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A current model of neural circuitry active in forming mental images

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My aim here is to formulate a compact, intuitively understandable model of neural circuits active in imagination that would be consistent with the current state of knowledge, but that would be simple enough to be able to use for teaching. I argue that such a model should be based on the recent idea of "concept neurons" and circuits of 2 separate loops necessary for recalling mental images and consolidation of memory traces of long-term memory. This paper discusses the role of the hippocampus and temporal lobe, emphasizing the essential importance of recurrent pathways and oscillations occurring in the upper layers of hierarchical neural structures, as well as oscillations in thalamo-cortical loops.

The elaborated model helps explain specific processes such as imagining future situations, novel objects, and anticipated action, as well as imagination concerning oneself, which is indispensable for the sense of identity and self-awareness.

I attempt to present this compact, simple model of neural circuitry active in imagination by using some intuitive, demonstrative figures.

Key words: **imagery • imaginary • imagination • episodic memory • working memory • short-term memory • top-down pathways • concept neurons • recurrent axons • hippocampus**

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Background

Imagination is a fundamental element of the most important cognitive processes such as remembering previously perceived objects, situations, formerly performed movements, and complex activities. It is necessary for problem solving, imagining and planning of social interaction, and all kinds of creativity. Remembering fragments of autobiography is also essential for the sense of identity and self-consciousness.

The number of papers devoted to formation of mental images has grown in recent years, but most naturalists, physicians, and scientists lack a theoretical model of neural circuits active in process of forming mental images. An understandable theory of this process is necessary to explain how the brain works. Such a model of neural circuits should be formulated and shared, especially for educational purposes [1].

Therefore, in this paper I present such a model by means of some figures. The 3 assumptions necessary for the consideration of these figure are: 1) recognition of the existence of 'object neurons', 2) the distinction of 2 different neural loops involved in mechanisms of memory, and 3) recognition of the significance of recurrent pathways (top-down connections) that enable recurrent excitations (oscillations) between the upper and lower levels of hierarchical structures.

Of course, these assumptions should be based on proven data about neural networks; therefore, we should bear in mind several previous findings on perception and recall of data from memory. The reader should be warned that the review of conclusions from recent experimental research may appear to be an unconnected set of facts and opinions, because these authors were not focused on a general theory of the imagery forming process. Therefore, I treat the elaborated figures as a link between these statements of experimental researchers and the theoretical model of mental imagery that I formulate

in this paper. The presented figures are, however, in line with the conclusions of the cited experimental papers.

Remarks About Object Neurons – The Highest Neurons of Hierarchical Neural Circuits Creating Perceptions

Advocates of the existence of object neurons, which represent particular known objects such as an apple, an orange, a face, and so forth, have been engaged for many years in a dispute with the adherents of more diffuse models of neural structures. Arguments for the existence of high-level 'object neurons' were made by several researchers [2–6]. Mishkin and Quiroga – supporters of the idea of existence of such 'object' or 'concept' neurons – have even expressed their convictions in popular science journals such as *Scientific American* [7,8]. For the visual 'objects', these neurons are located in the anterior part of the temporal lobes [4,5]. Thus, the visual pathways do not end in the occipital region, but are prolonged by superior structures placed above the occipital lobe. From the anatomical point of view, the visual pathways are bent, aimed towards the anterior parts of the temporal lobes and parieto-occipital cortex (Figure 1).

We should, however, additionally remember that according to the results of neurosurgical experiments performed by Ungerleider and Mishkin, both visual pathways generate visuospatial functions in still higher layers by means of the parieto-occipital cortex [10].

The idea of 'object neurons' is not inconsistent with the diffuse model of data processing, because any given object is represented by many such highest-level neurons, which constitute a set of multiple representations of the object. Parallel processing is also enabled by structures representing different aspects of the same object, such as shape, size, color, or texture, illustrated intuitively by Figure 2.

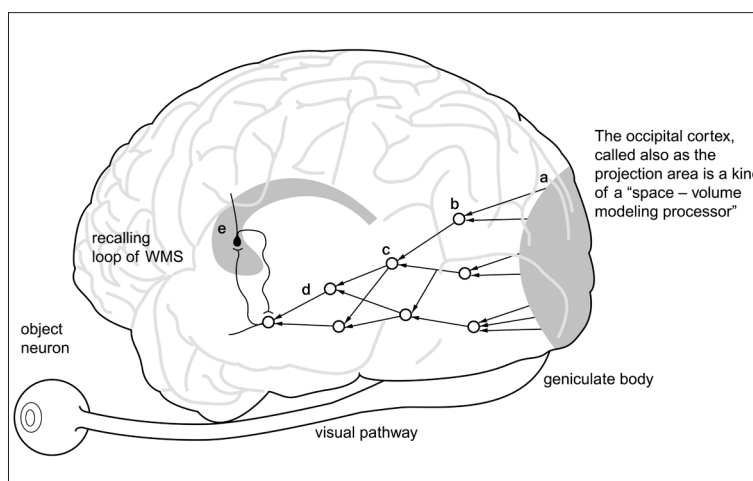


Figure 1. The visual pathways does not end in the occipital region, but is prolonged by superior structures placed the anterior part of the temporal lobe, where so called 'object neuron or concept neuron' can be found. These neurons are connected with the recalling loop of the working memory system.

