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On the evolutionary origins of executive functions

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ABSTRACT

In this paper it is proposed that the prefrontal lobe participates in two closely related but different executive function abilities: (1) "metacognitive executive functions": problem solving, planning, concept formation, strategy development and implementation, controlling attention, working memory, and the like; that is, executive functions as they are usually understood in contemporary neuroscience; and (2) "emotional/motivational executive functions": coordinating cognition and emotion/motivation (that is, fulfilling biological needs according to some existing conditions). The first one depends on the dorsolateral prefrontal areas, whereas the second one is associated with orbitofrontal and medial frontal areas. Current tests of executive functions basically tap the first ability (metacognitive). Solving everyday problems (functional application of executive functions), however, mostly requires the second ability (emotional/motivational); therefore, these tests have limited ecological validity. Contrary to the traditional points of view, recent evidence suggests that the human prefrontal lobe is similar to other primates and hominids. Other primates and hominids may possess the second (emotional executive functions) prefrontal ability, -but not the first (metacognitive executive functions) one. It is argued that metacognitive executive functions are significantly dependent on culture and cultural instruments. They probably are the result of the development and evolution of some "conceptualization instruments"; language (and written language as an extension of oral language) may represent the most important one. The second executive function ability (emotional/motivational) probably is the result of a biological evolution shared by other primates.

"Nothing in biology makes sense except in the light of evolution"
(Theodosius Dobzhansky, 1973)

1. What does "executive functions" mean?

"Executive functions" is a relatively new term in the neurosciences. Luria (1966, 1973, 1980) is the direct antecessor of the concept of executive functions. He distinguished three functional units in the brain: (1) arousal-motivation (limbic and reticular systems); (2) receiving, processing, and storing information (post-rolandic cortical areas); and (3) programming, controlling, and verifying activity, depending on the activity of the prefrontal cortex. Luria mentions that this third unit has an executive role. Lezak (1983) referred to "executive functioning" to discriminate cognitive functions from the "how" or "whether" of human behaviors. Baddeley (1986) grouped these behaviors into cognitive domains that included problems in planning, organizing behaviors, disinhibition, perseveration, reduced fluency, and initiation. Baddeley also coined the term "dysexecutive syndrome."

The definition of executive function includes the concept of mental flexibility and also ability to filter interference, engage in goal-directed behaviors, and anticipate the consequences of one's actions (Ardila & Surloff, 2007; Denckla, 1994, 1996; Goldberg, 2001; Luria, 1969, 1980; Stuss & Benson, 1986; Stuss & Knight, 2002). The concept of morality, ethical behaviors, self-awareness, and the idea of the frontal lobes as manager and programmer of the human psyche are also included (Anderson, Bechara, Damasio, Tranel, & Damasio, 1999; Damasio, 1994; Luria, 1980; Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005).

During the late 19th and early 20th centuries, clinical investigations documented diverse behavioral disorders in cases of frontal pathology. "Frontal lobe syndrome" was conceptualized by Feuchtwanger (1923). He correlated frontal pathology to behaviors that were not related to overt speech, memory, or sensorimotor deficits. He emphasized the personality changes in motivation, affective dysregulation, and the capacity to regulate and integrate other behaviors. Goldstein (1944) expanded the capacity of frontal lobe behaviors to include "the abstract attitude," initiation, and mental flexibility. Luria (1966, 1969) related prefrontal lobe activity with programming motor behavior, inhibiting immediate responses, abstracting, problem solving, verbal regulation of behavior, reorienting behavior according to behavioral consequences, temporal integration of behavior, personality integrity, and consciousness. During the 1970s, 1980s, and 1990s several books exclusively devoted to the analysis of the prefrontal cortex were published (e.g., Fuster, 1989; Levin, Eisenberg, & Benton,

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1991; Miller & Cummings, 1998; Perecman, 1987; Pribram & Luria, 1973; Roberts, Robbins, & Weiskrantz, 1998; Stuss & Benson, 1986). These works usually assumed that "frontal" ("prefrontal") syndrome was synonymous with executive dysfunction.

Progressively, it became apparent that "prefrontal syndrome" and "executive dysfunction" are not synonymous. The prefrontal cortex plays a key monitoring role in executive functions, but other brain areas are also involved (Elliott, 2003). Intact frontal processes, although not synonymous with intact executive functioning, are and integral part of it. Attempts to localize executive functioning to discrete frontal areas have been inconclusive. The emerging view is that executive function is mediated by dynamic and flexible networks. Neuroimaging results have also implicated posterior, cortical, and subcortical regions in executive functioning (Roberts, Robbins, & Weiskrantz, 2002).

