International Journal of Science and Research (IJSR)
ISSN (Online): 2319-7064
Index Copernicus Value (2015): 78.96 | Impact Factor (2015): 6.391

A Review: Psychophysiology of Tool Use in Non-Human Primates

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Abstract: ***The main aim of this work wasto conduct a systematic review of the scientific contributions to understanding the psychophysiological mechanisms related to tool use in non-human primates. Results showed thatthe tool use is observed in several species of non-human primates, which use tools to obtain food, even sequentially. In macaque and human species, it has been observed prefronto-parietal circuit activation.The intrinsic properties of this circuit are linked to the tool use in primates. Specific activation in the parietal lobe observed in humans could be a recent evolutionary feature in the primate order.***

Keywords: executive functions, primates, evolution, brain, tool use

1. Introduction

Approximately 55 million years ago, primates appeared on the earth. Arboreal in nature and with pensile tail, these mammals evolved through the geological eras, at the end of which arose the *Homo sapiens*[1]. The transition from arboreal life to the semi-arboreal life observed throughout the primate order, required adaptations in the central nervous system (CNS). Thus, diverse morphological and functional changes occurred during this process. Today, it is known that the development of the prefrontal cortex (PFC) and the associative areas of the encephalusin the primates are related with the performance of the superior cognitive functions [2]. As the result of the development ofthese cortical regions in these mammalsthere are complex behaviors such as the tool use. Tools can be defined as mechanical instruments that permit reaching goals that, in other manner, would be difficult or impossible to achieve [3,4]. Historically, the appearance of this behavior has been considered an important step in the evolution of primates and even for defining the genus *Homo*[5]. The tool use was considered for a long time as an exclusively human characteristic [6], however, currently there is evidence that other species, in particular non-human primates, can also use tools [7]. Primates are mammals adapted to life in the tropical forest. The presence of a basically primitive skeleton; especially in dentition, combined witharboreal life style and social organization, gave rise to the evolution of fingers and hands and well as to the evolution of language and telescopic vision. At present, nearly 175 species of primates are known, distributed in the tropical zones of America, Asia, and Africa. Phylgenetically, the primate order could be divided into three suborders: *Strepsirrhini* (formerly called Prosimians), *Tarsioidea* (tarsiers) and *Anthropoidea* (anthropoids)[8-10].In turn, the anthropoids are divided into three superfamilies: *Hominoidea*, which the great apes and humans are found; *Cercopithecoiea*, made up of the Old World monkeys, and *Ceboidea*, comprising the New World monkeys [1].

The living species of the great apes are divided into three families: Hylobatidae, gibbons and the siamangs belong; *Pongidae*, which includes the orangutans, gorillas, and chimpanzees, which are the currently existing anthropomorphic great apes, and *Hominidae*, which is composed of numerous genera, of which all but one have been extinguished at present: *Homo*, which at present, possesses a unique species: *Homo sapiens*[11]. On the other hand, the Old World monkeys live in tropical and subtropical regions in Asia and Africa, except for the macaque, which lives in Japan. The Old World monkeys do not have prehensile tails, but they do have ischial callosities around the tail and on the underside. These species preserve the tail (with the unique exception of the *Macacasylvanus*), presents more prominent faces, and their locomotion is basically quadruped [9, 10]. Among the Old World monkeys, there are twelve species of macaques, two species of mandrills, and four species of boons papions,also known as baboons, and the distinct species of macaques, the *Macacaarctoides* that most utilized primatein a broad gamma of areas of knowledge, among which psychology, medicine, and the neurosciences are highlighted.

The New World monkeys are divided into two families: *Callitricidae*, which includes the titís and the tamarins, and the *Cebidae*, which includes the spider monkeys and the howler monkeys. The habitats of the New World monkeys are the tropical and subtropical zones of South America and Central America. These monkeys present long tails in relation to their body mass and that are frequently prehensile as well as flattened snouts, with nostrils in a lateral position. They are very well adapted to tree life, possess long limbs, delicate hands, and a tail apt for balancing or easily catching hold of tree branches [9, 10]. In contrast with other primates, their thumbs are opposable. The smallest species of New World monkeys present the cerebral cortex with few grooves and incisions.