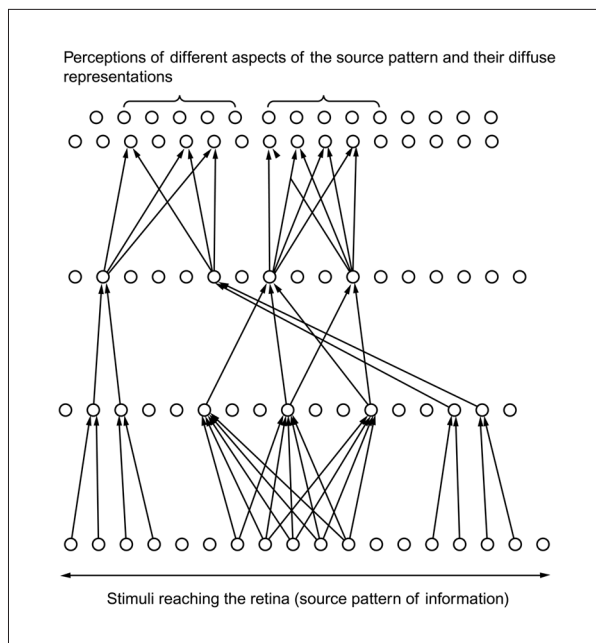


Figure 2. The perceived object is represented by multiple 'object or concept neurons', which are functionally equivalent. We should realize, that apart of this multiple representation some different aspects of the object, such as shape, size, color or texture are perceived, as result of the parallel processing.

Two Loops in Neural Circuitry: For Consolidation of Memory Traces of The Long-Term Memory and for Recalling Mental Images

Many years ago Brenda Milner found that neurosurgery performed on the hippocampus caused a profound and irreversible deficit of recent memory. Patients lost the capacity to form new long-term memories, but previously acquired long-term memories remained intact. Many years later she repeated her experiments [9]. It was later discovered that some hippocampal neurons exhibit 'long-term potentiation'. This means that long-lasting enhancement in signal transmission between 2 neurons occurs, which results from stimulating them synchronously.

If such neurons form a loop with certain cortical "object" or "concept" neurons, the circuit can easily fall into oscillations. The phenomenon of self-sustained, repetitive oscillations after the activation of an object neuron is important for consolidation of memory traces and also for recalling mental images [11,12].

Neurosurgical experiments performed on monkeys, however, proved that there are 2 separate but cooperating loops involved in the mechanism of memory [2]. The first loop, based on the hippocampal neurons, is necessary to maintain the arousal of a mental image activated from the side of the speech area.

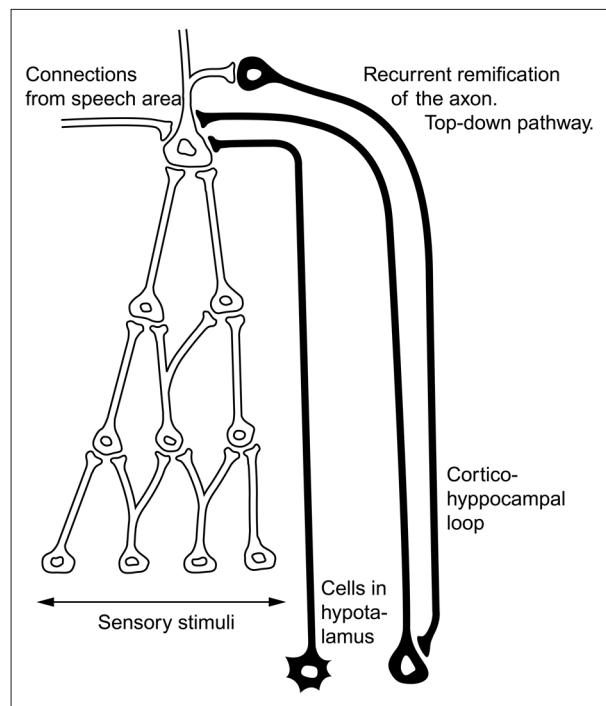


Figure 3. Two kinds of connections reach so called 'object neurons'. One of them, going from the side of hypothalamus and amygdale is active in the case of emotional arousal and take part in the consolidation of the long- term memory traces. The second connection constitutes the oscillating loop, which cause that the evoked mental image is aroused for the time necessary for the action of the working memory.

These loops are essential for short-term memory, also referred to as episodic memory or as recalling data from the working memory system. The second loop involves neurons situated in hypothalamic structures, especially in the amygdales nuclei. These structures are known as centers of emotional phenomena. The activation of the cortex- hypothalamic (limbic) loops is necessary for the consolidation of memory traces, leading to the formation of long-term memory. These loops are illustrated intuitively in Figure 3.

Details of the functional neuroanatomy of these 2 subsystems are not yet precisely defined. Considerable progress has been possible since the implementation of imaging methods based on fMRI. The authors of early papers based on fMRI indicate that the regions important for the working memory are the amygdale, hippocampus, and the temporo-parietal and parieto-frontal systems, as well as the right inferior frontal gyrus [13–15].

Some authors argue that important distinctions exist among different types of memories and the structures that mediate them [16]. Considerable effort has been made to understand the autobiographical memory and to distinguish it from the more elementary episodic and semantic memory [17].