Historically, Phineas Gage has become the most classical example for prefrontal lobe pathology, and disturbances in executive functions (Harlow, 1868). Phineas Gage was a reliable foreman for a railroad company who suffered a tragic accident in which a tampering rod was projected through his frontal lobes. Miraculously he survived, but after this accident, he was described as "profane," "irascible," and "irresponsible." Profound personality changes were reported, and according to Harlow, he began to behave as an animal. The Phineas Gage case is usually cited as a typical example of executive function disturbances. It is obvious however, that Phineas Gage's impairments were mostly situated at an emotional/motivational level, not at a purely cognitive (or "metacognitive") level. Overt behavioral changes were observed as frequently found in frontal lobe pathology, but purely cognitive impairments were ill-documented, partially due to the lack of appropriate cognitive assessment instruments.

Most frequently, executive functions are analyzed in experimental conditions using diverse research strategies, such as solving diverse problems, finding similarities between two words, providing an answer that requires inhibiting another, etc. A paradigm is created and the subject is required to solve it. The brain activity can be simultaneously recorded, using brain electrical activity or recording the regional level of activation (e.g., Osaka et al., 2004). Alternatively, executive functions are analyzed in brain-damaged populations in order to find the contribution of different brain systems (e.g., Jacobs, Harvey, & Anderson, 2007). This last approach represents the classical neuropsychological method. Executive functions, however, rarely are analyzed in natural ecological conditions. How, indeed, do people solve everyday problems? This is obviously a crucial question in understanding human behavior.

Tests for executive function typically represent *external tasks*, requiring the correct application of some intellectual abilities to be solved; for example, the Wisconsin Card Sorting Test (Berg, 1948; Heaton, 1981), the Tower of Hanoi (Simon, 1975), or the Stroop test (Stroop, 1935) represent unusual and unfamiliar tasks, requiring the development of new strategies, planning, thought flexibility, etc. Nonetheless, they are *emotionally neutral tasks*.

Although executive functions depend on extended networks including different brain areas, it is assumed that the prefrontal cortex plays a major controlling and monitoring role. Most important, prefrontal cortex does not only participate in those classically recognized executive operations (sequencing, alternating, inhibiting, etc.), but also plays a core role in coordinating cognition and emotion (Mitchell & Phillips, 2007). Most of the disturbances reported in Phineas Gage (and in many cases of prefrontal syndromes) refer to behavioral/emotional disturbances; or more exactly, disturbances in coordinating cognition and emotion/motivation. The prefrontal lobe has extensive connections to subcortical and limbic system areas (Barbas, 2006; Damasio & Anderson, 1993) and even its orbital portion could be regarded as an extension of the limbic system. It seems that no laboratory test for executive function taps into the ability to coordinate cognition and emotion, and in that regard, no executive function test has significant ecological validity.

By coordinating cognition and emotion, the prefrontal lobe plays a major function: controlling the limbic system impulses; that is, making limbic impulses "socially acceptable" (e.g., Beer, John, Scabini, & Knight, 2006; Blair, 2004; Lezak, Howieson, Loring, & Hannay, 2004). The inability to make basic biological needs socially acceptable, as clearly described in Phineas Gage's case, frequently represents a major disturbance in prefrontal patients. Of course, we all would like to hit somebody when frustrated, to take possession of anything we want, to stay at home instead of performing fatiguing work, and to approach any potential sexual partner. That is exactly what many patients with prefrontal lobe pathology frequently do.

2. Is there any fundamental core ability accounting for executive functions?

Some disagreement exists around the question of unity or diversity (non-unitary) of executive functions (e.g., De Frias, Dixon, & Strauss, 2006; Duncan, Emslie, Williams, Johnson, & Freer, 1996; Grafman, 2006; Kimberg, D'Esposito, & Farah, 1997; Parkin & Java, 1999). It is not clear what the particular unitary factor saturating the different executive function tests is. Behavior inhibition has been considered as a potential candidate, as the single factor responsible for successful performance in different executive tests (Barkley, 1997) or in combination with working memory (Pennington & Ozonoff, 1996). Salthouse (1996, 2005) suggested that reasoning and perceptual speed represent the underlying factors related to all executive functions. Salthouse (2005) observed that performance on two common tests of executive functioning, the Wisconsin Card Sorting Test (Berg, 1948; Heaton, 1981) and the Controlled Oral Word Association Test (Benton, Hamsher, & Sivan, 1994), were strongly correlated with reasoning ability and perceptual speed.

