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A Review on the Psychophysiology of Working Memory in Non-Human Primates

Manuel Alejandro Cruz-Aguilar[1,2], Miguel Angel Guevara[2], Marisela Hernández-González[3], Enrique Hernández-Arteaga[3], Mayra Liliana Ramírez-Rentería[3]

[1]Instituto Nacional de Psiquiatría "Ramón de la Fuente Muñiz", Dirección de Investigaciones en Neurociencias. Laboratorio de Cronobiología y Sueño, CDMX, México.

[2]Instituto de Neurociencias, CUCBA, Universidad de Guadalajara. Laboratorio de Correlación Electroencefalográfica y Conducta. Guadalajara, Jalisco, México.

[3]Instituto de Neurociencias, CUCBA, Universidad de Guadalajara. Laboratorio de Neurofisiología de la Conducta Reproductiva. Guadalajara, Jalisco, México.

Abstract: ***The main objective of this work was to conduct a review of the scientific contributions related to the working memory in non-human primates. In the great apes, there is evidence of good execution in working memory tasks. The neurophysiological bases of working memory have been studied mainly in the macaque, using electrophysiological recordings of the neuronal activity. These studies show the involvement of the lateral prefrontal cortex and the association areas. The study of the working memory in more primitive species than the New World monkeys, would allow understanding the remote origins of the cerebral mechanisms involved in the short-term memory inprimates.***

Keywords: Executive functions, evolution, cerebral cortex, short-term memory, primates.

1. Introduction

The development of the associative areas of the encephalus, mainly the prefrontal cortex, is considered the main key in the evolution of superior cognitive functions in primates [1]. The memory is included among these functions. Since 1936, year in which Jacobsen conducted the pioneer studies on short-term memory in macaques [2], a great amount of works concerning to the working memory in non-human primates have been carried out. These works intend to elucidate the neural mechanisms that intervene in theworking memory and that have served as a model to understand the human brain. The primate order is divided into three suborders: Strepsirrhini; Tarsioidea and Anthropoidea[3-5] In turn, the Anthropoids are divided into three superfamilies: *Ceboidea*, formed by New World monkeys, the Superfamily *Cercopithecoidea*, formed by Old World monkeys and*Hominoidea*, formed by great apes and humans [6]. One of the main differences among the distinct species is the development of the prefrontal cortex and the association areas of the brain, as well as the reciprocal connections among these. Therefore, it is possible to suppose that the comparison of the psychophysiological processes related tothe working memory among the variety of existing families, genera, and species of non-human primates allow determining some primitive neurophysiological elements that definethe working memory in the primate order. Thus, the objective of this work was to conduct a systematic review of the scientific contributions aboutthe psychophysiological mechanisms related to working memory in non-human primates.

2. Method

The databases PubMed, Google Scholar, Redalyc, Dialnet, and SciELO were employed for the bibliographic search of the following themes; *memory; working memory, and working memory in non-human primates.* As an inclusion criterion, it was taken into consideration that the works would permit to integrate each of the themes with scientific information, without the year of publication being a concern.

Likewise, all scientific works of working memory conducted in each species of non-human primates were included as well as all the neurophysiological and behavioral works related to the theme.

3. Results

3.1 Memory

Memory is the cognitive process by which the information is encoded, stored, and recovered [7, 8]. This information is acquired by means of sensorial perception, codified as an image, sounds, experiences, happenings or ideas, in order to later, during storage, be ordered and categorized, to finally recover the information at the time it is requested [8, 9].Memory can be classified based on its temporality, in to short-term and long-term memory; which alludes to the retention that is prolonged even for year [7, 8]. The short-term memory has brief duration, some seconds or minutes, permitting a logical sequence of behavior [10]. One type of short-term memory is the working memory.

