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Probable Relationship Between Neoteny in Human Brain Development and the Ability of Working Memory to Represent Novel Stimuli

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Abstract

In this review we detail a series of studies and investigations that lead us to ask: Is it possible that the neoteny experienced during our cognitive development could be related to the end of a General Learning process in non-human primates (a phase in which knowledge is acquired about the possibilities offered by objects and subjects in the environment and information about the possibilities offered by interactions with them, in addition to knowledge about the characteristics of the ecological and social environment in which we live)? Furthermore, the information analyzed in this work also leads us to ask: Is it possible that the end of this General Learning process in non-human primates could be due to the fact that their working memory could lose a significant part of its capacity to represent novel stimuli around the time of food independence? And if this were so, could the characteristic neoteny of human cognitive development (the condition presumably responsible for our exceptional cognitive ability) consist of H. sapiens maintaining the working memory capacity to represent novel stimuli active after youth, thus making General Learning possible during the adult stage of life? The analysis we have developed in this review leads us to give an affirmative answer to these questions, concluding that the capacity of working memory to maintain the representation of novel stimuli could have been, by continuing to function in the adult stage of life in the lineage of individuals that led to Homo sapiens, the necessary and sufficient quality for the distinct cognitive development that characterizes our species to begin.

Keywords

Neoteny, General Learning, Goal-Oriented Learning, Volitional Attention Cognitive System, Reflective Attention Cognitive System

1. Introduction

Evidence of Neoteny in Human Brain Development

Neoteny in cognitive and brain development is a condition inherent to primates. It is characterized by delayed and incomplete myelination, long periods of neuronal development, a large increase in synapse production, and prolonged and postponed synaptic pruning [1, 2], this generates a significant growth in the capacity to store and process information, which makes neoteny an eligible trait both in the evolution of primates and in that of the genus Homo [3, 4], so we can say that neoteny plays a major role in the structuring of human brain anatomy, in addition to being responsible for our exceptional cognitive abilities because it includes long periods of neuronal remodeling, adjustment and plasticity [5, 6]. The brains of

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children and young people are characterized by increased synchronization and plasticity, as well as by elevated neuronal metabolism. These juvenile traits may have been maintained into adulthood in certain human cortical neurons [3, 7]. Evidence of this is that our adult cerebral cortex exhibits increased synaptic activity, greater metabolism, and a very high degree of plasticity when compared to the adult cortex of other mammals, including non-human primates (NHP). This suggests that our neurons in association areas retain infantile characteristics into adulthood, and consequently, our brain would function during the adult stage of life in the same way as a juvenile brain [7].

Nine percent of our genes appear to contribute to delayed brain maturation compared to those of rhesus monkeys (*Macaca mulatta*) [8]. Similarly, the high expression of genes related to energy metabolism indicates that adult humans have a higher level of neuronal physiological activity than chimpanzees (*Pan troglodyte*) or macaques [9]. Likewise, adult humans exhibit levels of gene expression associated with cortical synaptogenesis and the retention of synaptic plasticity similar to those of adolescent chimpanzees [7, 10]. The fact that adult humans retain a set of brain developmental characteristics unique to young NHPs means that around puberty, our relatives would experience a noticeable decline in their ability to store and process information, so a significant decline in the ability to learn would have to be observed. However, there is no evidence that a significant decline in cognitive or learning abilities is observed in adult non-human primates when it comes to goal-directed learning [7, 13-26].

If, despite the end of prolonged periods of neuronal development, the cessation of incomplete and delayed myelination, and the termination of increased synapse production, our non-human relatives continue to learn and innovate (with respect to goal-directed matters) into their adult lives as if nothing had happened in their brains, then it is possible that not one, but two distinct learning processes are occurring, one based on these particular features of juvenile neuronal development (a process that would be terminated by a lack of these features), and another process subject to different conditions that would continue into the adult life stage of NHPs.

Evidence Suggests That a Learning Process Could Be Deactivated in NHPs, a Critical Period

Myelination of the cerebral cortex ends with sexual maturity in chimpanzees and macaques; however, axonal maturation continues until the third decade of human life [1]. Therefore, the preadolescent stage may play a very important role in the cognitive development of NHPs. Some research has shown that this age marks a turning point in several skills, such as double-checking in gaze following [27], mirror self-recognition [28], and second-order classification [29]. After the age of 2 (the age at which Pan monkeys reach adult performance), children continue to improve on physical and social cognitive tasks, whereas chimpanzees do not. In tests of attentional/motivational control, no difference in performance was found between human toddlers and Pan monkeys of the same age, and chimpanzees' performance does not increase thereafter [30].