Other authors challenge the existence of such a unitary factor. Godefroy, Cabaret, Petit-Chenal, Pruvo, and Rousseaux (1999) emphasized that certain frontal lobe patients perform well on some tests purported to assess executive abilities but not on others. Correlations among different executive tests are frequently moderate or low, and many times lacking statistical significance (Friedman et al., 2006; Lehto, 1996; Salthouse, Atkinson, & Berish, 2003).

Miyake, Friedman, Emerson, Witzki, and Howerter (2000) adopted an intermediate position. They studied three often-postulated aspects of executive functions (shifting, updating, and inhibition) and concluded that, although they are clearly distinguishable, they do share some underlying commonality. Based on the results of their study, the authors stated that executive functions are "separable but moderately correlated constructs" thus suggesting both unitary and non-unitary components of the executive system. By the same token, several authors have suggested different subcomponents of executive functions (e.g., Anderson, 2001; Delis, Kaplan, & Kramer, 2001; Denckla, 1994; Elliott, 2003; Hobson & Leeds, 2001; Lafleche & Albert, 1995; Lezak, 1983; Piguet et al., 2002).

3. Two proposed fundamental executive functions

It may be conjectured that there are two different, but closely related types of prefrontal lobe abilities (e.g., Fuster, 2001, 2002; Happaney, Zelazo, & Stuss, 2004):

(1) "*Metacognitive executive functions*" which include problem solving, abstracting, planning, strategy development and implementation, and working memory (the usual under-

standing of executive functions, generally measured in neuropsychology executive functions tests); these are abilities mostly related with the dorsolateral area of the prefrontal cortex (e.g., Stuss & Knight, 2002).The dorsolateral prefrontal cortex has been observed to participate in diverse planning, abstracting, problem solving, and working memory tasks. Using fMRI dorsolateral prefrontal activation has been found in tasks such as solving the Tower of Hanoi (Fincham, Carter, van Veen, Stenger, & Anderson, 2002), Controlled Word Association Test (letter fluency) (Baldo, Schwartz, Wilkins, & Dronkers, 2006), working memory (Yoon, Hoffman, & D'Esposito, 2007), and solving the Wisconsin Card Sorting Test (Lie, Specht, Marshall, & Fink, 2006).

(2) "*Emotional/motivational executive functions*," which is responsible for coordinating cognition and emotion. That means, the ability to fulfill basic impulses following socially acceptable strategies. In the last case, what is most important does not necessarily include what the best conceptual and intellectual result is, but what is in accordance with personal impulses (e.g., Bechara, Damasio, & Damasio, 2000). In that regard, the core function of the prefrontal lobe is to find acceptable justifications for limbic impulses. Following socially acceptable strategies actually involves inhibition of selfish or unsociable basic impulses in the first place, but not necessarily arriving at the best conceptual solution. The ventromedial areas of the prefrontal cortex are involved in the expression and control of emotional and instinctual behaviors (Fuster, 1997a, 1997b, 2002). This function is related with so-called "inhibitory control" of behavior (Miller & Wang, 2006). Clinical evidence (e.g., Luria, 1969; Stuss & Knight, 2002) as well as experimental research (e.g., Leung & Cai, 2007; Medalla, Lera, Feinberg, & Barbas, 2007) suggest that the neural substrate for this inhibitory function resides mainly in the medial and orbital portions of the prefrontal cortex. Fuster (2002) points out that "The apparent physiological objective of inhibitory influences from orbitomedial cortex is the suppression of internal and external inputs that can interfere with whatever structure of behavior, speech, or cognition is about to be undertaken or currently underway" (page 382).

There is no question that if metacognitive executive functions were indeed used in solving external problems without the involvement of limbic impulses, most world-wide problems would have been solved by man, because contemporary man has sufficient resources to solve all the major social problems (such as poverty and war). Human conflicts in general would also be significantly reduced.

Direct observation suggests that everyday problems usually have an emotional content: talking with a friend, a boss or a spouse; driving in the street; deciding how to approach somebody; spending money, etc., are not emotionally neutral activities, as are the Wisconsin Card Sorting Test (Berg, 1948; Heaton, 1981) and the Tower of Hanoi (Simon, 1975). When other people are involved, it is not easy to remain emotionally neutral. Social issues, simply speaking, are not emotionally neutral, because power/submission, personal benefits, and diverse biological drives are potentially involved (Smith, Bond, & Kagitcibas, 2006). Most likely, throughout evolution of mankind (i.e., during the last 150,000 years) fulfilling these drives has been the major application of the prefrontal functions: to get power, to have a dominant role, to take food and goods for ourselves, to get a sexual partner, etc. That means that emotional/motivational executive functions have played a crucial role in survival and reproduction (e.g., facilitating behaviors such as acquiring dominant roles, obtaining sexual partners, etc.).

