Review

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An Assessment of the Evolution of Executive Functions

Yürütücü İşlevlerin Evrimi Üzerine Bir Değerlendirme

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ABSTRACT

Cognitive evolution, as the core subject of fields like paleoanthropology, cognitive archeology, and neuropsychology, has begun to gain more interest in psychology in recent years. Executive functions are viewed from the perspective of cognitive evolution as basic advancements that are crucial to the evolution of language and contemporary cognition. As a metaphor, executive functions refer to advanced cognitive processes (working memory, inhibition, organization, cognitive flexibility, etc.) in the context of complex goal-directed behaviors. Sophisticated cognitive traits like executive functions emerged because of solutions to adaptive issues (survival, reproduction, and social group life) that human ancestors confronted over millions of years and passed them on to their offspring. Although it is accepted that Homo sapiens owes its evolutionary success to Paleolithic living conditions, explaining this process has not always been easy. In this review article, general information about executive functions is presented, followed by a review of scientific explanations about the evolution of executive functions. Evaluations have shown that these alternative scientific explanations based on archaeological, anthropological, and neuropsychological evidence for the evolutionary origins of executive functions do not fit all the pieces of the puzzle. It is believed that novel research models will clarify which of these alternative explanations are proximate causes and which are ultimate causes.
Keywords: Executive functions, cognitive evolution, evolutionary psychology

ÖZ

Bilişsel evrim, paleoantropoloji, bilişsel arkeoloji ve nöropsikoloji gibi disiplinlerin kalbindeki bir araştırma alanı olarak, son yıllarda psikolojide daha çok ilgi görmeye başlamıştır. Bilişsel evrim açısından bakıldığında, yürütücü işlevlerin dilin ve modern düşüncenin gelişiminde önemli rol oynayan temel kazanımlar olduğu düşünülmektedir. Bir metafor olarak yürütücü işlevler, hedefe yönelik karmaşık davranışlar bağlamında ileri seviyedeki bilişsel süreçleri (çalışma belleği, inhibisyon, organizasyon, bilişsel esneklik vs.) ifade etmektedir. İnsan atalarının milyonlarca yıl boyunca karşılaştıkları uyum sorunlarının (hayatta kalma, üreme ve sosyal gruplarda yaşama) çözümü ve bunların sonraki kuşaklara aktarılması yürütücü işlevler gibi sofistike bilişsel özelliklerin ortaya çıkmasına neden olmuştur. Homo sapiens'in evrimsel başarısını Paleolitik çağdaki yaşam koşullarına borçlu olduğu kabul edilse de bu süreci açıklamak her zaman kolay olmamıştır. Bu bağlamda, bu derleme makalede, yürütücü işlevler hakkında genel bilgiler sunulduktan sonra yürütücü işlevlerin evrim süreciyle ilgili ileri sürülmüş bilimsel açıklamalar gözden geçirilmektedir. Değerlendirmeler, yürütücü işlevlerin evrimsel kökenine ilişkin arkeolojik, antropolojik ve nöropsikolojik kanıtlara dayanan bu alternatif bilimsel açıklamaların yapbozun tüm parçalarını tamamlayamadığını göstermiştir. Yeni araştırma modellerinin bu alternatif açıklamalardan hangilerinin yakın neden (proximate), hangisinin asıl neden (ultimate) olduğunu netleştireceğine inanılmaktadır.
Anahtar sözcükler: Yürütücü işlevler, bilişsel evrim, evrimsel psikoloji

Introduction

Executive functions consist of top-down processes responsible for the regulation, control and monitoring of thought and behavior. Due to its domain-general nature, executive functions should be considered as a basic capacity involved in cognitive, affective, emotional, and motor processes (Heidlmayr et al. 2020). In recent years, executive functions have been reductively defined as a set of separate but interrelated elements that mediate the emergence of goal-directed thought and behavior (Doebel 2020). Although there is no clear taxonomy agreed upon in the relevant literature, cognitive processes such as working memory, inhibition, planning, organization, problem solving, emotional control and social behavior, monitoring, cognitive flexibility, attention control, verbal fluency and reasoning are all included under the title of executive functions.

Executive functions include the processes necessary to achieve good performance in complex tasks (Daimond et al. 2007). These information processing processes play crucial roles in human life, from mental and physical

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health to work and school success, healthy developmental processes, and well-being in life, and have significant functions in cognitive and social adaptation (Jurado and Rosselli 2007, Völter et al. 2022). In this context, understanding why and how executive functions emerged in the evolutionary process will make important contributions to the scientific explanation of the mental and behavioral characteristics of modern humans. Experts evaluate cognitive evolution from this perspective. "The human mind is the most complex natural phenomenon we have ever encountered, and Darwin's gift to those who want to understand it is evolution, the knowledge of the process that created it and gave it its unique organization" (Cosmides and Tooby 1992). In this context, the aim of the present article is to review the evolutionary explanations put forward for the emergence of executive functions. For this purpose, general information about executive functions will be given and then these explanations will be discussed.

Historically, the famous neurologist Alexander Luria, who first introduced the concept of executive functions, stated that processes such as planning, control, flexibility and monitoring are the basic elements of the executive function model and that the frontal lobe is responsible for this mechanism (Luria 1966, 1973, 1980). Simultaneously, Lezak (1982) defines executive functions as the capacity to set goals for effective and creative behaviors, to make plans, to realize what is planned and to execute them effectively and suggests that these capacities should be considered in the evaluation of executive functions.