Regardless of whether or not they are capable of using tools, long-tailed macaques (Macaca fascicularis) complete tool manipulation by the age of 4. This indicates that there is a critical developmental period until the age of 3.5, after which the skills necessary for tool use in natural conditions do not develop. Such critical periods have also been discovered in many other species, indicating that biological processes govern the ontogeny of the acquisition of perception-action routines [15]. In captive chimpanzees there is also a critical age (5 years) after which the skills to crack nuts are not acquired [31]. Thirteen chimpanzees in a zoo enclosure were given everything essential to crack nuts (walnuts, a wooden hammer and a wooden anvil), and they also passed various tests to determine the order in which they learned the necessary steps [32], however none learned. The authors concluded that because the chimpanzees were older adults, they were unable to develop the manipulative skills necessary for nut cracking because they were past the critical learning period [33], in other words, they failed because complex motor skills rely on pre-existing skills that are not acquired after the critical period [34] and because understanding of the physical forces and their effects involved in nut cracking is also not acquired after the critical period [35]. Captive adult chimpanzees face two main difficulties when learning to crack nuts with percussion tools [36], first, they usually do not strike objects against substrates, so they do not acquire the necessary motor skills, and second, by not exhibiting prolonged exploratory manipulation of stones, they also fail to learn the possibilities offered by objects, substrates, and actions [37].

Apparently, with NHPs reaching adulthood and the end of prolonged periods of neuronal development, incomplete and delayed myelination, and the termination of increased synapse production, the critical period that enables NHPs to learn primary manipulative skills, spatial relationships, and the possibilities offered by actions, objects, the environment, and substrates could end. Such a significant decline in the ability to learn could only occur, without affecting survival, if the subjects are already capable of surviving on their own at the time of food independence. Is this true?

The need for an important learning capacity to stop functioning

During the adult stage of life, our cortical neurons maintain infantile characteristics such as incomplete myelination, elevated synaptic activity, and great plasticity, which increases aerobic metabolism. This may contribute to the development of neurodegenerative diseases such as Alzheimer's disease or frontal dementia, since plasticity and elevated synaptic activity promote the development of abnormal deposits of β-amyloid peptides in the default mode network (DMN) [38, 39]. Also, with increasing age, incompletely myelinated neurons show increased metabolism and a marked tendency toward oxidative stress [40, 41], which could be the cause of the decline in the expression of genes related to learning and

memory as we age [42, 43].

Circumstances that would allow a learning process to end without affecting survival

In most mammals, food-finding and manipulation skills develop well before the first reproduction [44], for example, most mountain gorillas (*Gorilla beringei beringei*) reach adult levels of food manipulation before or at weaning, other studies also show that a wide variety of NHP species have already learned everything necessary for survival before food independence [45-49].

Studies on chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla beringei and Gorilla gorilla gorilla*) indicate that characteristic adult feeding rates and diet repertoires are achieved around weaning [17, 18]. In bonobos (*Pan paniscus*), chimpanzees, gorillas and orangutans all basic manipulations necessary for tool use are detected before or around weaning [34]. Orangutans (*Pongo pygmaeus* and *Pongo abelii*) reach adult dietary repertoires around weaning [47], as do chacma baboons (*Papio ursinus*) [45]. In bonnet macaques (*Macaca radiata*) adult competition in foraging also coincides with weaning, [46] and the same occurs in common marmosets (*Callithrix jacchus*) [50], in squirrel monkeys (*Saimiri sciureus*) [48] and brown lemurs of Mayotte (*Eulemur fulfus*) [49]. Adult foraging competence is only markedly attained after weaning in brown capuchins (*Cebus apella*) [51, 52], in Japanese macaques (*Macaca fuscata*), which achieve it around the time of first reproduction [53, 54], and in hamadryas baboons (*Papio hamadryas*) [55].

From 6 months onwards, young capuchins in captivity display all the basic forms of adult manipulation, including the use of the thumb and index finger in a precision grasp [56]. In general, this pattern seems to indicate that in NHPs, the age of foraging independence, rather than the age of first reproduction, marks the moment when individuals have acquired sufficient foraging skills to be able to survive in the future [47]. In our opinion, such a concentration of learning would make no sense if learning capacities did not experience a significant decline after weaning or after first reproduction, depending on the species.