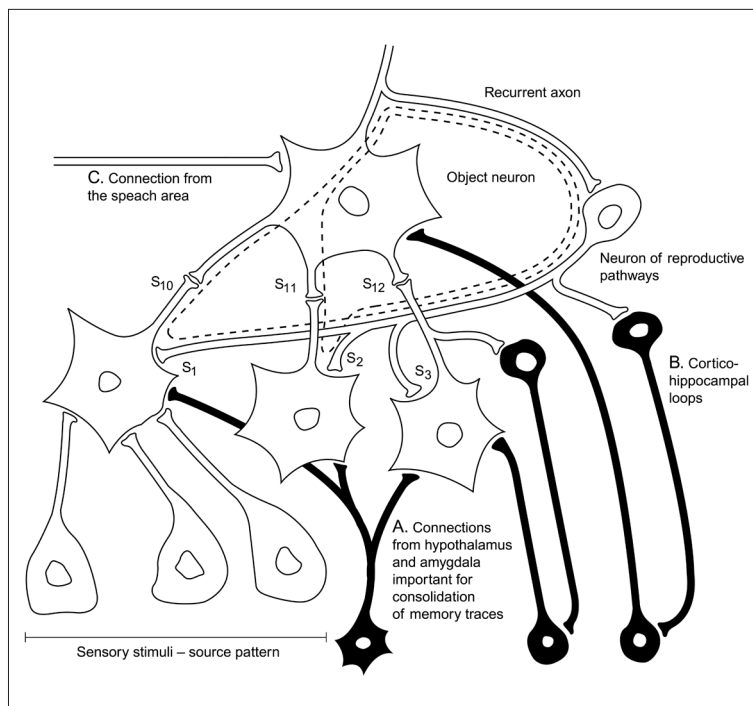


Figure 4. Three layers of the hierarchical structure of neurons integrating sensory information, for instance – in the visual pathways. The traces of long term memory are consolidated under the influence of connections from hypothalamus and amygdala (A). There are consolidated through two mappings: weights of receiving, ascending synapses (s_{10} , s_{11} , s_{12}) and synaptic weights of reproducing connections (s_1 , s_2 , s_3). The second, cortico – hippocampal loop (B) is necessary for temporary recalling of the mental image. The activation of the object neuron by this indexing loop causes the recurrent reactivation of neurons in lower layers. The dotted line indicate the pathways of repetitive circulations of stimuli in the upper layers of the hierarchical structure, what is the essence of mental imagery. The object neuron can be activated also from the side of speech area (C). Mental imagery is the essence of episodic memory, short term memory and is used for working memory activity.

The authors of the most recent works used sophisticated methods based on event-related fMRI, searching for regions that share a common pattern of functional connectivity [18]. Some evidence has emerged recently for the existence of parallel temporal-diencephalic pathways that function in a reciprocal manner between the hippocampal formation and the anterior thalamic nuclei. These extended pathways also involve the mammillary bodies, the retrosplenial cortex, and parts of the prefrontal cortex [19].

In my opinion, however, for educational purposes, information about the anatomical structure of the memory system should be presented in a simplified way, as in Figure 4.

Understanding the existence of at least 2 different loops involved in the consolidation of memory traces and the retrieval of mental images is aided by an appropriate understanding of functional concepts of the workings of the long-term and short-term memory.

The juxtaposition of long-term and short-term memory is important from the functional side, but we should understand that the same neuro-anatomical elements are engaged in both memory activities. Careful study of the presented figures will aid comprehension of this structural overlapping.

Figure 4 helps explain why we can say that the same structural elements are engaged in both long term and short-term memory. Memory traces essential for the long-term memory are formed by synaptic weights of afferent connections and recurrent pathways. In the moment of repeated perceptions, these

traces enable recognition of the pattern as one that is known. The upper layers of the same structure can be activated from the speech area. A sequence of words (e.g., some sentences) causes the activation of a set of object neurons representing an unknown or unusual configuration of objects and can constitute a problem that should be solved. The working memory maintains activation of this unusual configuration of an imagined object. The result of this manipulation, for instance finding that some objects are linked or related, can be memorized, but very often only for a short period of time. Therefore, we use the notion of the short-term memory.

The Neural Circuitry Necessary for Creating Mental Images

Early data obtained by means of neurological findings [20] and neural imaging confirmed that “the visual imaginary and visual perceptions rely on the same neural substrate” [21–24]. Researchers using psychological methodology draw similar conclusions [25–27].

A very important phenomenon essential for understanding the nature of creating mental images is the oscillation between neurons of the upper and lower levels of hierarchical structures creating perceptions; therefore, we should pay considerable attention to their occurrence.

The importance of top-down pathways in creation of mental images has been recognized for several years [28]. Marcel Mesulam, in an early theoretical review paper, wrote: “Many aspects of cognition may represent an iterative neural dialogue between sensory-fugal connections, which reflect the physical nature of ambient events, and sensory-petal connections, which infer the nature of the stimulus based on empirical accounts of past experience. These reciprocal pathways, embedded within the internally generated oscillations of the brain, are further modulated by top-down projections from high-order association cortices, most prominently located in prefrontal cortex. This set of top-down projections has the capacity to transcend experience-based representations and to insert internally generated priorities into the interpretation of ongoing events” [28]. Gilbert and Siegman expressed similar opinions in their review papers, but they emphasized the role of cortico-thalamic top-down influences [29]. Fietta, in a subsequent review paper, wrote: “Top-down projections from high-order associative cortices confer the ability to transcend experience-based representations, promoting individually-sculpted interpretations, as well as mental imagery, thought, and abstraction” [30]. This is a rather metaphorical dictum. A more concrete neurophysiological sense has been accorded to the phenomenon of oscillations. Zhang, in a previously mentioned review paper, stated that rhythmic neural activity exists all over the nervous system, in structures as diverse as the cerebral cortex, hippocampus, subcortical nuclei, and sense organs [11]. The theoretical review of known kinds of oscillations, as presented by Zhang, stresses the importance of top-down recurrences that occur between neurons in CA1 layers of hippocampal neurons and cerebral cortex for recall of data from memory [11].

A more recent experimental paper by Whitman et al. [12] pointed out that the fMRI-BOLD study is only able to capture states changing relatively slowly. They stress that the study of oscillations of significant importance in mental imagery should try to combine this technique with simultaneous EEG, MEG, and electrocorticography (ECoG) recordings, which have much higher temporal resolution. These authors are convinced that low- and high-frequency oscillations work in concert, coordinating neural activity into whole-brain functional networks [12].

It appears that oscillations between higher level neurons and lower level neurons of hierarchical structures have an essential character. This was appreciated and carefully discussed by Lou et al. [31], which I discuss in the subsequent paragraphs of this paper dealing with self-image and self-awareness.

To comprehend the importance of oscillations between subcortical structures (hippocampus, thalamus) and the cerebral cortex – for teaching purposes – it is useful to consider Figures 3 and 4.

Almost all cortical neurons have recurrent axons. This was demonstrated by Carpenter’s histological pictures of the

cytoarchitecture of the cortex. These ramifications are necessary to start top-down pathways to activate the lower levels of the hierarchical structures at the moment of the stimulation of an object neuron from the side of the speech area or during complex mental processes, especially problem-solving. When the neuron of a known object is stimulated, next the activation returns – by means of recurrent axons or generally by reproductive pathways – to lower levels of the hierarchical structure, consolidated previously during perceptions and the learning process. Downward activation can even proceed to a lower projection level, such as the occipital cortex, causing vivid dreams or hallucinations.