Executive functions consist of neural networks involving different regions of the brain, especially the prefrontal cortex, which is responsible for controlling and monitoring functions (Ardila 2008). In this sense, it should be noted that the first knowledge on executive functions was obtained from people with frontal lobe damage. Phineas Gage, one of the most popular cases called "No Longer Gage", which Harlow (1869) brought to the neuroscience literature, is a 25-year-old young man working as a foreman on the railroad. When the gunpowder used to break rocks during railroad construction negligently exploded, an iron crowbar weighing about 6 kg entered the left side of Gage's face and exited the upper left corner of his skull. This accident caused him to suffer serious brain damage. After months of hospitalization, Gage recovered, but began to exhibit bizarre behavioral traits. Although Gage has no problems with his intelligence or memory, his personality has undergone significant changes. Before the accident, Gage was an outgoing, responsible, and industrious individual. However, after the accident, he began to exhibit some characteristics of a maverick, someone who preferred to spend all his time wandering the streets, and someone whose judgments were subject to sudden change.

People who knew Gage expressed amazement when they heard that he was no longer the same Gage, that his personality had entirely altered, and that he displayed bizarre demeanors, according to Dr. Harlow (1969). Investigations revealed that Gage suffered from frontal lobe injury, which caused significant difficulties with cognitive functions including planning, organizing, establishing goal-oriented actions, developing strategies, and making judgments. After medical treatment, Gage was unable to regain his previous sanity. In this sense, the case of Phineas Gage is considered one of the milestone cases in neuroscience in terms of demonstrating the importance of healthy executive function processes.

Executive functions are grouped into two categories: "cold" and "hot" cognitive features. In contrast to hot cognitive functions, which are high-risk, reward/punishment-based information processing processes with affective, emotional, and motivational components, cold executive functions are abstract, context-independent procedures without affective aspects (Zelazo and Carlson 2012, Zelazo and Müller 2002). Although the distinction between cold and hot functions has been made in studies with people with brain injury, these processes are thought to be part of a general adaptive function that works together (Zelazo and Carlson 2012). In this context, hot functions have been shown to be more associated with emotional problems, while cold functions are more associated with academic success (Poon 2018).

Neuropsychology of Executive Functions

The human brain's frontal lobes have been shown to be more developed than other brain regions (Semendeferi et al. 1997). Because different regions of the frontal lobes are responsible for different executive functions, there is no single task to measure frontal functions, and because frontal functions have important effects on processes other than executive functions (psychosocial and emotional development, consciousness, awareness, etc.), it is difficult to clearly explain the relationships between frontal functions and executive functions (Stuss and Alexander 2000). However, we see that frontal functions and executive functions are commonly used as synonyms in the literature.

The prefrontal cortex, which is responsible for executive functions, anatomically consists of three parts: Dorsolateral, medial, and orbitofrontal areas. It is observed that the dorsolateral prefrontal cortex is responsible for cognitive tasks such as abstract reasoning, planning, organization, problem solving, and working memory, whereas the medial and orbitofrontal areas (called ventromedial areas) have more connections with the amygdala and limbic system and are mostly related to the integration of emotion and cognition and motivational responses (Ardila 2008, Happaney et al. 2004). The dorsolateral prefrontal region is associated with higher cognitive executive functions, while the ventromedial prefrontal cortex is associated with emotional/motivational executive functions (Ardila 2008). In this sense, dorsolateral frontal and orbitofrontal areas support different executive functions as two basic areas that work together interactively (Happaney et al. 2004).

In studies conducted with patients with ventromedial prefrontal damage, the importance of these areas in personality, memory, emotional expression, decision-making and social cognition has been emphasized, and dramatic changes have been observed in the personalities and social behaviors of these patients, as in the case of Gage (Schneider and Koenigs 2017). On the other hand, it has been reported that dorsolateral prefrontal cortex functioning plays a key role in executive functions and general intelligence, and lesions in this brain region cause general intelligence deficits (Barbey et al. 2013). Yuan and Raz's (2014) meta-analysis revealed a strong correlation between executive functions in healthy adults and prefrontal cortex size, particularly in the lateral and medial regions. Prefrontal cortex size and cortical thickness were found to be markers of excellent cognitive ability, supporting the "bigger is better" theory. According to the network model proposed by Salehinejad et al. (2021), it has been shown that the dorsal anterior cingulate cortex and lateral prefrontal cortex are associated with cold executive functions (inhibition, attention control, working memory, etc.), while the ventral anterior cingulate cortex, posterior cingulate cortex and medial-orbital prefrontal cortex are associated with hot functions. Using this network-based approach, researchers have been able to identify more efficient intervention strategies as well as comprehend the pathogenic processes behind neurological and mental illnesses.

Development of Executive Functions

Beginning in infancy and continuing through adolescence and maturity, executive function abilities continue to develop. Inhibition, working memory and cognitive flexibility are known as basic executive skills acquired during developmental periods (Best and Miller 2010, Diamond 2013, Miyake et al. 2000). It is accepted that inhibition is the most basic function that develops in the control of emotion, thought and behavior in childhood (Serpell and Esposito 2016). From childhood to adulthood, the decrease in gray matter and the increase in white matter and myelination in the frontal and parietal areas are parallel to the increase in cognitive capacity in these areas (O'Hare and Sowell 2008). Lateral, and medial prefrontal lobe volume and prefrontal cortical thickness have been shown to be associated with strong executive functions in healthy adults (Yuan and Raz 2014).