3.2 Working memory

The working memory has been defined as a temporary storage mechanism that at the same time allows to retain some informational data, comparing them, contrasting them, or instead, relating them among themselves. It is responsible for short-term storage, while simultaneously manipulating the information necessary for carrying out high-complexity cognitive processes, such as executive control and temporary storage [11]. There is a model of working memory formed bythevisuospatial sketchpad, the central executive and the phonological loop [11]. The central executive is responsible for supervising the information of the visual and phonological subsystems, distributing the attention assigned to each of the tasks to be carried out and to attention to the task and its adjustment to the demands within the context. The visuospatial subsystem is responsible of manipulating visual and spatial information. There is evidence that it is implicated in the organization and manipulation of visual images. On the other hand, the phonological subsystem is responsible of maintaining active and manipulating the information presented through the language, it is implicated in tasks that including linguistic, acoustic, word extension, misunderstood discourse, and articulatory suppression [11]. This model has been recently updated to include an episodic buffer, which functions as a facilitator of the informational constructions of multiple sources, so that it permits the entry of long-term information, whether of language or of visual semantics [12,13].

While the working memory model is theoretical, it is basedon brain structures that principally involve the functions of the prefrontal cortex and its interaction with other brain areas [14-16]. The works of Goldman-Rakic had an important influence on investigations about of the neural substrates of the working memory, with a great variety of cognitive tasks in humans as well as in non-human primates [15]. The findings suggest that there is a homologous neurobiological substrate (the prefrontal cortex) for working memory in primates [17-22].

3.3 Working memory in New World monkeys

The New World monkeys (*Platirrinos*) are divided into two families: the *Callitricidae*, which includes the tamaris, and the titis**,** and *Cebida*, which includethe spider monkeys and the howler monkeys. In the smallest species of New World monkeys the cerebral cortex presents few grooves and incisions, but these develop into the largest species, e.g.,spider monkeys.

There are scarce studiesrelated to the working memory in New World monkeys, however, Dias, Robbins and Roberts in 1996[23], describe the role of the prefrontal region in the execution of spatial-delay tasks. In this study, the authors trained marmosets (*Callithrixjacchus*) to respond to a homologable task to the Wisconsin card sorting task, which is used in humans.In this study the marmosets were placed inside a general Wisconsin test apparatus. The compartment where the monkeys were situated was divided by a window with a guillotine-type opaque screen that could be lowered and raised, while in the contiguous compartment two wooden boxes were placed into which the reinforcing stimuli were placed (food). The paradigm consisted of two phases; during the first phase,areward was placed in one of the boxes, and later, the opaque screen descended, and after a delay period, the second phase began. In the second phase, the opaque screen was removed and the marmoset was permitted to choose between the boxes. Success was considered if the marmoset chooses the box where the reward was, the animal then being allowed to take the reward. On the other hand, an error was considered when the marmoset chose the other box; in this case the animals were not permitted to take the reward. The training continued until the monkeys achieved more than 90% correct answers. After training, the prefrontal cortex was injured with quinolinicin lateral and orbital regions. Subsequently, these monkeys were required to the same paradigm in which they had been trained previously. The results showed that monkeys that had been injured presented a higher percentage of incorrect response compared with the control group (intact). These results are in agreement with that reported studies of prefrontal injury in Old World monkeys and even in humans [17, 23], and revealed that New World monkeys are capable to carry out tasks involving the cognitive process at the prefrontal level, such as the working memory.

In another work, Tsujimoto and Sawaguchi[24] conducted a comparative study on the execution of a working memory task. Utilizing a spatial-delay task that is homologable with the Wisconsin card sorting task using in humans, the authors compared the execution of marmosets (*Callithrixjacchus*) vs. squirrel monkeys (*Saimirisciureus*). These authors found that the squirrel monkey presented a greater percentage of correct responses compared with the marmoset. Nevertheless, both species were able to execute the task correctly, which demonstrated that the New World monkeys can perform working memory tasks.Likewise Tavares and Tomaz [25], published a work in which the authors trained capuchin monkeys (*Cebusapella*) in a delayed match-to-sample task. Once the monkeys were able to respond correctly to the majority of the assays, the experimenters manipulated the delay times and found that the monkeys continued to correctly perform the task despite having very long delays (up to 10 minutes). These results again confirm that, as with the Old World monkeys (*Macaca*), the New World monkeys have the capacity to executedelayed match-to-sample tasks.