When such a structure is activated from below by repeated perceptions, the object neuron is further stimulated by the cortex-hippocampal indexing loop. Thus, the structure of a known, recognized object is stimulated from 2 directions. When the object neuron is stimulated from the speech area, the mental image (a remembrance) is recalled. The neural mechanism of the mental imagery consists in the circulation of impulses up and down along superior levels of the hierarchical structure, which is maintained by the cortex-hippocampal indexing loops (see Figures 3 and 4).

It is also necessary to be aware that in the above-mentioned neuronal hierarchical structures active in recognizing objects, there are neurons that recognize situations and are active in additional aspects of perception such as spatial relations. Remembrances of a complex situation can be recalled from the memory by words such as “travel”, “holidays”, “harvest”, “wedding”, and “dancing”.

The excitation of such complex imagination begins from activation of neurons located above the temporal lobes. Greenberg et al., Bartolomeo, Deselaar et al., and Huijbers et al. proved that the regions of the brain active during complex mental imagery are: the hippocampus, posterior cingulate cortex, medial, dorsolateral, and ventrolateral prefrontal cortex, angular gyrus, dorsal and ventral precuneus, anterior and mid-cingulate cortex, and supramarginal gyrus [15,22–24].

Imagining Future Situations

We can recall from the memory different mental images, but it is possible also to imagine future situations that are more or less probable and we can imagine a novel object that we have never seen before. The implications from theoretical considerations indicate that imagining future situations and objects not seen before is accomplished through the use of elements of previous perceptions. Probably the working memory system of the brain performs the configuration of previously experienced elements and creates the design of neural circuits

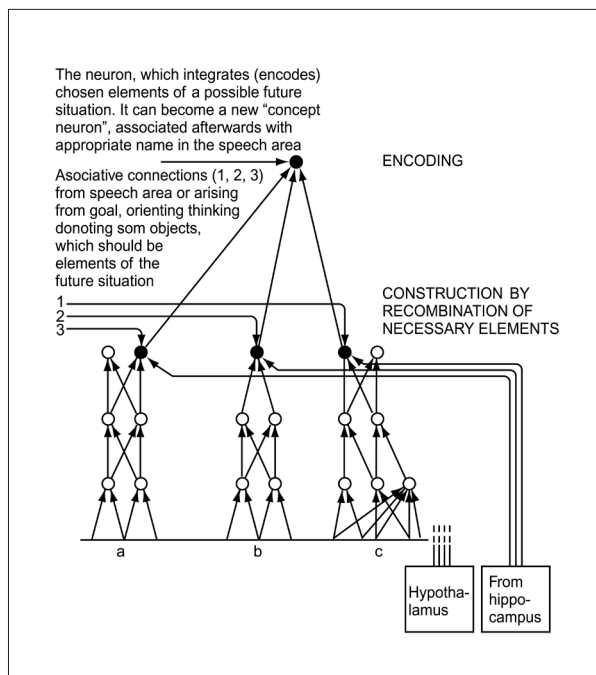


Figure 5. Intuitive illustration of the process of so called construction phase of the imagination of a future, possible situation. The working memory system (mainly left hippocampus) is accessing the episodic memory and recombine appropriate details. Afterwards mainly the anterior part of the right hippocampus encodes the pattern of a possible future situation. The encoding consists on alignment of elements, their integration and memorization at least for a certain period of time.

that constitute this kind of imagery. An interesting question is whether contemporary experimental findings confirm these theoretical assumptions.

Location of neural substrates for past and future events

Recently some researchers attempted to determine the location of neural substrates that are involved in such cognitive processes on the basis of sophisticated imagining techniques like fMRI and connectivity studies.

These studies also attempted to determine which neural substrates are involved both in recalling past events and imagining possible future situations. One of first studies to establish common and distinct neural substrates for both remembering past events and imagining future situations was done by Okuda et al. [32].

It is now established that both remembering past experiences and imagining future events rely on a common network of brain regions, including medial prefrontal, medial and lateral parietal, and medial and lateral temporal regions, along with

posterior visuospatial regions and the left hippocampus [33–36]. However, despite this overlap, the right anterior hippocampus is preferentially engaged by imagining future events in comparison to remembering past events [33,37,38].

Phases of imaginative processes

Recently, several phases of imaginative processes have been discerned. Usually the construction phase and the elaboration phase of the imagery are discerned. The recall of the past event is elicited by sentences like “Remember visiting the Eiffel Tower in Paris” and imagining a future situation by a sentence like “Envision the birth of your future child”.

Participants in an experiment by Addis et al. were cued with a noun for 20 seconds and instructed to construct a past or future event within a specified time period (a week, a year, or 5–20 years) [33]. Once participants had the event in mind, they pressed a button and for the next 20 seconds elaborated on the event. The elaboration of the constructed event consisted of retrieving and generation of as many details of the mental image as possible. The researchers, using fMRI techniques, tried also to determine which neural centers are involved in the implementation of these distinguished phases of the imaginative process [33,37]. They concluded that future event construction mainly engaged the right hippocampus. In contrast to the construction phase, elaboration was characterized by a remarkable overlap in regions comprising the autobiographical memory retrieval network engaged during elaboration, including self-referential processing and contextual and episodic imagery. They also emphasized the finding that amnesic patients exhibit deficits in both past and future thinking, which confirms, according to these authors, that the episodic system contributes importantly to imagining the future.

A detailed discussion on the essence of the constructions of images of future situations was provided by Schacter [39]. In the present paper, I try to illustrate the process of the “constructing of the future situation” by means of intuitive, demonstrative, didactic Figures 5 and 6.