The maturation process of executive functions takes place with certain developmental leaps that are specific for each function (Jurado and Roselli 2007). For example, it has been found that working memory skills, which progress from childhood, show a developmental leap between the ages of 11 and 15-19, reaching a maximum level in early adulthood (Anderson et al. 2008). The results of the study conducted by Poon (2018) showed that the progress in cold executive functions such as working memory, attentional control, cognitive flexibility, and inhibition was relatively slow in the early adolescence years and made a developmental move around the age of 14; planning skills made progress around the age of 16. A bell-curve pattern of development was obtained in hot functions during adolescence. Reward and choice impulsivity peaks in mid-adolescence (14-15 years of age) and maturation begins at 17 years of age. With the anatomical changes that occur in the brain with advancing age, executive skills also decline. A research on this subject, for instance, revealed that working memory and inhibition begin to deteriorate in the 30s and 40s and continue to do so until old age (Ferguson et al. 2021).

Measurement of Executive Functions

One of the challenges is the difficulty in measuring and rehabilitating executive functions with valid and reliable tools due to their complex and modular nature (Chan et al. 2008). Although they have been criticized for their ecological validity, we see that executive functions are mostly assessed with performance-based tests. Situations such as some patients being successful in one test but not in another, and the same test measuring two different executive functions cause test practitioners to doubt the content of the test (Jurado and Rosselli, 2007). Furthermore, it is noted that rating scales are widely utilized, despite several debates concerning their drawbacks. While performance measures are used to provide information about cold cognitive skills, rating scales are more commonly used to assess the use of hot functions (emotional/behavioral) and skills based on hot functions in daily life (Isquith et al. 2013).

The most used standardized tests to assess executive functions and frontal lobe damage are the Wisconsin Card Matching Test (WCMT), Stroop Color and Word Test (SCWT), Tower of Hanoi Test (THT), Trail Making Test (TMT), and Controlled Word Association Test (CWAT). The WCMT, developed by Berg (1948), is considered as the gold standard in assessing executive functions (Kopp et al. 2021). In the test, which consists of target and response cards with different colors and shapes from different categories, the person is asked to correctly match each of the response cards with the target card presented. The test material in the current version consists of four stimulus cards with different colors and amounts of shapes and two decks of 64 cards each with the same type of shapes. The matching category changes after 10 consecutive correct matches. In the test, which was adapted to Turkish culture by Karakaş et al. (1999), 13 different scores are calculated. These include the total number of wrong and total number of right answers, the number of categories finished, the number of perseverative and non-perseverative errors, the percentage of perseverative errors, the number of responses used to finish the first category, the number of conceptual level responses, the percentage of conceptual level responses, and the inability to maintain the set-up score. This test, in which feedback is provided to the participant throughout the application, specifically measures set shifting, inhibition, cognitive flexibility, organization, and abstraction (Miyake et al. 2000).

The SCWT is based on the Stroop Effect explained by Stroop in 1935, which is based on the comparison of the time to read the color names with the time to name the colors themselves and shows the interference effect of reading on naming. The SCWT is a test that evaluates skills such as inhibition of attention directed to an irrelevant stimulus, suppression of the interference effect, and conflict resolution (Heidlmayr et al. 2020). In this sense, the Stroop task reveals an information processing that requires restrictive control (Kaynak & Erdeniz, 2019). The Stroop Test, which was developed by utilizing the original test created by Stroop (1935), is among the tests frequently used all over the world today with its different versions. The Stroop Test TBAG Form, adapted to Turkish culture by Karakaş et al. (1999), consists of five sections (black color names, colored color names, colored circles, colored neutral words, and colored color names) in which four cards are presented.

The Tower of London Test (Shallice 1982) is one of the tests measuring planning and inhibition skills developed based on the Hanio Tower Test (Simon 1975). The standardization of the test in Turkish culture was carried out by Atalay and Cinan (2007). Another test for frontal lobe function measurement is the TMT (Armitage 1946). Originally, this test consists of A and B forms. In part A, the participant is required to draw 25 series of 25 circled numerals in numerical sequence to link them. In part B, the participant is expected to combine 25 circled numbers and letters in the correct order, arranged in numerical and alphabetical order. The standardization of the TMT in Turkish culture for a sample aged 50 years and older was conducted by Cangöz et al. (2007). Executive functions such complex attention, planning, set switching, and response inhibition are evaluated, particularly in form B (Cangöz 2009). The quantity of mistakes made during the allotted time for sections A and B, as well as the quantity of corrections, are factors considered in the scoring process. Eight different scores are calculated for the entire test.

The Iowa Gambling Test (IGT) is one of the popular psychological tests in which a patient's decision-making behavior is assessed in a simulated real-life task. Developed by Bechara et al. (1994) and used to assess impairments in real-life decision-making processes of patients with ventromedial prefrontal damage, the IGT is based on the concepts of uncertainty, choice, reward, and punishment. Patients were presented with four different decks and were expected to choose cards that would make or lose money. Advantageous cards are less likely to win but less likely to lose. Disadvantageous cards have a higher probability of winning more money but a higher probability of losing it. Low scores on the IGT, a test designed specifically to measure hot executive functions, have been linked to disorders like impulsivity (Burdick et al. 2013), eating disorders (Brogan et al. 2010), gambling addiction (Linnet et al. 2010), and alcoholism (Maurage et al. 2014). In this test, whose normative data in a healthy Turkish sample were examined by İçellioğlu (2015), a total net score and five separate net scores for each of the 20 cards are calculated. The total net score is obtained by subtracting the number of disadvantaged decks selected throughout the entire test from the number of advantageous decks selected throughout the entire test.

