensory dorsal pathways towards the PHC (TH and TF areas), where it is fused with other cortical contribution from Default Mode Network’s components (such as RSC and OPFC, blue in the figure), and provides a fine elaboration of the contextual features of the environment, the episodic *where* and partially the *when*, and the ground for scene perception. Eventually, the functional roles of these two Rhinal regions are becoming better understood, with the main directions being a high-level abstract representation of environmental features for use in spatial navigation, memory processes, sense of self (relying on the Default Mode Network), social cognition and other cognitive functions requiring enriched representations. The PRC and the PHC were placed respectively inside the Anterior Temporal System and the Posterior Temporal System.

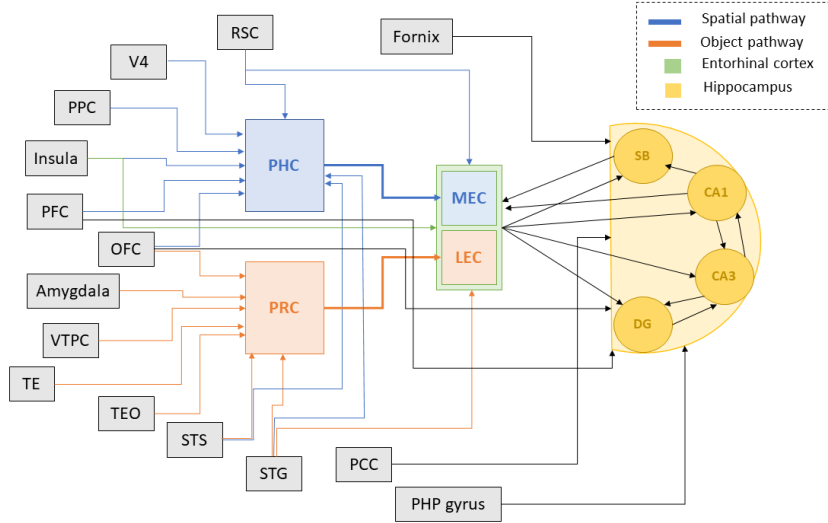


Figure 8: **Diagram of the input streams to the Hippocampal formation** - SB Subiculum, CA1 Cornu Ammonis 1, CA3 Cornu Ammonis 3, DG Dentate Gyrus, MEC Medial Entorhinal Cortex, LEC Lateral Entorhinal Cortex, **PHP gyrus ??**, PCC Posterior Cingulate Cortex, STG Superior Temporal Gyrus, STS Superior Temporal Sulcus, TEO TE temporal regions, VTPC Ventral Temporo-Parietal Cortex **missing ref**, OFC Orbito-Frontal Cortex, PFC Pre-Frontal Cortex, PPC Posterior-Parietal Cortex, RSC Retro-Splenial Cortex - Only the moderate-strong connections have been considered; acronyms same as before, **reciprocal connections are not mentioned for clarity**

Continuing the journey downstream, from the Rhinal cortex, the information is passed to EC (green in the figure), where the spatial and object data remain separated. The MEC receives projections mainly from the PHC and it constitutes an additional stage in spatial processing and context memory, thanks also to the presence of grid-cells, the precursors of the Hippocampal place-cells (Neher, Azizi, and Cheng 2017). **Thus, this Para-hippocampal route provides the elements for answering the *where* of an episodic memory, defining its spatial content.** Meanwhile, the LEC has afferent connections from the PRC and it further elaborates information about the object and it starts to link spatial and contextual data. **As such, this route could account for the *what* part of an episodic memory, as it provides an high-level and multi-dimensional picture of the items at play.** However, the mechanisms accounting for the *when*, namely the temporal features, turned more subtle to identify. The encoding of the sequence of events is thought to be partially propagated by means of the population behaviours like the theta-gamma code, network-level synchronizations where spatial cells fire in specific order, and neuron-level behaviours like phase precession, a shift of timing of the firing activity. Both these properties are shared by MEC and Hippocampal neurons.

Finally, objects, context and locations arrive in the Hippocampus formation, the yellow semi-circle, where in a few words they get orthogonalized in the DG, effi-

ciently merged in CA3, re-coded in CA1, and then returned to the Neocortex via the Fornix, with feedback connections to the upstream input areas.

6.2 Interest in a deeper comprehension of network connectivity and dynamics in encoding Episodic memory

Memory, and episodic memory especially, plays an essential role in our mental life. It is at the centre of a plethora of important cognitive processes ranging from decision-making to language and abstract reasoning. By means of the deep connections of the areas involved in its formation with cerebral networks devoted to perception and emotions, memory has a lot to do in the construction of our personal identity, the self, and our interaction with the external world (Williams, Conway, and G. Cohen 2008). Gaining a better comprehension of its development could have a great impact on sectors such as Neuropsychology, where it could provide a wide framework to favour the tracking of some aspects of the cognitive decline in neurodegenerative diseases. In this regard, well known are the marked memory deficits in Alzheimer patients, about which some studies have individuated part of the causes in the atrophy of the medio-Temporal cortex and their lead in impairing the formation of new episodic traces (Carlesimo and Oscar-Berman 1992; Chan et al. 2001; Wenk 2003). Likewise, in Parkinson’s disease patients the impairments in memory have been traced back to atrophy right in the Hippocampal core, in CA3 and CA2 (and to a lesser extent in CA1 and Sb), pivotal components for encoding and recollecting old episodes (Das, J. J. Hwang, and Poston 2019; Economou, Routsis, and Papa-georgiou 2016; La et al. 2019).

Moving on more computational fields like Cognitive Science and AI, having an insight of how the brain implements its one-shot learning algorithm would be an invaluable treasure for building machines more efficient in terms of time, energy, and memory requirements (Lake et al. 2011; S. W. Lee, O’Doherty, and Shimojo 2015; Thompson et al. 2020). Moreover, a fast learner should be much more flexible and able to generalize better to new domains (transfer of knowledge). Current Machine Learning is still struggling in finding effective strategies to do this, and instead requires incredibly large training datasets (thousands or millions of inputs) and a considerable amount of time. Although some solutions found so far might be claimed capable of learning a new object class or task in one go (Romani, D. J. Amit, and Y. Amit 2008), most of the times, they eventually rely on special training tricks that do not exactly configure in a one-shot learning paradigm as genuine as the biological brain does (Bertinetto et al. 2016; Vinyals et al. 2016). Maybe the solutions rely in the spiking neural network approach, closer to the real brain environment, and some promising solutions in this direction have been devised (Edmund T. Rolls, Tromans, and Stringer 2008). Combining more sophisticated network architectures might allow developing optimal training procedures.

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