Significance of the hippocampus

The role of the hippocampus in imagining the future is important, but its function is very specific. Martin et al. performed a functional fMRI study and concluded that the hippocampal activity associated with imagining may reflect the encoding of a future event, not its construction [40]. This study was conducted by asking the participants to imagine the future events in response to person, place, and object cues. A post-scan recall test can determine whether an imagined future event was successfully encoded or not, it means if it was memorized efficiently [40]. A comparison of successfully and unsuccessfully

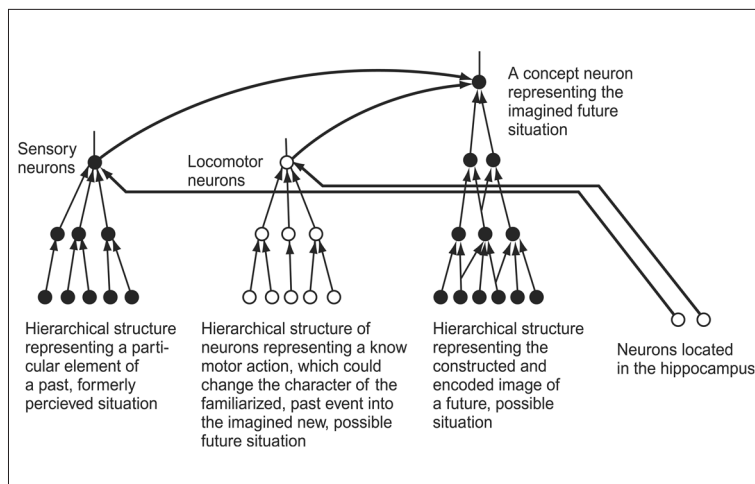


Figure 6. The process of elaboration of the image of a possible, future situation. The construction consists on selection of neurons representing images of past events and of structures responsible for movements and actions, which are able to transform the known, past situation.

encoded events revealed anterior and posterior right hippocampal clusters. When imagined events were successfully encoded, both anterior and posterior hippocampus showed common functional connectivity to a network including parahippocampal gyrus, medial parietal and cingulate cortex, and medial prefrontal cortex. When encoding was unsuccessful, only the anterior hippocampus, and not the posterior, exhibited this pattern of connectivity. These findings demonstrate that right hippocampal activity, observed during imagination of the future event, may reflect the encoding of the simulations into memory. This function is not essential for constructing future scenarios and may explain why some patients with hippocampal damage are still able to imagine the future. The authors maintain that their study provides a more comprehensive understanding of hippocampal contributions to the construction and encoding of detailed future simulations. They localized 2 regions of the right hippocampus involved in this process: 1 anterior and 1 posterior, with the connectivity between these and with other parts of the core autobiographical network being particularly necessary for successful encoding [40].

A growing body of research on hippocampal function suggests that its action is important for implementing the schemes and building material for goal-oriented thinking and problem solving. I illustrate the mechanisms of this activity by means of Figures 7 and 8.

Addis et al. wrote that hippocampus function is more important for imagining the future than for remembering the past [37]. They maintain that it is possible that this hippocampal activation retains for a period of time the recombining details into coherent scenarios and facilitate the encoding of these scenarios into memory for later use. These authors developed a new framework that highlights 3 component processes of the constructions of a future possible event: accessing episodic details, recombining details, and encoding simulations. The authors maintain that different component processes of the

simulation of the future may be differentially affected by hippocampal damage [37].

Recombination for the formation of a novel future event

Zeithamova et al. emphasize the role of the hippocampus in inferential reasoning – the ability to form relationships between items or events that were not experienced together [41]. Intuitively, inferential reasoning can be treated as the process by which elements of individually existing memories are retrieved and recombined to answer a novel question. Zeithamova et al. argue that such flexible retrieval is performed by the hippocampus using special hippocampal encoding mechanisms. The hippocampus is able to create newly formed and existing memories [41].

According to Zeithamova et al., such integration would underlie the formation of networks of related memories that extend beyond direct experience to anticipate future judgments about the relationships between items and events. Such integrative encoding enables the hippocampus to form schemas and prospective concepts. Thus, created and encoded memories are actively constructed to anticipate future decisions and actions [41].

The authors of many of earlier works on remembering past events and construction of possible future events confined their research to considerations of episodic memory. However, results of recent research suggest that the recall of past events and the construction of possible future events involve utilization of resources of semantic memory [42,43].

Significance of temporal lobes

The hallmark of amnesia is the inability to remember autobiographical experiences from the past. Neuroimaging studies and data from amnesic patients indicate that the medial

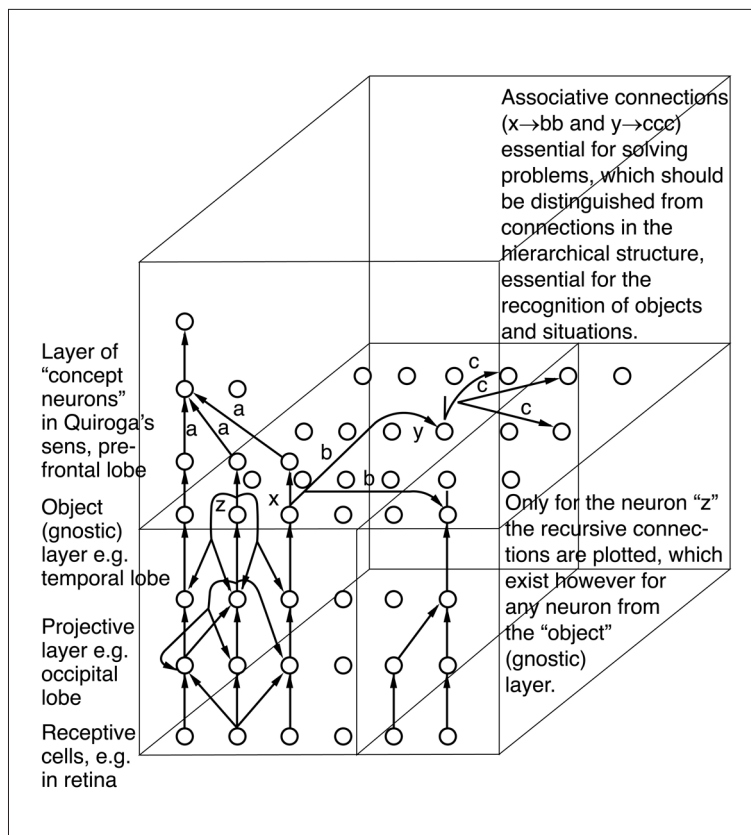


Figure 7. The hippocampus (working memory system) realize goal oriented thinking and problem solving, what requires the use of associative connections that are here marked in the horizontal plane as opposed to perceptive hierarchical structures seen here in the vertical plane.