The main tests used in children and adolescents are the Behavior Rating Inventory of Executive Functioning (BRIEF; Gioia et al., 2002), which assesses the executive functions of children and adolescents aged 5-18 years and preschool children through their behaviors in daily life, and the Childhood Executive Functioning Inventory (CHEXI; Thorell & Nyberg, 2008) for children aged 4-7 years. There are parent and teacher versions of BRIEF, totaling 86 statements in both formats. The validity and reliability study of BRIEF, which is assessed with a three-point Likert-type scale, was conducted by Batan et al. (2011). High raw scores and T scores ($t>65$) indicate advanced executive dysfunction. The adaptation of the CHEXI into Turkish was conducted by Kayhan (2010).

Studies on the validity and reliability of the teacher form and parent form of the CHEXI, which were designed for 48-72-month-old children, were carried out by Arslan-Çiftçi et al. (2020) and Hamamcı et al. (2021), respectively. A 5-point Likert scale is used on the forms for parents and teachers. Both forms include 24 items total and are divided into two subscales: working memory and inhibitory control. High scores on the scales indicate executive function difficulties.

One of the measures and inventories that is often used worldwide to evaluate behavioral, emotional, and cognitive symptoms associated with everyday tasks and to identify executive dysfunctions is the Executive Dysfunction Scale for Adults (Pedrero-Pérez et al. 2015). The Scale for Assessing the Development of Executive Functions in Children was created in our nation by Taşkın-Gökçe and Kandır (2020) to measure the development of executive function in young children (48-72 months old). Working memory, empathy, and inhibition of self-regulation are the three qualities measured by this 116-item test, which is based on information from instructors.

Relationship of Executive Functions with Psychopathology

The literature provides a comprehensive examination of the association between deficiencies in executive function and the psychopathologic picture that manifests in a variety of ways. Although different opinions continue to be reported on whether executive function deficits are the cause or the consequence of psychopathology, its link to psychopathology has been shown in many studies conducted with children (Martel et al. 2017, Zelazo 2020), adolescents (Bloemen et al. 2018), young adults (Lantrip et al. 2016, Romer and Pizzagali 2022), and older adults (Zainal and Newman 2023). The higher-order construct model (Michelini et al. 2019) explains psychopathology in general hierarchically with a top-level p-factor and five lower-level factors. These five specific factors in the psychopathological structure include symptoms such as externalizing (disobeying rules, attacking people), internalizing (anxious or depressed mood), neurodevelopmental (attention deficit and hyperactivity), somatization (pain, vomiting) and dissociation (withdrawal, refusal to talk). Romer and Pizzagali (2021) employed this model to conduct a longitudinal study with children ages 9 to 12 years, controlling for gender, age, race, history of psychopathology, parental education, and income level. The study's findings indicated that executive function deficits are a consequence of general psychopathology as well as a predictive factor (a risk sign). In this regard, it is important to understand how executive function deficiencies may contribute to the development of juvenile psychopathologies.

Neurodevelopmental Disorders

Executive function deficits have an important place in the etiological explanation of neurodevelopmental disorders. It has been observed that children aged 8-14 years with attention deficit hyperactivity disorder (ADHD) and specific learning disabilities (SLD) are behind in inhibition and set switching tasks compared to their healthy peers, and specifically, verbal, and visuospatial task distinctions of working memory differentiate ADHD and SLD profiles (Crisci et al. 2021). Individuals with ADHD fail more on visuospatial tasks, while those with SLD fail more on verbal tasks. In one study, executive dysfunctions (inhibition, set switching, emotional control, working memory, and planning/organization) observed around the age of four years were shown to be predictors of autism spectrum disorder (ASD) and ADHD features observed 2-3 years later (Otterman et al. 2019). Specifically, it has been reported that deficits in set-shifting skills are more associated with ASD symptoms, while inhibition, working memory, and planning/organization deficits are more associated with ADHD and ADHD-like clinical symptoms.

In studies, oppositional defiant disorder (ODD) was found to be associated with hot executive functions (Iowa Gambling Test) compared to ADHD, while deficits in cold executive functions are different from the profile in ADHD (Antonini et al. 2015, Hobson et al. 2011, Yang et al. 2011). It has been suggested that reward-punishment functioning is associated with ODD, but not with ADHD symptoms. On the other hand, impairments in cold/hot executive functions as well as cognitive delay in ADHD have been shown to be associated only with hot functions (Rastikerdar et al. 2023). It has been reported that clinical groups consisting of ODD, ODD+ADHD fail in cold executive tasks (e.g., planning) and hot executive tasks (e.g., delay of gratification and externalization) compared to healthy groups (Dolan and Lennox 2013).

According to Barkley (2015), there is an important link between the capacity for self-control and executive functions. Self-control is a functional trait that has emerged evolutionarily largely for a range of social functions, such as self-defense, social exchange, collaborative coalitions, and vicarious learning. Indirect learning and imitation create an evolutionary advantage for human ancestors to benefit from the experiences of others in the most costless way (Barkley 2001). In this regard, it seems that more research is needed to understand social dysfunctions such as self-regulation problems in ADHD.

Another neurodevelopmental illness known as Tourette syndrome is caused by frontostriatal malfunction. Individuals with Tourette syndrome experience uncontrollable repeated behaviors such as tics. Executive dysfunctions have also been identified in studies on this syndrome. It has been reported that executive dysfunctions are specific to this syndrome, mostly in inhibitory control and cognitive flexibility, but with less severe impairments in planning and decision-making (Morand-Beaulieu et al. 2020).