Mitchell and Phillips (2007) have argued that emotion can affect executive function ability. They propose that mild manipulations of negative mood appear to have little effect on cognitive control processes, whereas positive mood impairs aspects of updating, planning, and switching. This effect of emotion on cognition has been supported for different executive function tasks, such as working memory (Spies, Hesse, & Hummitzsch, 1996) and planning (Oaksford, Morris, Grainger, & Williams, 1996)—using the Tower of London (Shallice, 1982) as a paradigm. In other words, when emotion is involved, metacognitive executive function ability decreases. Mitchell and Phillips (2007) emphasize that current evidence on the effects of mood on regional brain activity during executive functions demonstrates that the prefrontal cortex represents an area of integration between mood and cognition.

These two types of executive functions ("metacognitive" and "emotional/motivational") depend on relatively different prefrontal areas, and as a matter of fact, two major variants in the prefrontal syndrome are frequently distinguished, one mostly impairing cognition (or rather, cognitive control, that is, "metacognition"); the other one mostly impairing behavior:

(1) *Dorsolateral syndrome.* Cummings (1993) indicated that the dorsolateral circuit is the most important to executive functioning. The most noted deficit is an inability to organize a behavioral response to novel or complex stimuli. Symptoms are on a continuum and reflect capacity to shift cognitive sets, engage existing strategies, and organize information to meet changing environmental demands. Various researchers, including Luria (1969), have noted perseveration, stimulus-bound behavior, echopraxia, and echolalia. Lateralization has been noted in executive dysfunction (Goldberg, 2001). Ventral and dorsal portions of prefrontal cortex are bilieved to interact in the maintenance of rational and "non-risky" decision making (Manes et al., 2002). According to Fuster (1997a, 1997b, 2002), the most general executive function of the lateral prefrontal cortex is the temporal organization of goal-directed actions in the domains of behavior, cognition, and language.

(2) *Orbitofrontal and medial frontal syndrome.* Orbitofrontal damage has been associated with desinhibition, inappropriate behaviors, personality changes, irritability, mood liability, tactlessness, distractibility, and disregard of important events (Stuss & Knight, 2002). These patients are unable to respond to social cues. Noteworthy, it was observed by Laiacona and colleagues (1989) that these patients have no difficulty with card sorting tasks. Eslinger and Damasio (1985) coined the term "acquired sociopathy" to describe dysregulation that couples both a lack of insight and remorse regarding these behaviors. The orbitofrontal cortex appears to be linked predominantly with limbic and basal forebrain sites. Medial frontal lobe damage causes apathy or abulia (a severe form of apathy). Acute bilateral lesions in the medial frontal area can cause akinetic mutism, in which the individual is awake and has self-awareness, but does not initiate behaviors (Ross & Stewart, 1981). According to Fuster (1997a, 1997b, 2002) the ventromedial areas of the prefrontal cortex are involved in expression and control of emotional and instinctual behaviors.

It is evident that the two prefrontal syndromes can have rather different clinical expressions (metacognitive and emotional/motivational) depending upon the specific location of the damage.

4. Metacognitive executive functions as an internalization of actions

As pointed above, disagreement persists around the potential unitary factor in executive functions. I will suggest that "action representation" (i.e., internally representing movements) may constitute at least one basic metacognitive executive function factor. I will refer to "action representation" and "time perception," derived from it; both ultimately potentially depending upon one single core ability ("sequencing?").

Two departing observations are important to support the involvement of prefrontal cortex in motor representation:

1. *Anatomical observation*. Prefrontal cortex represents an extension and further evolution of the frontal motor areas. It may be conjectured that the prefrontal lobe should participate in complex and elaborated motor ("executive") activities.
2. *Clinical observation*. A diversity of motor control disturbances are observed in prefrontal pathology, such as perseveration, utilization behavior, paratonia, primitive reflexes, etc. (e.g., Ardila & Rosselli, 2007a; Victor & Ropper, 2001).