Due to the complexity of the tool use that is observed in primates, the executive functions are the cognitive abilities are those that are probably related to this behavior. The executive functions are defined as a series of processes whose objective is to facilitate adaptation to new situations and to modulate the most basic motor and cognitive abilities [12]. It has been proposed that they have the capacity to filter information that interferes with the task, involving themselves with behavior directed toward an objective, foreseeing the consequences of their actions and drive the concept of mental flexibility [13-17]. There is evidence that the executive functions in primates depend to a great degree on the prefrontal cortex [14-20], and on the association areas, mainly the parietal cortex [21-29]. The prefrontal cortex participates in the control, regulation, and efficient planning of behavior. To it is attributed an essential role in creativity, the development of the formal operations of thought and decision making [30-31]. On the other hand, the parietal cortex is related with the processing of somatosensory information processing, [32] and has been considered important for attention and spatial perception, as well as for polysensory integration [33-35]. Diverse studies suggest that the posterior parietal cortex also participates in intention movement and decision making [21-29].

Therefore, it is possible to suppose that the comparison of the psychophysiological processes related with the tool use among humans and the variety of families, genera, and species of existing non-human primates would allow for the determination of some cognitive, behavioral, and neurophysiological elements that underlie the tool use in the primate order. Thus, the objective of the present work was to perform a systematic review of the scientific contributions concerning the understanding of thepsychophysiological mechanisms related with the tool use in non-human primates.

2. Method

The databases PubMed, Google Scholar, Redalyc, and Dialnet were utilized for the bibliographic search of the following themes: *tool use in non-human primates; neurological basis of the tooluse in primates,* and *psychophysiology of the prefrontal-parietal circuit.*The keywords belonging to each theme were searched for independently and also were combined among themselves for the search for themes. 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. Similarly, works were included on the tool use of all of the species of non-human primates and all the neurophysiological and behavioral works referring to the theme.

2.1 Tool use in non-human primates

In the international literature, there is evidence that non-human primates possess the capacity to manipulate an object (tool) with the hand to act upon other [36-39]. In orangutans[40-43]and gorillas [44-46], tool use is related mainly with obtaining food. Similarly, there is evidence that gorillas can use branches to explore the depth of a river[47]. In the chimpanzee, the tool use is also found to be related with obtaining food [42, 48, 49]; however, this has been observed mainly in females. It has even been reported that these primates are capable of using tools to hunt down vertebrates [42, 50]. With regard to Old World monkeys, in macaques, it has also been observed that females, in comparison with males, utilized tools with greater frequency (stones) to obtain food [51]. With respect to the New World monkeys, there is evidence thatthe capuchin monkey is one of the most studied specieand even its capacity to elaborate its own tools [52,53].In capuchin monkeys, it has been observed that males, use tools with greater frequency [54-55]. In this species, the capacity to create, reutilize, and transport tools to obtain food has also been observed [56, 57]. In a longitudinal study conducted in the species *Cebus* spp., the spontaneous use was observed of stones to dig and obtain food [58]. Likewise, the spider monkey, is capable of employing tools in the wild to scratch itself [59]. With respect to the oldest primates, tool use has been studied under laboratory conditions in two species of lemur [60-62], observing, in all cases, the use of tools to obtain food.

In non-human primates, the sequential tool use has been documented. Only a limited number of primate species are capable of utilizing tools sequentially, where a tool to obtain another tool is utilized, which later will serve to obtain an out-of-reach objective. The paradigm that is commonly employed to evaluate sequential tool useconsists of presenting to the subjects a reward that is out of their reach and an easy-access tool that is which is not sufficiently long to reach the reward, but that is sufficient for reaching another tool, which can be utilized for obtaining the reward. [63].

The study of chimpanzees has been the model to evaluate the primitive traits that characterize the sequential tooluse in hominids [64-66]. However, the spontaneous sequential tool use has also been reported in gorillas and orangutans [44], as well, and in capuchin monkeys [67]. In chimpanzees, there isevidence of the use of five tools sequentially to obtain food [42-44]. Likewise, the orangutan and the bonobo possess the capacity to use up to five tools to obtain food [42]. It has been reported that after some training sessions, macaques [68] and titís[61] can also use tools sequentially to obtain food, as well as primates of the species *Sapajus*spp, [69]. There is evidence that capuchin monkeys and the great apes exhibit these behaviors in the wild. Figure 1 presents a summary of the scientific works that refer the tool use in non-human primates.