Executive Functions in Psychiatric Disorders

Healthy information processing requires healthy executive functions. Therefore, impairments and deficits in these functions are thought to be precursors to many psychopathological conditions. Many studies have shown a strong correlation between executive function problems and psychiatric disorders. For example, schizophrenia (Haugen et al. 2021), personality disorders (Garcia-Villamisar et al. 2017, Gvirts et al. 2015), obsessive-compulsive disorder (Olley et al. 2007), major depression (Matsuo et al. 2007), anxiety disorders (Warren et al. 2021), eating disorders (Blume et al. 2019, Diaz-Marsa et al. 2023). A fMRI study conducted with 1129 young people with an average age of 15 years found that psychotic symptoms were associated with hypoactivation in the left dorsolateral prefrontal cortex, while behavioral symptoms were associated with hypoactivation in the frontoparietal cortex and cerebellum. On the other hand, anxiety and sadness symptoms were found to be associated with hyperactivation in the executive function network (Shanmugan et al. 2016).

Obsessive Compulsive Disorder

Prefrontal dysfunction is recognized as one of the main causes of obsessive-compulsive disorder (OCD). Planning, decision-making, conceptualizing, and encoding challenges in nonverbal memory are signs of executive dysfunction in individuals with OCD (Kashyap et al. 2013). In a study comparing OCD patients with active symptoms, OCD patients in remission and panic attack patients, inadequacies in set switching and inhibition were observed in OCD patients. Research has revealed a connection between OCD and abnormalities in the anterior cingulate cortex, superior medial prefrontal, and dorsolateral prefrontal brain regions (Kashyap et al. 2013). Cortico-striato-thalamo-cortical circuit impairment was discovered during executive tasks in an fMRI research including OCD patients (Del Casale et al. 2015). It has been determined that executive function deficits in OCD remain constant over time, and in this sense, these deficits have acquired trait characteristics (Bannon et al. 2006). Conversely, some researchers contend that poor executive function utilization leads OCD patients to employ more adaptive strategies (excessive control) that reduce anxiety, which exacerbates OCD symptoms and limits the therapeutic benefits for patients (Synder et al. 2015).

Schizophrenia

Schizophrenia is a severe mental illness with neuropsychological disorders (attention, executive functions, etc.) along with positive (hallucinations, delusions, movement disorders, etc.) and negative symptoms (withdrawal, monotonous affect, asociality, etc.) (Choudhury et al. 2009). Brain imaging studies on working memory and executive function disorders in schizophrenia have found abnormalities in the frontal and medial temporal lobes (Raffard and Bayard 2012). Schizophrenia patients with predominant positive symptoms showed lower performance in all cold executive functions (such as working memory, planning, and cognitive flexibility) compared to healthy individuals (Ruiz Castañeda et al. 2022). However, patients with schizophrenia have also been reported to have deficits in hot executive functions such as emotion recognition and theory of mind. It was found that 81.5% of these patients had dorsolateral, 77.8% had anterior cingulate, and 59.3% had orbitofrontal syndrome.

Executive dysfunctions in schizophrenia are quite heterogeneous. Some patients fail in three tasks, while others fail in one or two tasks. These differences are assumed to result from the diversity of executive functions and the effects of general cognitive factors such as intellectual level and general processing speed (Raffard and Bayard 2012). In a study conducted on this subject, it was found that many schizophrenia patients have poor insight due to inadequate executive functions (Choudhury et al. 2009). In this study, it was observed that 70 percent of the participants did not have sufficient awareness about their illness.

Bipolar Disorder

People with bipolar disorder (BD) face many cognitive and emotional challenges, the most important of which is executive dysfunction. For instance, compared to euthymic bipolar patients, manic bipolar patients have been observed to have more impairment in hot executive processes (Bernabei et al. 2018). Manic individuals were shown to perform much worse than healthy controls on tasks involving cool executive function. These results suggest that hot executive functions are more closely related to mood than cold functions. In a research on bipolar disorder, impaired set switching and increased risk-taking were identified as indicators of the condition in relation to frontolimbic connectivity problems (Linke et al. 2013). Regarding the phases of the disorder, it was found that verbal fluency and processing speed worsened in the depressive and hypomanic/mixed phases, and inhibition control worsened in the manic phase (Ryan et al. 2012).

Personality Disorders

The genesis of personality disorders is significantly impacted by impairments in executive functioning. In borderline personality disorder, which is characterized by symptoms such as suicidal tendency, substance use, risk taking and suicide attempts, it has been found that there are problems in executive functions, especially planning, working memory, attention, and problem solving (Gvirts et al. 2012, Ruocco 2005). Emotion regulation difficulties seen in borderline personalities stem from problems in cognitive control. In a research using brain imaging, individuals with borderline personality disorder showed decreased activity during negative affect in the regions of the amygdala, anterior cingulate, and dorsolateral prefrontal cortex when compared to healthy subjects (Ruocco et al. 2013). It has been found that the cognitive load brought on by the pursuit of high self-interest causes maladaptive behaviors, including conscious and unconscious inhibition and working memory issues, in individuals with antisocial personality disorder (Stuppy-Sullivan and Baskin-Sommers 2019). However, a study conducted with 524 healthy adults aged 21-35 found that high levels of antisocial impulsivity and fearlessness-dominant psychopathy traits were associated with serious self-control problems (Lantrip et al. 2016). It was concluded that antisocial impulsivity traits are manifested by monitoring problems, and impulsivity is a general feature of psychopathy.