In summary, it is possible that since delayed myelination, high plasticity, and an overproduction of synapses can cause oxidative stress, a critical period would be established in NHPs during which a very intense learning process develops, allowing individuals to learn the vast majority of everything they will need to survive as independent adults before weaning.

2. Evidence That Two Learning Processes Could Be at Work

As we discussed, there is strong evidence that NHPs continue to learn after weaning, but there is also evidence that they also stop learning, which leads us to propose that two learning processes could interact instead of one. A General Learning process that enables our relatives to learn primary manipulative skills, spatial relations, and the possibilities offered by actions, objects, the environment, and substrates. And another distinct learning process aimed at achieving goals. Could this be the case? We will use examples of tool-based learning where both learning processes are clearly seen in action. To identify them, we will use (A1) for General Learning and (A2) for Goal Learning.

The use of an object as a tool (A2), according to the perception-action theory, requires producing and managing spatial relationships between the object we hold and other objects or surfaces (A1) [57, 58], this hypothesis proposes that the actions we perform separately with objects and surfaces (A1) precede the actions that combine them (A1 and A2) since the spatial and temporal aspects (A1) of an action sequence must first be learned separately so that they can then be combined into a monitored action sequence (A2). In other words, initial tool use (A2) reflects pre-designed action routines (A1) [14, 57] since learning to use an object as a tool (A2) is achieved through extensive prior exploratory activity that provides the opportunity to learn about the possibilities of actions, objects, surfaces, and the spatial relationships that occur between them (A1) [57, 58].

Infant long-tailed macaques (*Macaca fascicularis*), during the tool-learning process, initially pick up objects, touch them, and then manipulate them repeatedly with their hands and mouths, and usually move them back and forth over short distances (A1). A little later, they develop actions in which they begin to combine the objects used (food and stones). It is also in this phase that percussion appears, but at this initial moment it lacks any objective (A1). The initial exploratory manipulations do not give the impression of having a purpose or being directed toward a specific objective, such as obtaining food. They seem to be motivated by an intrinsic impulse that makes the subjects want to perform the different actions with the stones, since these manipulations, by themselves, do not provide either food or reward to those who perform them (A 1). In a second phase, the manipulations begin to resemble actions typical of tool use, but the order in which the actions are chained, within the framework of the behavioral sequence, is most often erroneous (A1 and A2) until full competence is finally achieved (A 2). Although inept actions are still occasionally performed at this stage of learning, subjects stop performing simple (goalless) manipulations with stones and food (A1) and limit manipulative actions to those strictly necessary for effective tool use (A2) [15].

The findings in long-tailed macaques seem to support the Perception-Action perspective, which predicts that tool use is an activity that develops over several years. During this time, inexperienced subjects first randomly develop a wide range of different simple manipulations with the objects involved in tool use (A1), with the form, characteristics, and frequency of the different manipulations varying throughout the self-learning process. In the second stage, a very wide range of inept

combinatorial manipulations emerges that simultaneously involve food and hammers (A1). And finally, in the third phase of the learning process is when the actions are channeled towards achieving the objective (A2), varying by trial and error the actions and the order of the sequence in which they are carried out, until finally the correct sequences appear that enable the effective use of tools to obtain food. (A 2)" [15].

Stone manipulation through object play (A1) has been observed in all macaque subspecies belonging to the fascicularis macaque taxonomic subgroup [59, 60], and these behaviors develop in a similar manner [59], suggesting that phylogenetically, macaques have a biological tendency to manipulate stones (A1), a tendency that could drive the first exploratory perception-action routines with stones, routines that would enable the use of tools under favorable conditions (A2) [61, 62].

Chimpanzees (*Pan troglodytes*) and capuchins (*Cebus*) manipulate tools and food extremely frequently before becoming competent (A1) [13, 33, 63, 64], and young chimpanzees touch and pick up stones and nuts in simple actions (A1) before starting to combine stones, nuts, and anvils in various ways (A1 and A2), resulting in initially correct but ineffective action sequences that eventually become successful (A2). Chimpanzees acquire competence after years of observing other members of their group cracking and tasting nuts, in addition to playfully manipulating stones and nuts during this time (A1). Infants begin by exploring objects and surfaces, then percuss the substrates with the objects they carry, also using objects to strike other objects they have previously placed on a substrate (A1). Subsequently, for months, they execute different sequences of actions (necessary for nut cracking) by varying the objects and substrates involved (A1 and A2). Eventually, they manage to select the ideal substrates and percussion tools for the activity, in addition to becoming capable of executing the successful action sequence in the correct order (A2) [17, 65].