Table 1: Studies on the use of tools in non-human primates

Family	*Species*	*Author*	*Type of tool*	*Objective of th use of the tool*
Great apes	**Orangután:**			
	(*Pongo pygmaeus*)	Fox et al., 2004	Branches	Obtain food
	(*Pongo abeli*)	Schaik and Knott, 2001.	Branches	Obtain food
	(*Orongoabeli)*	Martín-Ordas et al., 2012.	Sequential use of 3-5 sticks	Obtain food
	(*Pongo pygmaeus*)	Call and Tomasello, 1994.	Sticks	Obtain food
	Gorilla:			
	Gorilla (*Gorillagorilla*)	Mulchay and Call, 2005.	Sequential use of two sticks	Obtain food
	Gorilla (*Gorillagorillagorilla*)	Pouydbat, 2010.	Branches, substrate	Obtain food
	Gorilla (*Gorillagorillagorilla*)	Pouydebat, 2005.	Branches	Obtain food
	Gorilla (*Gorillagorilla*)	Breuer, 2005.	sticks	Explore depth of a river to cross it
	Chimpanzee:			
	Pan troglodytes	Mulchay and Call, 2005.	Sequential use of two sticks	Obtain food
	Pan troglodytes	Martín-Ordas et al., 2012.	Sequential use of 3-5 sticks	Obtain food
	Pan troglodytes Verus	Pruetz et al., 2015.	Branches	Hunt vertebrates
	Pan paniscus	Boose et al., 2013.	Branches	Obtain food
	Pan paniscus	Martín-Ordas et al., 2012.	Sequential use of 3-5 sticks	Hunt vertebrates
Old Worldmonkeys	**Macaque:**			
	Macaca Fascicularis aurea	Gumert et al., 2001.	Stones	Open foods without skin (oysters, crabs, nuts, etc.]
	Macaca fuscata	Hihara et al., 2003.	Sequential use of two canes secuen	Obtainfood
New Worldmonkeys	**Capuchin:**			
	Cebusapella	Westergaard and Suomi, 1994.	Branches	Obtain food
		Westergaard and	Stones	Obtain food
		Suomi, 1996.	Stones	Obtain food
	Cebuslibidinosus	Spagnoletti et al., 2011.	Stones	Obtain food
		Spagnoletti et al., 2012.	Stones	Obtain food
		Elisabetta et al., 2013.	hammer stone	Obtain food
		Mannu and Ottoni, 2009.	Branches and stones	Obtain food, dig
	Cebusspp.	Moura and Lee, 2004.	Branches and stones	Obtain food
	Sapajusspp.	Sabbatini et al., 2014.	Sequential use of two sticks	Obtain food
	Spider monkey			
	(*Atelesgeoffroyi*)	Lindshield and Rodrigues, 2009	Branches	Scratch himself
	Cotton-top tamari			
	(*Saguinusoedipus*]	Santos et al., 2005a.	Canes	Obtain food
Strepsirrhins (Prosimios)	**Lemur:**			
	EulemurFulvus	Santos et al., 2005b.	Canes	Obtain food
	Lemurcatta	Laurie et al., 2005.	Canes	Obtain food
	Aye-Aye (*Daubentoniamadagascariensis*)	Sterling and Povinelli, 1999.	Vines	Obtain food

2.2 Neurobiological bases of tool use in non-human primates

In the international literature, there is evidence that in macaques and in humans, cerebral activity related with tool use has been studied through neuroimaging techniques. In these studies, it has been found that the observation of subjection actions carried out with simple tools activate the prefrontal-parietal circuit, which is also activated during the observation and the execution of the subjection movements of a tool [70-72]. In both species, observation of tool use activates the occipital, temporal, intraparietal, and ventral premotor cortex, in bilateral fashion. In humans, the observation of the tool use is related with the specific additional activation of a rostral sector of the left inferior region in the parietal lobe. In these works, the activation of this region is suggested for being considered as a characteristic of the human brain, because it was not observed in the monkey studied, even after the latter received training [70-73]. These studies suggest that the observation of a hand that use a tool activates similar regions in humans and macaques, and that there exists a specific additional sector of the left inferior region of the parietal lobe, which appears to be specialized from the tools use in the*Homo sapiens*. It is noteworthy that the neural basis of the sequential tool use has not been documented in any species of the non-human primates.