Executive Functions in Neurological and Physical Diseases

Many forms of dementia are associated with executive function impairments. It was shown that although executive dysfunction is a main feature of frontotemporal dementia (FTD), it is also associated with dementia with Lewy bodies (DLB), albeit not as strongly as FTD (Johns et al. 2009). In one study, impairments in executive functions and working memory were detected in patients with mild to moderate Alzheimer's disease (AD) and vascular dementia (VD), but no significant difference was observed between the two patient groups (McGuinness et al. 2010). A different investigation on executive skills, working memory, and attention revealed qualitative differences between FTD and Alzheimer's patients (Stopford et al. 2012). While it was observed that performance in Alzheimer's disease was affected in terms of information load and working memory capacity, the impairments seen in FTD patients were found to be related to frontal executive processes such as attention, set switching, and response inhibition. These results point to frontal lobe abnormalities in FTD and temporoparietal abnormalities in Alzheimer's disease.

Evolutionary Explanations for Executive Functions

Due to their enormous brains and intricate neurological systems, our ancestors were able to walk upright, make tools, utilize fire, and talk, setting them apart from other members of the primate family in the evolutionary lineage. The continent of Africa is acknowledged as the hub of human emergence. Most of the fossils of the first human species, Homo habilis (skilled man), have been found in East Africa. Beginning with the creation of the first tools, the Paleolithic Age (also known as Old Stone) was the longest and most challenging time in human history, lasting two million years (Şimşek 2017). Homo sapiens (wise human), who emerged in the Upper Paleolithic period and lived in social groups in hunter-gatherer communities, rapidly spread around the world for centuries, establishing countries, civilizations, and cultures.

It is acknowledged that the human mind is a creation of evolutionary processes (Coolidge & Wynn, 2001). One of the common goals of cognitive archaeology, social anthropology, and evolutionary psychology is to explain the evolutionary history of modern human thought with scientific evidence. Although paleoanthropologists emphasize the importance of the Upper Paleolithic period in the evolution of cognitive abilities based on symbolic signs of modern culture such as ritual and art, it has not always been possible to explain this process easily (Coolidge and Wynn 2001). On the other hand, to recall the famous quote of geneticist Theodosius Dobzhansky (1964): "Without the light of evolution, nothing in biology makes sense."

"As an evolutionary adaptation with distinctive features for solving adaptive problems in the human brain, executive functions are universal, complex, improbable, and have signs that they are designed for a purpose"

(Barkley 2001). It is insufficient to explain the question "why and how did executive functions emerge?" with social and cultural factors; these questions also require evolutionary explanations. The human mind is functionally designed to solve adaptive problems, and understanding these problems is the best way to discover how the human mind works (Tooby and Cosmides 1989). In this context, many alternative (albeit speculative) views have been proposed to explain why and how executive functions emerge in primates (Adornetti 2016, Ardila 2008, Barkley 2001, Coolidge and Wynn 2001, Dunbar and Schultz 2017, Rosati 2017). When considered independently, these various viewpoints are shown to fit together some parts of a complicated jigsaw, but not enough to finish it. Further research on this topic is expected to expand our knowledge and comprehension of various factorial models that are validated by scientific data.

In human evolutionary history, the emergence of executive functions has been associated with toolmaking as a purposeful behavior. There are notable correlations between population density, geographic distribution, brain size, and technological advancements (Ambrose, 2001). The earliest humans to employ stone tool technology, Homo habilis, acquired this skill to solve challenges in everyday life and, consequently, to ensure their survival. Cognitive evolution should be thought of as a mosaic, with some features emerging first (e.g., spatial cognition) and others later (e.g., executive functions) (Wynn and Coolidge 2016). Chiseling stone is a skill that requires monitoring how past, present, and future actions relate to each other in a planned manner to achieve a final goal (Adornetti 2016). The development of toolmaking abilities is believed to occur concurrently with frontal lobe activities because they involve the planning and coordination of several subtasks (Ambrose, 2001). Furthermore, a highly developed visuospatial sub-memory capacity of working memory that is independent of language function is linked to toolmaking (Coolidge and Wynn 2005). It is assumed that the executive system is shaped through several evolutionary stages based on verbal and non-verbal working memory. For example, the imitation skill required to make tools has a non-verbal function (Barkley 2001). In this perspective, we may conclude that the Acheulean stone culture of Homo ergaster and Homo erectus during the Lower Paleolithic Period (the ancient stone age) contains the earliest indications of the growth in the ability for action control and organization.

Ardila (2016) considers the cognitive abilities that Homo sapiens acquired 150,000 years ago to survive as pre-adaptations of new cognitive abilities such as grammatical language and executive functions. The construction of prehistoric stone tools is attributed to the process of discourse coherence, which is fundamentally related to the level of action organization and behavioral control (Adornetti 2015). Discourse coherence is one of the pragmatic functions of language mediated by the executive functions of planning, control, and organization. The coherence principle is believed to help structure the sequence of communicative activities and support the evolution of language function in humans by increasing the coherence of speech. In other words, discourse coherence, which is supported by executive functions and represents the pragmatic feature of language, is a prerequisite for the emergence of grammar (Adornetti 2016). Similarly, action perception is recognized as a pre-adaptation for executive functions and grammar, two cognitive skills that emerged simultaneously in human evolution (Ardila 2015, 2016). Thus, the emergence of executive functions in the Homo lineage is attributed to indirect relationships between toolmaking and the origin of language.