All these studies show that two different learning processes could operate almost simultaneously. A process that would be responsible for carrying out General Learning about the physical forces involved in actions, about the possibilities these offer us, as well as allowing us to learn about the objects, surfaces, events, and subjects in our environment and the relationships established between them (causal knowledge of the world). And another learning process whose main purpose is the achievement of survival-related objectives.

2.1. The General Learning Process Is Characterized by the Absence of the Reward System

In this space we will try to explain that, contrary to what happens during the goal-directed learning process, the general learning process does not occur supported by the reward system, since its direct purpose is not the satisfaction of basic life needs.

2.1.1. Importance of Exploratory Manipulation

Visual investigation of objects and their exploratory manipulation are essential elements for infants of our species to learn about these objects, their inherent physics, and the physical properties of the world around them. [66-73]. Exploration is the way that allows human babies to learn what objects, substrates, elements and subjects in the environment are for and how to make them satisfy our needs, and it also allows them to acquire information about the consequences of their interaction with each other. This causal understanding of their properties, the possibilities they offer us and the harm that the elements of the environment could cause us exponentially expands the cognitive baggage we have available to face new problems since the causal essence of such knowledge makes it transferable to other contexts [74-78]. The exploratory tendency of infants of our species is so important for their future cognitive development that the greater or lesser propensity for it determines the subject's better or worse cognitive performance, both current and future. This indicates that the exploratory manipulation of objects, substrates, elements, and subjects in the environment is predictive of the individual's advanced cognitive development [78-80].

Since the 1950s, it became evident that many animal species, like us, feel an impulse towards exploration unrelated to biological needs or environmental stimulation [81] because exploration also seems to serve to learn about objects, substrates, elements and subjects in the environment [82-88] with such exploratory manipulation being completely independent of goal achievement [70-72, 78, 89]. Everything indicates that the exploratory manipulation of objects could be responsible for a very important part of the learning about how the physical world in which we exist works. Through it, the cognitive potential of naive subjects is converted into real knowledge useful to face the challenges of subsistence and into essential skills for achieving this goal, such as: the basic handling of ecologically relevant objects (food or nesting substrate) and complex skills such as those involved in the extractive search for food or the use of tools [73].

Multiple studies in different primate and non-primate species point to a positive correlation between exploratory tendency, problem-solving ability and innovation likelihood [90-95], for example in orangutans (*Pongo abelii*) success in problem solving depends on persistence and variability of exploratory behavior [96]. In fact, in primates the propensity towards exploration and its diversity and flexibility seem to be more intense and frequent than in other taxa [97], there is a clear trend, from strepsirrhine primates to Old and New World monkeys and apes, indicating that the drive towards exploration becomes increasingly stronger [97] and the manipulations become much more varied [97, 98], involving more different parts of the body (using fingers more and more frequently than the mouth) [72, 97], that is, the exploratory tendency has been increasing with each new lineage of primates. Great apes show the highest levels of exploratory drive, with bimanual manip-

ulations that also involve other parts of the body. These manipulations are more varied, flexible, and complex because they combine objects with each other and with different substrates [98-101], although they are less complex than ours [102, 103].

Immature, non-tool-using bonobos (*Pan paniscus*) show much lower rates of exploratory manipulation and less diverse types of it than do tool-using chimpanzees, suggesting that the highly complex tool use of our species, as opposed to the lesser tool use of primates, may be due to the differences in the frequency and complexity of exploratory manipulation found between human and great ape infants [102, 103]. As we saw, in macaques the tendency to manipulate stones is essential for the emergence of perception-action routines that under the right conditions make the use of tools possible [61, 62], since through exploratory manipulation they probably discover the properties of rocks and how they serve to modify the environment [61, 64, 77], in short, learning to use an object as a tool is achieved during the course of a long exploratory activity since this is what allows subjects to learn about the possibilities of actions, objects, surfaces and about the spatial and causal relationships that are established between them [57, 58].

2.1.2. Learning Causal Relationships During General Learning

"Associative learning consists of the gradual assignment of associative strength to the connections or associations formed between mental representations of different events that occur in temporal contiguity, whether the mental association established between the word "open" and the opening of the door or the association between eating food X and developing an allergic reaction" [104]. "Many psychologists have proposed that the learning of causal relationships is associative learning like any other learning, whether classical conditioning, instrumental conditioning, concept learning, or spatial learning" [104]. In fact, causality is thought to be a cognitive illusion [105] because much of our understanding of how a cause causes a certain effect is based solely on simple associations (temporal or spatial, static or dynamic) that we perceive, without any true understanding of how causally linked events or elements relate to each other. This lack of understanding is known as the illusion of explanatory depth [106].