3.4 Working memory in Old World monkeys

The neural bases of working memory have been widely studied in Old World monkeys, mainly in the macaque. Pioneer studies on the neurophysiology of memory were conducted in macaques[2, 26]. These works are, in their majority, invasive electrophysiological studies, in which the electrodes are placed directly in the cerebral cortex and some subcortical structures. Theneurophysiological studies conducted on macaques during the last decades have allowed for great progress in understanding the cerebral circuits relate to working memory in humans. Among the paradigms commonly utilized in primates for evaluating working memory, we find the delayed match-to-sample task. In this procedure, a stimulus is presented (sample) to a subject for a short time lapse. Then, the stimulus is removed and short time period is waited (delay). Afterward, the same stimulus is presented with another new stimulus, and the subject is asked to identify which of the two stimuli was presented previously. This procedure is repeated in a determined number of assays. The neural circuits implicated in the working memory in primates are generally activated during a delay period, that is, the time comprising that between the presentations of the stimulus-sample up to the presentation of the stimulus-test. Thus, this paradigm employs different delay times to evaluate the working memory. This procedure constitutes the conceptual basis of memory paradigms known as delayed match-to-sample task.

In a pioneer study that utilized delayed match-to-sample task to elucidate the neural bases of the working memory in macaques, it was reported that among the neurons of the cerebral cortex that continue to discharge even after the sensorial stimulation, precisely at the moment when the monkeys remembered the stimulus [27]. The later works of Patricia Goldman-Rakic and colleagues demonstrated that these persistent neural discharges varied depending on the properties of the stimuli retained by the memory, for example, the position of a visual stimulus [28]. Currently, there are neurophysiological studies carried out in macaques in which persistent neural activity was registered during the interval retention of delayed match-to-sample task, mainly in the dorsolateral prefrontal cortex (DLPFC). It has been observed that, on reducing this activity, the memory deteriorates [29-31], suggesting that the cellular activity registered in the DLPFC, which persists even after the perception of the stimulus, is mnemonic in character and reflects the active storage of past sensorial representations, this event constitutes the cellular basis of memory. These findings offered, to our knowledge for the first time, a mechanism by which the neurons could encode retained information.

Working memory studies conducted in macaques have permitted the development of complex models of DLPRC functions. Based on injury data and the unitary registry of neurons in the cerebral cortex of macaques, Goldman-Rakic (1987) developed one of the most important theories that exist on the functions of the DLPFC. By means of retention paradigms in delayed-response tasks, it has been shown that the persistent activity of the DLPFC neurons reflect the temporary storage of some characteristics of the stimulus, such as the position or the form [29,32-34], while the lesions in zone 46 in the LCPFC diminished the capacity to maintain the sensorial representations in line, which are not yet present in the environment, but that are necessary for remembering the stimulus (that is, it causes forgetting of the information). Based on these facts, Goldman-Rakicproposes that the main function of the DLPFC is to create and maintain internal representations of sensorial information. Miller and Cohen (2001) [35] suggest that in addition to storing recent sensorial information, the DLPFC controls the integral representations of the task contingencies, and even abstract rules. This idea is similar to the theory of Fuster(36), in which the author emphasizes that the DLPFC is responsible for the temporary integration and the measurement of separate events in time. For Fuster, the persistent activity of the DLPFC during the delay of the sustained period reflects the maintenance of various objective-directed representations, including past sensorial events. Likewise, these neuronal discharges could also be representations of the anticipated action and preparatory activity [37-38].All of these models emphasize that DLPFC play an important role in the temporary maintenance and storage of information through the persistent neuronal activity.

Other studies conducted with macaques also indicate a crucial role of the DLPFC in a variety of processes that are necessary for the correct execution of the working memory [17], such as the selection of relevant information. This process is defined as the operation by which sensorial information becomes relevant, in such a way that it can be maintained and, finally, utilized for selecting an adequate motor response [17]. The DLPFC does not store sensorial events; notwithstanding this, it participates in the regulation of other posterior regions that in reality are those that do store the information, such as the parietal cortex [17, 35, 39-41]. Therefore, the activity sustained in the DLPFC does not reflect the storage of the representations *per se*, but instead reflects some maintenance operation or a regulation process of posterior zones of the cerebral cortex.