The Oldowan culture (chipped pebble culture), produced by Homo habilis in the Lower Palaeolithic, consists of the first simple stone tools chipped from another stone. Acheulean technology, on the other hand, consists of sophisticated, pointed tools that can be used for many purposes such as cutting and chopping, and can be produced from materials such as bone and plants, as well as hard stones such as flint. A team of archaeologists made up of Oldowan and Acheulean technologists was requested to create an example of these tools to comprehend the variations in executive function control that occurred in early humans with the transition from Oldowan to Acheulean (Stout et al. 2008, Stout et al. 2010). When the brain activations of the participating archaeologists were measured during this stone chiseling activity, activation was recorded in the posterior parietal and ventral motor areas during Oldowan tool production, while no significant activation was detected in the prefrontal areas, indicating that Oldowan tool production requires minimal executive function control (Stout et al. 2008). The activation observed in the ventrolateral prefrontal cortex (no activation was found in the dorsolateral prefrontal cortex) during Acheulean toolmaking suggests that Acheulean toolmaking requires hierarchically more organized sensorimotor action sequences. Although toolmaking requires more organizational and planning skills, the increased activation observed in parietofrontal areas and Broca's area in both hemispheres indicates strong connections between toolmaking and language skills. The overlap of activation in toolmaking with language circuits suggests that these two skills have a more complex and general cognitive basis for goal-directed action. These findings are considered evidence of indirect relationships between toolmaking and the presence of executive functions.

The complexity of the ecological environment in which species live and their foraging behaviors are considered one of the factors determining brain evolution (Dunbar and Schultz 2017). Hunter-gatherers' preference for larger habitats than other primates and their willingness to explore remote areas in search of unique food sources contributed to the increase and strengthening of their cognitive capacity (Rosati 2017). According to this perspective, controlling hunter-gatherers' responses by suppressing their tendency to consume the food obtained before returning to their home (inhibition) may have naturally served the emergence of sophisticated executive functions. The best example of response inhibition is agriculture, where harvested crops are stored for the next planting season. According to Coolidge and Wynn (2005), it is not possible to speak of such response inhibition for the Upper Paleolithic period, as we do not have sufficient scientific evidence at present.

Executive functions are late achievements in the cognitive evolution of the Homo species. Under these circumstances, there does not appear to be much agreement on Neanderthal cognitive ability. It has been suggested that the working memory capacity of Neanderthals who lived during the Middle Paleolithic period may have been lower than that of Homo sapiens (Wynn and Coolidge, 2004). In a neuroanatomical study, differences were observed between species in the cerebellum, which has important functions in information processing such as language, attention, and working memory, and it was found that Homo sapiens had larger cerebellar hemispheres than Neanderthals (Kochiyama et al. 2018). Paleoneurological evidence supports this conclusion by demonstrating that both modern humans and Neanderthals had growing and enlarged parietal cortices. Additionally, cognitive archaeology demonstrates that Homo sapiens is the only species that has specialized in working memory and visuospatial skills, in contrast to all other extinct human species, including Neanderthals (Bruner and Colom 2022). Contrary to what has been claimed, Ambrose (2002) asserted that Neanderthals could speak like their common ancestor, Homo heidelbergensis, indicating that Neanderthals possessed considerable executive capabilities that they employed to adapt to evolutionary constraints.

There is no characteristic that distinguishes humans from other animals in terms of cognitive superiority in nature; rather, it is our more adaptable and diverse cognitive capacities that set us apart (Laland and Seed 2021). Differences in the ecological conditions to which non-human primates are exposed have also favored their acquisition of strong executive functions in the evolutionary process (Rosati 2017). For example, when chimpanzees and bonobos were compared in terms of competition for food, bonobos were found to have lower levels of social inhibition than chimpanzees (Wobber et al. 2010). In a study comparing the performance of chimpanzees and humans in working memory tasks, while there were similarities in the anatomy of the prefrontal cortex, the working memory span was 2 ± 1 in chimpanzees and 7 ± 2 in humans, known as the famous Miller's law. It was also found that the working memory performance of chimpanzees corresponds approximately to the working memory performance of 4-5-year-old children in humans (Read et al. 2022).

There are research results showing that absolute brain size is the best indicator of primate cognitive abilities (Deaner et al. 2007, MacLean et al. 2014, Rosati 2017, Stevens 2014, Striedter 2005). When the waiting responses of thirteen primate species (such as lemurs, long-tailed macaques, orangutans, bonobos, gorillas, chimpanzees, etc.) for delayed reward were evaluated in terms of factors such as body size, absolute brain size, relative brain size (brain volume ratio relative to body size), home range distance (the distance between the houses where the group lives), and group size, different results were obtained in terms of the variables examined (Stevens 2014). Significant differences were found between species in terms of willingness to wait for a delayed reward (liquid or solid food). While body mass, absolute brain size, home range size, and life span variables significantly predicted waiting time, no such result was obtained for relative brain size and social group variables. According to the cognitive ability hypothesis, species with higher cognitive abilities were expected to have longer waiting times for delayed reward, and this hypothesis was supported by the findings. These results suggest that evolutionary pressures have different effects on different species in terms of decision-making and cognitive abilities.

A neuroimaging research compared the brains of live humans with the brains of gorillas, chimpanzees, orangutans, gibbons, and macaques that had passed away naturally at a zoo to investigate the size of different species' brains. It was found that humans had the largest absolute brain and largest frontal lobe volume (30.8% macaque, 31.8% gibbon, 27.5% orangutan, 29.7% gorilla, 38.1% chimpanzee, and 35% human); the relative frontal lobe size in humans was similar to other primates (28.1% macaque, 3.1% gibbon, 35.3% orangutan, 32.4% gorilla, 35.9% chimpanzee, and 36.7% human). Humans also showed no relative size difference in the dorsal, mesial, and orbital portions of the frontal lobes. There was very little difference between the relative volumes of the frontal lobes in humans and chimps. As a result, humans have much larger hemispheres in absolute terms, while they do not have a larger frontal lobe than would be expected from a human-sized primate brain (Semendeferi et al. 1997).