Causal relationships are understood as the transfer of some type of force [107]. If phenomenon A causes phenomenon B, it is because A exerts a causal power whose result is B. Cause and effect are temporally related because the cause always precedes the effect [108]. Causality can also be inferred when no force intervenes [109]. For example, the end of an event or the disappearance of a phenomenon can also generate an effect, such as when it stops raining, the trees wither, or when a domino piece is removed from the base of the building, the tower falls.

The Michotte effect is also important in understanding causality. When we see on a computer screen that an object, A, is moving in front of it, while another, B, is moving behind it, we infer that B is chasing A, although since these are digital objects, they have no motivation of their own. Very similar is what happens when an object, A, moving toward the position of B, who is stationary, stops when it reaches B, who immediately begins moving in the same direction as A. Here, we assume that A caused B's movement [110].

2.1.3. The Role of Curiosity in General Learning

The idea that humans inherited a drive to explore from a common ancestor is supported by the fact that there are strong similarities between our exploratory behavior and that of great apes [73]. The driving force of exploration, and therefore of General Learning, could be curiosity, defined as an innate impulse towards information and discovery [111-115], since curiosity, transformed into exploration, facilitates the acquisition of knowledge, in addition to learning, by reducing uncertainty [111, 114, 116]. According to Oudeyer and colleagues, curiosity, driven by internal motivations, is capable of generating satisfaction and pleasure when we unleash our exploratory impulse [117, 118]. For example, juvenile capuchins (*Cebus*), between 1 and 3 years old, manipulate objects more frequently than other age groups [119]. This manipulation is unrelated to feeding, suggesting that manipulation is intrinsically rewarding for them [120].

The distinctive feature of the General Learning process is that, since it does not seek goal achievement, there are no rewards for learning; rather, the only motivation for learning comes from the satisfaction provided by exploratory manipulation and curiosity itself. If information lacks reward value, and therefore no reinforcement occurs to make learning possible, how do we learn everything we've just described during the General Learning process? Because the same networks and structures are involved in both the General Learning process and the Goal Learning process, we will attempt to answer this question in the section devoted to the memory encoding and retrieval function of the default network.

2.1.4. General Learning During Adulthood Could Be What Makes Us Different from Other Primates

So far we have presented a series of studies that, on the one hand, seem to indicate that there could be two very different learning processes (General Learning and Objective Learning), with General Learning probably ceasing to occur when the critical learning period ends and NHPs achieve food sovereignty [1, 27, 29, 31]. And on the other hand, we mention research that shows that in the same period in which General Learning would cease to occur, the characteristics of the high cognitive development shown by our primate relatives during childhood and youth (incomplete myelination, long periods of neuronal development, the great increase in the production of synapses and high neuronal metabolism) also cease to be present [3, 7-9, 11, 12]. This leads us to a first question, could the

end of late myelination, of the long periods of neuronal development, of the great increase in synapse production and of the elevated neuronal metabolism be what causes the end of the General Learning process (the end of the critical learning period)? If this were the case, if the end of these characteristics of elevated cognitive development is the cause of the termination of the General Learning process, and if these characteristics of young NHPs, due to the neoteny of our cognitive development, remain active during the adult stage of life in H. sapiens, would it be justified to think that what differentiated us cognitively from the rest of our primate relatives is the novel and unique quality of keeping active and functioning beyond youth the cognitive capacities that make General Learning possible (the critical learning period)?

The fact that the cognitive capacity that allows humans to carry out General Learning during adulthood (learning for much of life what NHPs can only learn during the critical learning period) could be the distinctive cognitive characteristic that differentiates H. sapiens from the rest of the primates, makes it necessary for us to focus now on trying to explain how learning occurs during General Learning, when there is no reinforcement learning linked to reward value.

2.2. The Role That Working Memory Would Play During the General Learning Process

If, as previously explained, during the General Learning process, there is no goal-directedness, and therefore, in this case, learning does not depend on reward-related reinforcement, how and through what mechanisms is information transformed into long-lasting knowledge during General Learning? To answer this question, it is first necessary to focus attention on the neural networks that involve the structures that have undergone neoteny in our species, since these brain areas are the ones that maintain the characteristics (delayed and incomplete myelination, long periods of neuronal development, greatly increased synapse production, and elevated neuronal metabolism) that presumably make General Learning possible in NHPs.