temporal lobes play an important role in retrieving and recombining details from memory in the service of novel simulations. Impaired retrieval and recombination of details may lead to impairments of both episodic and semantic memory. It seems that the medial temporal lobe contribute to scene construction and the process of mental time travel [44].

Weiler et al. maintain that future thinking (i.e., the imagining of novel events) requires the recombination of stored elements into a new event [45]. It requires additional resources that are not shared by episodic memory. These authors examined 2 patients with lesions in the medial dorsal thalamus. This nucleus of the thalamus is involved in executive aspects of memory (strategic retrieval), which are presumably more important for future thinking than for episodic memory. The authors found that the patients' descriptions of novel events lacked content and spatio-temporal relations. Considerations of the characteristic features of this deficit lead to the conclusion that is unlikely to attribute this deficit to disturbances in self-projection, scene construction, or time concept. According to the authors, it can be explained by a deficit in recombination of stored elements into a new event [45].

Significance of the "default-mode network"

Interesting links were found between the structure and function of neural circuits active in the recall of mental images and

reconstruction of past events, as well as the construction of future situations and the function of the "default-mode network". Ostby et al. emphasized that a core brain network engaged in remembering the past and envisioning the future shares neural substrates with the default-mode network. These authors promote the intriguing hypothesis that default-mode activity, measured at rest, is related to performance in separate attention-focused recall and imagination tasks [38]. They showed that functional connectivity of the default-mode network in children and adolescents is related to the quality of past remembering and future imagination.

They concluded that that mental time travel is modulated by the task-independent functional architecture of the default-mode network in the developing brain.

Imagery of Novel Objects Not Yet Perceived, and Planned, and Anticipated Action

In describing the neural substrates active in imagination of future events, we take into account the "phase of the construction" of the mental image. Certainly, neurons participate in such construction, which represents relational aspects of elements of the new situation, sometime the same that are active in application of grammar rules. It is assumed that neurons are

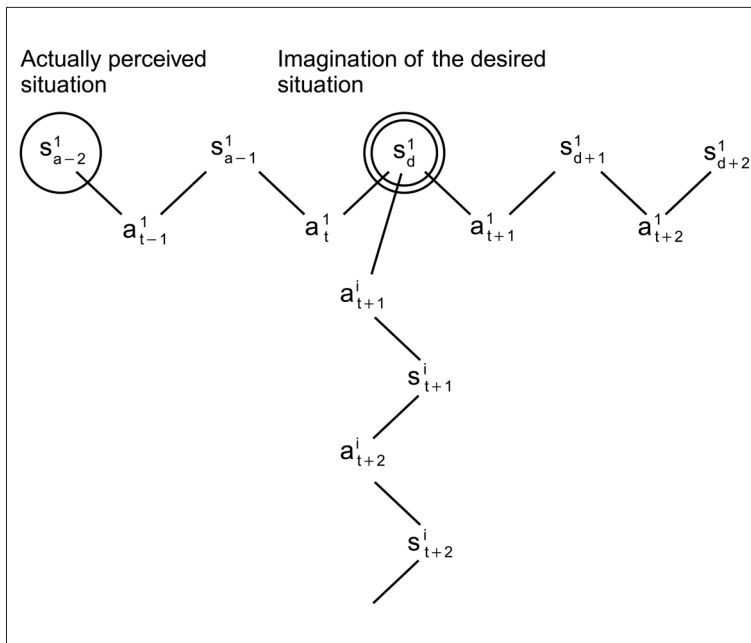


Figure 8. The functional, local map of the associative cortex. We attempt here to illustrate intuitively one of the mechanisms involved in problem solving. The juxtaposition of current and desired situation incites the configuration performed by the working memory system of a “chain of possible passages”. Triggering of nearby concept neurons, representing the current and desired situations stand out these neurons, which starts the search for a “chain of passage”. Working memory system is “looking for transitions” from $s_{(a-2)}^1$ to s_d^1 , by browsing “actions” $a_{(t-1)}^1 \dots a_{(t)}^1$ able to transform – step by step the actual situation (a) for a desired situation (d). It is necessary to realize that cortical neurons of the considered chain are depicted here as a map of the horizontal plane as opposed to perceptive hierarchical structures shown on the Figure 7 in the vertical plane.

active in the course of constructing the image of a future situation, which represents movements and actions necessary to pass from actual to planned future situations.

Planned, anticipated, potential actions are utilized neurons of these centers of the brain when imagining the future, which are involved during real movements of the body [46–50].

Hétu et al. performed a meta-analysis of 75 papers related to recent investigations of neural network involvement in motor imagery [46]. These authors concluded that motor imagery consistently recruits a large fronto-parietal network and some subcortical and cerebellar regions. They found that although the primary motor cortex was not shown to be consistently activated, the mental imagery network includes several regions known to play a role during actual motor execution [46].