The results of electrophysiological studies in macaques, together with some brain imaging findings in humans, have demonstrated that the neural activity sustained during the delay period is not only observed in the DLPFC, but also it can be observed in the posterior parietal and inferior temporal cortexes, in the dorsal premotor cortex during spatial working-memory tasks, and in the ventral premotor cortex during non-spatial working-memory tasks. This pattern of cerebral activity could reflect maintenance of relevant information prior to the motor action, that is, the retrospective sensorial information is maintained until the motor acts (behavioral responses) are carried out [42].

3.5 Working memory in the great apes

The live specimens of the great apes are divided into three families: *Hylobatidae*, in which gibbons and siamangs belong; *Pongidae*, which includes orangutans, gorillas, and chimpanzees; the currently existing anthropomorphic great apes, and *Hominidae*, which comprises numerous genera, nevertheless at present possesses a sole species, the *Homo sapiens sapiens*.

Diverse studies postulate a close relationship between the great apes and humans, due to that we share the same common ancestor, thus share a high percentage of the genetic load (96.4 of the DNA of orangutans, 97.7% with gorillas, and nearly 99% with chimpanzees and bonobos) [43, 44]. Despite the high degree of genetic, anatomical, and physiological conservation, there are noteworthy differences in behavior. Nevertheless, it has been observed in diverse studies, that the non-human great apes are capable of carrying out superior cognitive processes. For example, utilizing a modified version of radial arm maze where food was placed randomly on different arms [45, 46], it was demonstrated that these primates exhibited excellent spatial memory, because they are very precise in remembering on which arm the food was found. Other studies have shown that these primates also develop efficient localization strategies of hidden food; for example, Menzel (1973) [45] found that chimpanzees in captivity engaged in strategies to localize food that was previously provided in order to obtain it at a shorter distance. Likewise, studies conducted with gorillas [46]and orangutans [47]showed that these species exhibited precision in the exploration and searching for foodtask. Other recent studies performed in chimpanzees demonstrated that these primates are capable of recognizing and learning sequentially the numbers 1 to 9 and even present a better response than humans in short-term memory tasks. Additionally, after training, chimpanzees are capable of learning and utilizing Arabic numbers to label sets of objects in real life with the corresponding number, when the experimenter showed them images with different amounts of objects [48-53].

Inoue and Matsuzawa [54],in a masked task; which is a similar task to sequence replication, but which consists of that at the moment that the chimpanzee pushes the number 1 on the touch screen, the remaining number disappear and the subjects are required to remember the localization of the numbers and push them in the correct order, the position of the numbers is completely random,the authors observed that the great majority of the chimpanzees could solve the task (remembering the numerical elements and their position) with the nine items presented in only 0.5 seconds. Also, they were capable of replicating the test on various occasions with high accuracy time after time, until achieving 100% accuracy. The authors conducted these tests following the same procedure in humans (children and university adults); the results revealed that the humans were not capable of remembering the correct order in the majority of occasions and their responses were slower compared with those of the chimpanzees. Despite the deficiencies in solving this task in humans, the children obtained better scores with respect to the university adults. This could explain, together with other studies also carried out humans with certain memory tasks, in which children aged 5 to 11 years exhibited better task execution than the adults [55, 56]. Studies conducted with chimpanzee fetuses have demonstrated that they are capable of generating associative learning over classical conditioning [57]. This study was carried out in three pregnant females and consisted of stimulating the mother's abdomen with vibroacoustic stimuli; this was performed one a week from day 201 of gestation up to delivery (around day 233). Each session comprised 6-10 assays. After the birth, the behavioral tests were carried out on postnatal days 33 and 58, and it was demonstrated that the chimpanzees presented a better response to the 500-Hz tone and memory persistence during at least 2 months. This was of great interest due to that studies with nursing infants report a lower temporality of memory [58,59].