From an evolutionary perspective, the observed relationships between brain size and differences in executive function capacity among primates require different approaches to the issue. Dunbar and Schultz (2007) propose that an increase in brain size results in a disproportionate rise in the availability of executive functions, which in turn leads to an increase in sophisticated social behaviors. The capacity of neocortex size (particularly the frontal area) to accommodate ecological adaptive pressures in species determines group size and hence social behavior (Dunbar and Schultz 2007). That is, group size and the level of social complexity are thought to be linked to brain volume in primates, and brain size reciprocally influences social behavior and social behavior reciprocally influences brain development. An analysis of forty-four research on the subject revealed that while diet composition and life history are associated to relative brain size, absolute brain volume, neocortex size, and proportion are related to a species' degree of sociability and cooperation (Schultz and Dunbar 2022). In addition, total brain volume significantly predicts the ecological environment in which the species lives, and neocortex significantly predicts social group size. All these findings imply that ecological, social, and biological factors have different effects on cognitive evolution. This is because a species' cognitive and social traits are closely correlated with the total size of the brain, the relative size of the forebrain, and the quantity of neurons (Schultz and Dunbar 2022). Important relationships have also been discovered between the relative size of the brain and the energy needs and food preferences of species.

The best indicator of human cognitive superiority is having the highest number of neurons among primates. The Homo lineage is distinguished by a larger brain with a larger number of neurons despite their lower physical size, whereas greater hominid apes (the ape lineage) have smaller brains despite their larger bodies (Herculano-Houzel 2012). However, hominid monkeys could not have brain sizes proportional to their body size because they could not afford the metabolic cost of supporting a larger number of neurons. Brain size is a costly and expensive trait as it requires more energy; therefore, smart foraging is seen as an adaptive behavior that distinguishes primates from non-primates in terms of discovering original food sources and inventing original tools (Dunbar and Schultz 2017). In this respect, humans' use of fire for cooking helped them consume food faster and allowed them to meet the metabolic needs of their neurons more easily. Thus, the ability to use other neurons for competition has created an evolutionary advantage for the human species (Herculano-Houzel 2012).

Over the course of evolution, human ancestors became selfish cooperators, living in groups to meet specific environmental selection pressures that arose earlier (Barkley 2001). In this regard, sociability is thought to have had the greatest influence on the development of the primate brain (Dunbar and Schultz 2017, Schultz and Dunbar 2022). All content features of the human mind are socially constructed; the human mind consists of functionally specialized, context-dependent cognitive adaptations (Cosmides and Tooby 1992, 2013). In support of these views, Barkley (2001) argues that the executive function system emerges to solve adaptive pressures (such as mutual altruism and social coalitions, imitation, tool use, mimetic and communication, self-defense against social influence) that emerge as social problems arising from the conditions created by group life. The prefrontal cortex has been shown to be critical for adaptive functioning, as the reciprocal exchange required by living in social groups requires remembering the past (especially delayed), making predictions about the future, and controlling behavior (Barkley 2001).

Conclusion

"Human cognitive uniqueness is not due to traits that are absent in animals, but to their interactions with each other and the feedback provided by cultural and developmental factors that build on and reinforce evolving biological differences" (Laland and Seed 2021). In this sense, executive functions, which are common to the primate family in the evolutionary process, are considered an umbrella concept consisting of a series of mental components responsible for the control of complex goal-directed behavior, thought, and action. Executive functions are generally regulated by the prefrontal cortex. The distinction between purely cognitive executive functions (cold) versus affective-based or reward-centered (hot) functions is demonstrated by the neural specialization found in the prefrontal cortex. Pure cognitive executive processes such as abstraction, problem solving, and planning were found to be associated with the dorsolateral prefrontal cortex, while affective and motivational processes were associated with ventromedial and orbitofrontal areas. The findings obtained from frontal lobe lesions and brain imaging studies continue to enrich our knowledge and reasoning about the mechanisms of psychiatric and neurological disorders and reduce our question marks in this regard.

It has been suggested that executive functions are the fundamental evolutionary achievements that led to the development of modern cognition (Coolidge & Wynn, 2001). As a result of retrospective evaluations in the light of archaeological and anthropological information, various scientific explanations have been put forward for the emergence of human executive functions in the evolutionary past. These explanations include the connection between the construction of the first stone tools and the origins of language, discourse coherence, differences in the ecological environment in which species live, foraging strategies, brain size, differences in the number of neurons, sociability, and adaptive problems caused by living in social groups. It is believed that future research models will clarify which of these alternative factors is the proximate cause and which is the main cause.

Important innovations that have emerged in the human lineage throughout the evolutionary past, such as shared attention and language, have changed the rules of the game while improving the performance of other elements of human cognition (Laland and Seed 2021). In this context, while the selection pressures of nature have an important role in determining the behavioral traits of modern humans, approaching these traits only from this perspective would be a one-sided and reductionist view. According to Tooby and Cosmides (1989), the evolutionary process is slower than the development of history and culture. Although it is accepted that some historical changes, such as food production and disease prevention with population growth in the post-Neolithic period, contributed to the success of adaptation, it cannot be claimed that this is the case for all adaptations. Therefore, even if natural selection has a limited and sluggish corrective capacity, it is thought that this power would eventually fix the aberrations brought about by human destructiveness.

To conclude, while the current review article offers insightful and captivating scientific insights into the evolution of executive functions, it was noted that numerous studies lacked a cohesive explanatory framework, with numerous points being incoherent, unclear, hypothetical, or lacking. Due to the multifaceted nature of cognitive evolution, there is a need for explanatory systems developed from a causal perspective that considers existing and potential factors.

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