2.3 Psychophysiology of the Prefrontal-Parietal Circuit

As its name indicates, this circuit is constituted of the prefrontal and parietal cortexes, and of the reciprocal connections that exist between these. There is evidence that this circuit initiates with the send of projections from areas 9 and 10, as well as from area 7a of Brodmann to the dorsal region of the caudal head [74]. The prefrontal cortex, on the one hand, has been associated with superior cognitive operations and the executive functions[75-90].

The prefrontal cortex functions are determined by their associative nature, integrating multimodal information. It also possesses wide connections from subcortical and limbic regions. It performs an important role in prioritizing stimuli, referencing them to internal representations, appropriately directing the attention, monitoring the time sequence of the happenings permits the understanding of abstract concepts and carrying out executive functions [91]. In particular, the posterior parietal cortex is tightly interconnected with the prefrontal cortex, and it has been demonstrated that they exhibit similar properties across a broad gamma of experimental situations. Likewise, it has been documented that the posterior prefrontal cortex of primates is activated during tasks related to spatial working memory [92,93], during decision making [94], planning [95-99], the expectation of a reward [100,101], the rules [102], sorting/classifying [103,104], cognitive associations [105], and quantifying [106-110].

At present, it is known that in primates, the dorsal convexity of the frontal and parietal lobes forms a network that is implicated in attention. This network comprises the cortex along the intraparietal sulci, the inferior parietal lobe, and the dorsal premotor cortex, including the frontal ocular field. These regions are strongly interconnected with recurring fibers that pass through the superior longitudinal fasciculus. The posterior parietal cortex in primates possesses information elaborated in the sensory cortex and of representations of behavioral goals and expectations deriving from the dorsolateral prefrontal cortex and the premotor cortex [111]. Likewise, in the international literature, there is evidence that the prefrontal-parietal circuit is sustained by the interconnections of the posterior parietal cortex, the dorsolateral cortex, and the cingulum. The interconnections of the posterior parietal cortex are more prominent with the posterior zone of the cíngulum, while the dorsolateral prefrontal cortex maintain the most prominent interconnections with the anterior cingulum.

In humans, the posterior parietal cortex is a zone around the intraparietal sulci that includes its own intraparietal sulci, the lateral intraparietal area, which is in reality the lateral branch of the intraparietal sulci, the inferior parietal gyrus(approximately the zone corresponding to area 39 of Brodmann) and zones of area 7 of Brodmann, possibly zone 7a for visual attention and zone 7b somatosensory attention [112]. Likewise, the posterior parietal cortex, of right predominance, constitutes the main settlement of a posterior attentional system that controls the selective and focalized attention.

3. Discussion

Historically, the appearance of the tool use has been considered as an important step in the evolution of primates, even for defining the genus Homo[5]. In effect, the international literature supplies evidence that the use of tools is present in a great amount of non-human primate, which suggests that all primates are capable of utilizing tools, from the most ancient species to up to the great apes, among which humans are found.

Therefore, one of the most important points in this review has to do with the question: Which psychophysiological mechanisms are shared by the primates that permit them to use tools? According to this present review, it could be said that they share the great majority of psychophysiological processes, except those related with oral language social intelligence, or remembering the personal life story present in humans. There is great anatomical, structural, and neurochemical homology in the brain of the primates, and there is evidence of the activation of common cerebral areas, above all of the prefrontal-parietal circuit, in the motor and cognitive processes implicated in the tool use as humans as well as in non-human primates [113]. Only a small difference has been reported, and that is that humans present a specific activation in the left anterior supramarginalgyrus of the inferior parietal cortex during the observation and execution of tool use, which is not observed in macaques [72,73].