4. Discussion

According to the international literature, there is evidence that the great apes can successfully perform in diverse types of tests that involve the working memory. Distinct studies postulate a close relationship between the great apes and humans, due to that we share a high percentage of the genetic load (96.4% of DNA with orangutans, 97.7% with gorillas, and nearly 99% with chimpanzees and bonobos) [43, 44]. In this regard, it is known that the DLPFC and the areas of association of the great apes present prominent development, and there is evidence that the working memory possesses a physiological substrate in these brain areas [17-22]. Another interesting aspect that was detected in the scientific literature is that the study of the neural mechanisms of the working memory in non-human primates have been performed utilizing the behavioral analyses with concomitant neuronal firing recordingof different brain areas.On the other hand, we observed that the study of the working memory of the oldest primates, e.g., strepsirrhini, is limited. There are studies that show that New World monkeys can execute working-memory tasks; however, these works have been principally behavioral [17, 23-25]. Actually, the brain processes of the working memory in primates phylogenetically farthest from the human being have been scarcely explored. The study of this type of memory in species more primitive than the New World monkeys, would allow understanding the remote origins of the cerebral mechanisms involved in the working memory in the primate order.

5. Conclusions

The neural bases of the working memory have been explored principally in macaques. These studies have made it possible to understand the neural mechanisms and circuits that underlie the working memory, especially the participation of the DLPFC and the associative areas. The working memory study in older primates than New World monkeys would allow understand more about primitive cerebral mechanisms implicated in the working memory intothe primate order.

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Author Profile

Manuel Alejandro Cruz-Aguilar, Psychologist by Autonomous Mexico State University.Doctorate in Biological Sciences by Metropolitan Autonomous University, Unit-Iztapalapa.Postdoctoral fellowship from CONACYT / Institute of Neurosciences, University of Guadalajara.Appointment, Tenured Researcher in Medical Sciences into the Chronobiology and Sleep Laboratory, Neuroscience Division, National Institute of Psychiatry Ramón de la FuenteMuñiz, CDMX, Mexico. Manuel Cruz is primatologist and specialist in sleep neuroscience. Develops research related to executive functions in New World Monkeys. Likewise, develops research related phylogeny, neurophysiology, pharmacology and psychophysiology of sleep.

Miguel Angel Guevara, PhD in Physiological Sciences by the Center of Neurobiology of the National Autonomous University of Mexico. Dr. Guevara is responsible for the Laboratory of Electroencephalographic Correlation and Behaviour of the Institute of Neurosciences at the University of Guadalajara, Mexico. Dr. Guevara develops specialized methods and techniques for EEG analysis. It also studies the participation of the prefrontal cortex in cognitive and motivated processes. He has published national and international articles and chapters in various research books, as well as several computer programs designed for the capture and analysis of electroencephalographic signals and computerized application of tasks that evaluate cognitive processes.

Marisela Hernández-González, PhD in Physiological Sciences by the Neurobiology Center of the National Autonomous University of Mexico. Postdoctoral fellowship at the Peripheral Unit of the Biomedical Research Institute, National Autonomous University of Mexico, and at the Faculty of Psychology of the University of Tromsø, Norway. Marisela Hernández-González is responsible of Neurophysiology of Reproductive Behavior Laboratory at the Institute of Neurosciences, University of Guadalajara, Mexico. Her line of research focuses on the neural basis of sexual and maternal behavior.Using the electroencephalographic technique as the main tool, she has performed multiple works in both humans and rats that have been published internationally.

Mayra Liliana Ramírez-Rentería, Master in Behavioral Science, with Neuroscience orientation, granted by the Institute of Neurosciences of the University of Guadalajara, México. Mayra LilianaRamírezRentería is currently completing a PhD in the Laboratory of Neurophysiology of Reproductive Behavior of the Institute of Neurosciences at the University of Guadalajara, Mexico. Has held stays at the University of Guadalajara in the Laboratory of Neurochemistry and Neurophysiology, by Dr. Alberto Morales Villagrán. Her line of research focuses on the study of epilepsy and the basic mechanisms involved in the behaviors motivated in animal models.She has published national and international articles and chapters in books.

Enrique Hernández-Arteaga, Master in Behavioral Science, with Neuroscience orientation, granted by the Institute of Neurosciences of the University of Guadalajara, Mexico. Enrique Hernández-Arteaga is currently studying the doctorate in Behavioral Science at the Neurophysiology of Reproductive Behavior Laboratory at the Institute of Neurosciences, University of Guadalajara, Mexico. His line of research has focused on the investigation of the effects of stress both at the behavioral, hormonal and neural level (through the technique of analysis of electroencephalographic activity) on motivation and sexual execution, as well as on cognitive aspects such as working memory. These studies have been published in book chapters and international journals.