2.2.1. Structures That Experience Neoteny in Cognitive Development

Adult human association areas, such as the ACC (anterior cingulate cortex), appear to have retained a high degree of plasticity and synaptic activity through an increase in the expression of certain genes related to brain development [121] and there are also many neotenic genes whose expression in humans corresponds to that occurring in the dorsolateral prefrontal cortex (DLpfc) of young chimpanzees [10], the dlPFC and ACC are closely related to WM (working memory) [122-125]. Furthermore, some association areas of our brain, related to cognitive functions, seem to retain a high synaptic activity and a great neuronal plasticity during adulthood since they show high levels of aerobic glycemia, among them we have the DLpfc, related to working memory (WM) and the DMN (integrated by the VMpfc (ventromedial prefrontal cortex), the DMpfc (Dorsomedial prefrontal cortex), the PCC (posterior cingulate cortex), the inferior parietal lobule (IPL), the lateral temporal cortex, the hippocampus and its surroundings), related to autobiographical memory, planning, social interaction and navigation, theory of mind and moral decision making [38, 126]. In summary, the frontoparietal net and executive control net (FPN-ECN) (related to WM) and the DMN (on which WM acts) contain the neuronal structures that experience neoteny during cognitive development in our species.

2.2.2. The Importance of CPDL for Working Memory, Cognition, and Learning

The CPDL does not store the representation of the processed stimuli [127, 128], but rather generates a descending signal that activates the posterior regions, where the representations are actually stored [127, 129].

2.2.3. Importance of Working Memory for Cognition and Learning

The increase in the capacity of WM to retain the representation of stimuli predictably has a lot to do with the cognitive skills that made possible the construction of the complex and sophisticated world in which we live today [130-135], but it is not as important the quantity of what WM retains as its quality [136], this is because the ability to acquire knowledge and skills depends on WM [137, 138]. Efficient performance on WM tasks guarantees good results in reading [139], arithmetic problem solving [140] and good calculation skills [141, 142]. Moreover, good WM is also responsible for correct language learning, reading [143] and motor skills [144, 145]. And WM is also directly related to fluid intelligence and academic performance [137, 146-151].

2.2.4. Neoteny in the ACC and dlPFC

Several tests performed on a group of 11 transgenic rhesus macaques (carrying human copies of the MCPH1 gene, important for brain development and evolution) indicated an altered pattern of neuronal differentiation that resulted in delayed nerve cell maturation and delayed myelination of neural fibers, a modification similar to the neoteny experienced by our brains. Most notably, these transgenic individuals exhibited improved short-term memory and faster reaction times in the delayed matching-to-sample task (which also demonstrates a greater capacity for WM) [152]. This study could be evidence that neoteny may not be directly linked to learning itself, but rather to the capacity of WM (related to the dlPFC and the ACC, the structures that experience neoteny in cognitive development) to keep the representation of what needs to be known active.

2.2.5. Learning in the Absence of Reward-linked Reinforcement

The general learning process in non-human primates is extremely intensive, as before reaching food independence, subjects have learned almost everything necessary to survive as independent adults [44, 46, 48, 49, 153, 154]. What would make it possible to learn so much in such a short period of time? An important function of the default mode network (DMN) is the encoding and retrieval of episodic memory [155] through its connections with the retrosplenial and hippocampus, the medial prefrontal cortex (MPFC) has encoded and represents objects, contexts, events and adaptive responses (semantic information), so it plays a role in the retrieval of a recent event; but initially the MPFC is not sufficient to retrieve the new memory since the relationship between the context and events with the adaptive responses (the arbitrary visuomotor mapping) of that event will be encoded only in the hippocampus in the form of episodic memory, therefore both the hippocampus and the MPFC are necessary to retrieve a recent memory [156, 157].

The repetition of a memory representation over time causes the synapses that support it to consolidate in the MPFC, thus converting the relationship between the subject, the object, and the event with the adaptive response into a long-term memory within the MPFC. At this point, the hippocampus is no longer necessary for its retrieval, so during the retrieval of remote memories, the hippocampus disconnects, as it is the MPFC that represents and stores the context-event-response mappings [156-159]. In fact, "when stimuli are learned by repetition, they are better remembered and retained in memory for longer because repetitive learning more strongly activates the hippocampus and the connectivity between it and the posterior regions of the Mpfc, which leads to successful retrieval of associative memory" [160]. Everything seems to indicate that after learning by repetition, memory performance improves significantly and is maintained for much longer [161], since repetition improves the relational associations between the different elements that are the object of memory [162, 163], in short, repetition is one of the most powerful variables that positively affect memory and the ability to retrieve memories [164-167]. This would be so because the encoding of information in the WM depends on attention activating the perceptual representation of objects when we do not see them and this occurs through a rehearsal process (repetition of the representation) that keeps the information activated through reverberant signals (from top to bottom) generated in the frontoparietal network that activate the regions that contain information related to that which is represented in the WM [168].