However, this small difference barely refers motor specialization and does not explain the abysmal difference that exists between the tool use in humans and non-human primates. Human adults without experience are capable of understanding a priori, the causal relationship between the tool use and the results obtained [114]. Thus, humans are capable of imagining, creating, perfecting, and even intentionally transforming the tools, solving a different problem from that for which they were created [115]. This suggests that distinct areas of the prefrontal cortex and the areas of association that controls the executive functions, as well as limbic-system structures related to the regulation of emotions and creativity, could make up part of the psychophysiological mechanisms comprising the broad behavioral repertoire of tool use, principally in humans. Likewise, the tool use related with the architecture, technology, science, art, and the use of arms are importantly determined by the development of the prefrontal cortex circuits and the association areas, which evolved in a different manner from to give rise to distinct species of primates, achieving greater development in humans [115,116]. In this respect, it is interesting to observe that in the international literature, there is no evidence that non-human primates build or use tools to harm other beings of their own species, or to intentionally destroy the ecosystem. The latter appears to also be an intrinsic property of human nature: a high cost of the evolution of the CNS in the primates, a brain that evolves to adapt itself and to self-destruct.

A third aspect that is highlighted in the present review is that in non-human primates, the sequential tool use has been documented, however, only the capuchin monkeys and the great apes exhibit these behaviors in the wild. Evidence exists that the proportion of the cerebral cortex and the encephalization coefficient of are associated with the tool use in the primate order [113].It is interesting to observe that New World monkeys have a cerebral-cortex proportion similar to that observed in capuchin monkeys and macaques [117], and an encephalization quotient equivalent to that of the chimpanzee [118-119]. This suggests that the cytoarchitectonic characteristics of the prefrontal and parietal cortex, the proportion of the cerebral cortex, and the encephalization quotient, as well as the cognitive and motor capacities, can comprise factors that are related with the sequential tool use in primates.

The most part of studies conducted to explore the neural bases of tool use in primates have utilized neuroimaging techniques [73, 74], which possess great spatial resolution, but very little temporal resolution. Tool use implies process of attention, planning, spatial orientation, and motor execution, which take place within a well-organized time sequence, thus the importance of employing high-resolution techniques, as is the case of Electroencephalographic (EEG); a non-invasive technique that permits the registry of electric cerebral activity, even in freely moving non-human primates [120,121]. EEG activity can be defined as voltage oscillations originating from intra- and extra neuronal ionic currents in a large population of cells that are radially disposed to the surface, which are activated synchronically [122,123]. The registry and analysis of EEG activity has been employed for many years as one of the most sensitive tools that permit the examination of cerebral functioning in relation to the different physiological states, permit among these the executive functions. Therefore, we consider that the study of the psychophysiological mechanisms of the tool use in non-human primates by means of EEG activity, would allow study the cortical mechanisms related with tool use. Finally, it is noteworthy that, there are scarce neurophysiological works on the tool use in New World monkeys and oldest monkeys. The study of these species could increase knowledge on the behavioral strategies and cerebral mechanisms implicated in the tool use into primate order.

4. Conclusion

The tool useis presents in a large number of non-human primate species, which suggests that all primates are capable of utilizing tools, some even in sequential fashion. The specific activation of the inferior left rostral region of the parietal lobe, which is only observed in humans during the use of tools, suggests that this is a recent evolutionary trait in the primate order. The cytoarchitectonic and functional characteristics of the prefrontal-parietal circuit could be factors that are related with tool use in primates. The study of the psychophysiological mechanisms of the use of tools in non-human primates utilizing analysis of the EEG activity would permit more delving deeper into the cortical mechanisms related with the use of tools in the primate order.

5. Acknowledgments

Dr. Manuel Alejandro Cruz-Aguilar is grateful to the InstitutoNacional de Psiquiatría “Ramón de la FuenteMuñiz”, CONACyT and to the Universidad de Guadalajara for the facilities granted to him for the carrying out of his postdoctoral fellowship (2015-2017) that endorse the present work. The authors of this paper declare that they have no conflict of interest.

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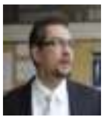

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