Van Elk et al., in an fMRI study, investigated the neural mechanisms supporting the retrieval of the semantic knowledge of action [47]. A novel motor imagery task was administered when participants of the experiment were required to imagine planned actions with a familiar and unfamiliar object, either goal-related or grasp-related. Planning actions related to unfamiliar objects were associated with increased activation in the bilateral superior parietal lobe, the right inferior parietal lobe, and the right insula. The parietal areas are involved in motor imagery. The planning of familiar actions resulted in increased activation of the anterior prefrontal cortex. The authors concluded that action semantic knowledge is activated most readily when actions are planned in a goal-directed manner [47].

Marc Toussaint refers to different experiments on planned behavior [48]. He argued that nervous systems use internal models to perform predictive motor control, imagery, inference, and planning. He proposed the concept of a sensorimotor map to represent such an internal model. Such a map is similar to self-organizing maps but is inherently coupled to sensor and motor signals [48].

Paulus et al. considered how a novel functional object is represented in a neural substrate, highlighting the role of the action systems [50]. They investigated whether people are able to acquire object representations just by imagining the use of novel objects, taking into account that previous findings suggested that executed and imagined actions share a common representational format. The authors trained the participants in the experiment by use of novel objects in a motor imagery condition. Their findings suggest that motor imagery can facilitate the acquisition of novel object representations [50].

Beauchamp et al. argued that studies of the essence of the representations of different categories of objects, including tools, have spurred the development of the sensory-motor model of object concept representation [51]. They maintain that information about objects is represented in the same neural subsystems that are active during perception and in the course of its use. Authors highlight that it provided insight into the brain mechanisms of the utilization of a tool, when 3 types of information are important for identification: 1) “the characteristic motion with which they move, such as the up and down motion of a hammer, 2) their visual form, and 3) the way that they are manipulated” [51]. The authors suggest the existence of a mapping between specific brain regions and these fundamental

identifying properties of tools. They consider neuroimaging studies of the left posterior middle temporal gyrus. This brain region is active both when people perceive moving tools and when they answer questions about tools [51]. It is important that the authors try to explain how low-level receptive field properties could give rise to the high-level category-related representations observed in functional imaging experiments [51].

Considering the results of research on the neural representation of perceived objects and novel objects not seen before, it is worth noting the results obtained by Justa et al. [52]. They applied a simple experimental model based on obtaining fMRI scans after imagination, evoked by a noun, of simple visual objects like an apple or an orange. The authors discovered that any such simple imagined object has 3 representations: 1) possible manipulation, 2) shelter, and 3) eating. Each factor is represented in 3 or 4 brain locations that correspond to a cortical network active in non-linguistic tasks [52].

The idea of Just et al. was expressed similarly in earlier papers by Alex Martin [53] and Weisberg et al. [54]. Alex Marin wrote that evidence from functional neuroimaging of the human brain indicates that equally important are information about such properties of an objects what it looks like, how it moves, and how it is used. This information is stored in sensory and motor systems active when that information was acquired. So, concepts of objects belonging to different categories (e.g., animals and tools) are represented in partially distinct sensory and motor neural networks [54].

Weisberg et al. believe that our ability to identify everyday objects does not rely solely on information about their appearance [54]. They used fMRI to examine subjects given the task of matching pictures of novel objects before and after extensive training, which consisted on manual manipulations with different tools. After training, neural activity emerged in regions associated with the motion (left middle temporal gyrus) and with the manipulation of common tools (left intraparietal sulcus and premotor cortex). However, the activity is more focal and selective in regions representing their visual appearance (fusiform gyrus) [54]. The authors state that the distributed network is automatically engaged in support of object identification. They even suggest that as a result of training, these previously novel objects have attained the conceptual status of “tools” [54].

Image of Oneself, Sense of Identity, Autobiographical Memory and Self-Awareness

Considering the neural substrates of imagery, it is impossible to omit comments on the substance of the image of oneself, which is the basis of self-awareness and sense of identity.

A rational definition of these processes should highlight that self-consciousness requires the use of the memory about one's past and consists of imagining oneself on the background of the image of the world. The key element of the process comes down not only to self-perceptions, but also to the imagery of oneself.

The recent literature on investigations into cognitive processes is scarce. I present here brief statements related to this subject made by a few authors.

Prebble et al., in the abstract of a not-yet published paper, emphasize that intuitive insight and some theoretical considerations link the autobiographical memory and sense of self [55]. They proposed a novel framework for sense of self and memory. This simple model delineates 2 dimensions: 1) the subjective *versus* objective and 2) the present *versus* temporally extended aspects of sense of self. According to these theoretical assumptions, autobiographical memory is important for the formation and maintenance of a mental representation of the objective self in the present moment and across time [55]. These considerations are supported by findings in patients with dementia [56].

Fivush considered the development of autobiographical memory during the lifespan [57]. He remarks that autobiographical memory integrates memories of past experiences into an overarching life narrative. He highlights that autobiographical memory is a gradually developing system across childhood and adolescence, which depends on the development of a sense of subjective self and that develops within specific social and cultural contexts related to individual, gender, and cultural differences. The author remarks that mothers who reminisce with their young children in elaborated and evaluative ways have children who develop more detailed, coherent, and evaluative autobiographical memories [57].

Ortigue et al. discern an “emotional brain” (medial temporal lobe and amygdala) and discuss the formation of more sophisticated emotions like jealousy on the basis of fear and anger [58]. These sophisticated emotions play important roles in the perceptions and imagination involving oneself [58].