Because of what we have just exposed, we believe that everything that NHPs learn during the General Learning process (the properties and possibilities of objects, subjects, actions and events; the physical properties of the natural environment and the peculiarities of the social environment, in short, semantic learning), would predictably occur with the prominent participation of the WM capacity to activate and maintain again and again the episodic memories of the hippocampus so that the information they contain becomes long-term (semantic) memories within the Mpfc [156-158]. Thanks to this semantic learning of how the world around us works, the DMN is thought to put into operation some form of probabilistic estimation of past, hypothetical and future events, estimation that is used in both social and ecological events [38, 155, 169-172]. This semantic knowledge would allow the DMN to continuously predict the environment using mental images [173]. Could the WM capacity to activate and maintain representations be the cognitive tool that makes it possible for NHPs to learn in the short time from birth to food independence almost everything they will need to survive for the rest of their lives, both in terms of General Learning and in terms of Goal Learning?

2.2.6. Working Memory Would Enable the Repetition Necessary for Learning, When Reinforcement Learning Is Not Available

Intelligence growth could be related to the increase in WM's capacity to maintain novel stimuli in mind [174]. Everything that needs to be learned is new, but depending on whether the stimulus currently being worked with is familiar or not, WM functions differently in both H. sapiens and NHP [175-179]. What is familiar to us (a place, an object, an action or an individual) is automatically recognized very quickly since it is not expensive for the WM to keep the representation of something known activated [180-182], on the contrary, when it comes to unknown stimuli (which are precisely the object of learning) the representation is slow, complex and above all, expensive (it requires a high metabolic activity) [35, 175, 180, 181, 183]. In fact, new stimuli require controlled processing that requires great effort [184]. In this process, in our case, the left DLPFC, the left anterior insula, the superior parietal cortex, the anterior cingulate cortex and the pre-supplementary motor area are activated [123-126], but above all, the fronto-striatal circuit that is responsible for the encoding of novel stimuli is very important [185-192] and finally, the perirhinal cortex (PRh) also plays a key role in the processing of novel objects [193-195].

Although there are studies that seem to show that WM in macaques is not activated when the stimuli are unknown [178, 196-198] there are also others that show that macaques are able to categorize novel stimuli by recoding them according to their biological relevance, animation and kinship with other stimuli [196-202]. This suggests that the capacity of WM to maintain the representation of unknown stimuli may have appeared 32 million years ago [203, 204]. A high WM capacity (during the infant-juvenile stage of NHPs) to activate and maintain the representation of novel stimuli encoded in the episodic memories of the hippocampus could perhaps support the rapid acquisition of the wide arsenal of knowledge exhibited by our primate relatives shortly before weaning, by making it possible, through the repeated activation of novel stimuli, for these episodic memories to be transformed into long-lasting semantic knowledge encoded in the MPFC.

2.2.7. Representing Novel Stimuli During Adulthood May Be What Allows Us to Develop General Lifelong Learning

Having shown that in the absence of reward value, learning probably requires more than ever a large working memory capacity to activate and maintain the representation of novel stimuli, and that because this capacity is extremely complex and metabolically costly, it could provoke oxidative stress, being therefore susceptible to being significantly reduced in NHPs with the arrival of food independence, could the end of late myelination, of the great proliferation of synapses and the cessation of the enormous neuroplasticity cause a considerable decrease in the capacity of WM to activate and maintain the representation of novel stimuli that must be learned? If this were the case, could the cessation of the great capacity of WM to maintain representations of unknown stimuli be the event that puts an end to the General Learning process, the end of the critical learning period? And if this were to happen, could it be that by maintaining the H. sapiens brain (as a consequence of the neoteny of our cognitive development) the late myelination, the great neuroplasticity and the overproduction of synapses, what in practice happens is that our WM maintains during adulthood a high capacity to represent novel information, thereby making it possible for General Learning to continue functioning well beyond maturity in our species? Let us remember, the growth of intelligence could be related to the increase in the capacity of WM to maintain novel stimuli in the mind [177].