Esch et al. discuss the significance of the reward system for the formation of feelings like love and compassion [59]. They remark that the reward system is based on function of prefrontal or orbitofrontal cortices, cingulate gyrus, amygdala, hippocampus, and nucleus accumbens [59]. Experiencing feelings such as love and compassion participates in formation of self - identity [59]

Jankowiak-Siuda et al. emphasize that perception of one's own emotions involves internally simulating the affective states and

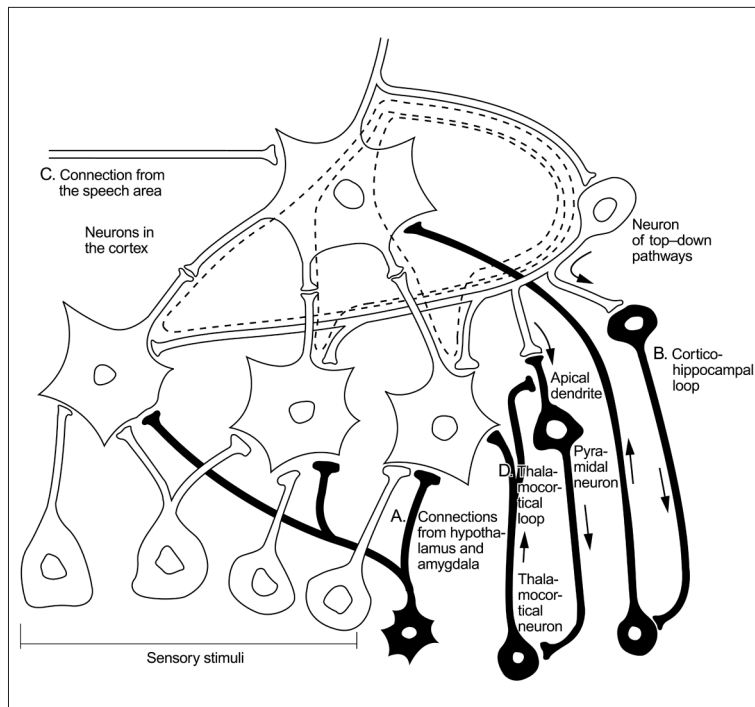


Figure 9. Intuitive and symbolic depiction of some layers of the hierarchical structure of neurons integrating sensory information and of three coordinating networks. The drawings is similar to the Figure 4. It also illustrates the circuits responsible for perceptions and recalling of mental images. The significance of depicted elements are determined in the legend of the Figure 4. However, here we highlight the existence of the thalamo – cortical loops. Neural activity in the period of a deep sleep is limited to the oscillations of thalamo – cortical loops reaching only the lower parts of the cortex. The frequency of these oscillations are in the theta and delta range. In this situations only a core element of the imagery process is active. The figure enable to understand why perceptions and imagery stimulate further the oscillations in these loops, what increase the frequency of oscillations. The core element of the imagery process is acting permanently without external stimuli.

cognitive mental states of others [60]. Neuroimaging studies indicate that the same areas of the brain are activated when people experience their own emotions and when they observe others' emotions. The authors argue that there are at least 2 modes of information processing involved in empathy. The mirror neuron system is engaged in bottom-up automatic processing [60]. Understanding others' feelings by taking their perspective is another aspect of empathizing. When we try to understand what others feel, autonomic neural pathways responsible for empathizing can be inhibited by top-down circuits involving mainly prefrontal areas of the brain [60]. Thus, empathy can also refer to our ability to take the cognitive perspective of other people, which is usually the action of the 'theory of mind' circuits. It helps us to understand the experiences, intentions, and needs of other people [60]. Thus, the sense of self is also based on observations of behavior of others [60].

An intriguing theory was formulated by Lou et al., who link the retrieval from autobiographic memory with a very basic process of recurrent thalamo-cortical oscillations [31]. This theory concerning essential assumptions about general features of the brain is based on experimental evidence [31].

The authors used magneto-encephalography and "Granger causality analysis" to test if specific autobiographic memory retrieval can enhance recurrent interaction between higher order, modality non-specific, brain regions and the thalamus. The authors examined neuronal activity in a paralimbic network, which participates in autobiographic memory retrieval and self-reference. According to the authors, this network

includes medial prefrontal/anterior cingulate, and medial parietal/posterior cingulate cortical regions, together with the pulvinar thalami. They demonstrated that the pre-stimulus condition is characterized by recurrent oscillations that are maximal in the lower gamma range (30–35 Hz). When retrieving a specific autobiographic trace, this activity was dramatically increased [31].

The obtained results inclined the authors to consider the 2 main opposing visions of the organization of the brain and the mechanisms underlying the phenomenon of consciousness. One vision is that the brain responds to external stimuli, the nervous system is organized as a set of complex neuronal connectivity patterns triggered into action by the outside world, and behavior is fundamentally the resultant of the external world. The authors have a different vision, believing that the work of the brain is mainly an intrinsically generated neuronal activity, with sensory inputs acting as modifiers of such intrinsic activity [31]. They maintain that recursive activity in cortico-thalamic interaction may bootstrap neuronal processing to elicit conscious experience.

According to this view, emergence of conscious experience is achieved through oscillatory binding of disparate regions in the brain. Authors opting for such an understanding of brain organization and the neural ground of consciousness rely on some earlier works [61–63].

The perspective of Lou et al. and Llinas et al. correspond to the old ideas promoted by psychologists related to notions such as Freudian “id” and Jungian “self”. Through these concepts psychologists attempted to determine what is the core element of the self-image. I try to explain intuitively the essence of neural circuits related to these intriguing concepts by means of Figure 9.

Conclusions

This review of recent experimental data has allowed me to elaborate intuitive, demonstrative figures enabling comprehension of a model of neural circuitry active in imagination. This model facilitates abandonment of the concepts of “boxes and transfers among buffers” that were used to discuss mechanisms of recall from memory. It helps to be aware of the sophisticated data storage by the human brain, which consists, in some sense, on activation of parts of a “lighting tree” from

different directions for different periods of time. Apart of the discussion of neural substrates active in imagination, the intuitively comprehensible neural mechanism is presented.

The model explains the sophisticated processes involved in imagining future situations, novel objects, and anticipated actions, as well as construction of the image of oneself, which is indispensable for the sense of identity and self-awareness.

The presented theory raises some challenges. It would be necessary in the future to take a position regarding the significance of the thalamo-cortical oscillations for understanding of self-awareness. An advanced model of the problem-solving processes active in the working memory system is needed.

The presented model, however, could be helpful, especially for educational purposes. It improves the understanding of the common basis of numerous cognitive processes and general features of the action of the brain.

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