3. Discussion

Against these two questions, which we have reached as conclusions 1 and 2, is the fact that much of what we presented in the first part of this review, regarding the General Learning process, links it to exploratory manipulation [66-72]. So, why not consider that the characteristics of neuronal development in juvenile nonhuman primates (high neuronal plasticity, tremendous synaptic development, and late myelination), which, as a consequence of neoteny, remain active in adult H. sapiens, are related solely to exploratory manipulation? Studies of the ontogeny of exploratory behavior in human infants show that visual, manual, and oral object manipulation peaks around 2 years of age and then declines [79, 205], with the exploratory tendency also decreasing as exposure time and familiarity with the object increase [72], from which it can be inferred that the neotenic characteristics of human cognition could not predictably be related solely to exploratory manipulation since, as in non-human primates, this is not maintained in us either.

On the other hand, why couldn't the neuronal neoteny experienced by H. sapiens simply be a consequence of a superlatively increased cognitive and learning capacity in structures such as the DLpfc, the ACC and the DMN? After all, what happens in the juvenile stage of our primate relatives is an increase in synapses, a greater degree of neuronal plasticity and a delay in myelination [1, 2], characteristics that contribute to an increase in the capacity for storing and processing information [3, 4]. As we saw, when reinforcement learning linked to rewards is not involved, learning occurs because the repeated representation of an episodic memory in the hippocampus ends up becoming a long-term memory in the Mpfc [158-160]. Although our cognitive development is characterized by the overproduction of synapses, high plasticity and late myelination until adulthood [1, 2], when we want to learn many things (not directly linked to survival) in a short period of time, such as when we study for an exam. We are forced to incessantly repeat, using the great capacity of our WM to represent novel stimuli, the contents that we want to become long-term memories in the Mpfc. Something that would not be necessary if neoteny consisted simply in an overcapacity for learning and cognition since everything would be automatically encoded for us and therefore there would be no need to study for exams. Furthermore, as we saw, human neoteny is linked to a greater learning capacity, but apparently, through an increase in the retention capacity of WM [152].

4. Conclusion

Despite all the ideas we have just presented during the discussion to try to validate the importance that conclusions 1 and 2 described above could have, I have not found studies that show that there could be a significant decrease in the capacity of WM to maintain the representation of novel stimuli during the transition of NHPs to the adult stage of life. However, the ability of an adult NHP to maintain the representation of unfamiliar stimuli [203, 204] by associating them with other stimuli in relation to their biological relevance, animacy, or relatedness [197, 200, 202] might be less complex and much less metabolically costly than maintaining the representation of novel stimuli during the first years of life [35, 175, 180, 181, 183] (when there is nothing or little with which to relate all the new things that need to be learned) This circumstance described leads us to think that, if there were a considerable decrease in the capacity of WM to represent novel stimuli during the transition from youth to adulthood in NHP, this could have been overlapped in the studies and research carried out by the fact that presumably in the adult stage of life it could be easier and less costly to represent unknown stimuli by associating them with the wide arsenal of knowledge that adults have.

Finally, I would like to point out that even if evidence were found of a significant change in the capacity of WM to maintain representations of novel stimuli during the transition from juvenile to adult life in NHPs (which would allow us to think that, given its predictable implications in making General Learning possible during the adult stage of life, this fact could have contributed to the evolutionary process followed by our species), it would still be necessary to explain how the first carriers of a brain that would generate oxidative stress from weaning onwards, making it incompatible with the proper functioning of cognition, could have survived. More than enough reason to take the conclusions of this review with great caution.

5. Recommendations

Although empirical data seem to indicate that there are not one, but two distinct learning processes that complement each other and occur simultaneously during the early life stages of our primate relatives, many more studies on the capacity of working memory to represent novel stimuli in early childhood are needed to either refute or confirm the hypothesis presented in this review.

Abbreviations

NHP	Non-human Primates
DMN	Default Mode Network
A1	General Learning
A2	Goal Learning
ACC	Anterior Cingulate Cortex
DLpfc	Dorsolateral Prefrontal Cortex
WM	Working Memory
VMpfc	Ventromedial Prefrontal Cortex
DMpfc	Dorsomedial Prefrontal Cortex
PCC	Posterior Cingulate Cortex
IPL	Inferior Parietal Lobule
FPN	Frontoparietal Net
ECN	Executive Control Net
MPFC	Medial Prefrontal Cortex
PRh	Perirhinal Cortex

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Author Contributions

Lic Hernan Perez Ramos is the sole author. The author read and approved the final manuscript.

Conflicts of Interest

The authors declare that there is no conflict of interest, as this work is the responsibility of a single author who received no funding for its completion.

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