Several authors have argued that thought, reasoning, and other forms of complex cognition (metacognition) depend on an interiorization of actions. Vygotsky (1929, 1934/1962, 1934/1978), for instance, proposed that thought (and in general, complex cognitive processes) is associated with some *inner speech*. Vygotsky represents the most classical author suggesting this interpretation for complex cognition. More recently, Lieberman (2002a, 2002b) suggested that language in particular and cognition in general arise from complex sequences of motor activities.

Vygotsky (1934/1978) developed the concept of "extracortical organization of higher mental functions" to account for the interaction of biological and cultural factors in the development of human cognition. Vygotsky's (1934/1962, 1934/1978) understanding of "higher mental functions" is roughly equivalent to "metacognitive executive functions." A major factor in systemic organization of higher cognitive processes, according to Vygotsky, is the engagement of external instruments (objects, symbols, signs), which have an independent history of development within culture. This principle of construction of brain functional systems was called by Vygotsky the principle of "extracortical organization of complex mental functions," implying that all types of mankind conscious activity are formed with the support of external auxiliary tools or aids. However, different mediators and means, or significantly different details within them (e.g., the direction of writing and degree of letter-sound correspondence, orientation by maps or by the behavior of sea-birds, etc.) may develop, and in fact are developed in different cultures. Therefore, the analysis of cognitive processes must necessarily take into account these cross-cultural differences (Kotik-Friedgut & Ardila, 2004).

The central point in Vygotsky's (1934/1962) idea is that higher forms of cognition ("cognitive executive functions") depend on certain mediation (language, writing or any other); the instruments used for mediating these complex cognitive processes are culturally developed. According to Vygotsky (1934/1962), the invention (or discovery) of these instruments, will result in a new type of evolution (cultural evolution), not requiring any further biological changes. Thinking is interpreted as a covert motor activity ("inner speech").

Vygotsky (1929) assumes that thought and speech develop differently and independently having different genetic roots. Before two years of age, the development of thought and speech are separate. They converge and join at about the age of two years, and thought from this point ahead becomes language mediated (verbal thought). Language in consequence becomes the primary instrument for conceptualization and thinking. According to Vygotsky (1934/1962), speech develops first with external communicative/social speech, then egocentric speech, and finally inner speech. Vocalization becomes unnecessary because the child "thinks" the words instead of pronouncing them. Inner speech is for oneself, while external, social speech is for others. Vygotsky considered that thought development is determined by language.

Vygotsky (1987) separated two different types of concepts: spontaneous and scientific. Spontaneous concepts are developed in a parallel way with language, whereas scientific concepts are concepts learned at school. Children progressively develop reflective consciousness through the development of scientific concepts. School is intimately related with learning a new conceptual instrument: reading. Written language is an extension of oral language, and represents the most elaborated form of language.

Luria further extended Vygotsky's ideas and attempted to find the neurological correlates for different components of complex cognitive processes. He clearly stated that mental functions are "...social in origin and complex and hierarchical in their structure and they all are based on a complex system of methods and means..." (Luria, 1973, p. 30).

In brief, Vygotsky (1934/1962) argued that complex psychological processes (metacognitive executive functions) derives from language internalization. Thinking relies in the development of an instrument (language or any other), that represents a cultural product.

Lieberman (2002a, 2002b) refers specifically to the origins of language. He postulates that neural circuits linking activity in anatomically segregated populations of neurons in subcortical structures and the neocortex throughout the human brain regulate complex behaviors such as walking, talking, and comprehending the meaning of sentences. The neural substrate that regulates motor control (basal ganglia, cerebellum, and frontal cortex) in the common ancestor of apes and humans most likely was modified to enhance cognitive and linguistic ability. Lieberman (2002a, 2002b) suggests that motor activity is the departing point for cognition. Speech communication played a central role in this process. The neural bases of mankind linguistic ability are complex, involving structures other than Broca's and Wernicke's areas. Many other cortical areas and subcortical structures form part of the neural circuits implicated in the lexicon, speech production and perception, and syntax. The subcortical basal ganglia support the cortical–striatal–cortical circuits that regulate speech production, complex syntax, and the acquisition of the motor and cognitive pattern generators that underlie speech production and syntax. They most likely are involved in learning the semantic referents and sound patterns that are instantiated as words in the brain's dictionary.

The cerebellum and prefrontal cortex are also involved in learning motor acts (e.g., Matsumura et al., 2004; Hernandez-Mueller, Mulas, & Mattos, 2005). Lieberman (2002a, 2002b) proposes that the frontal regions of the cortex are implicated in virtually all cognitive acts and the acquisition of cognitive criteria; posterior cortical regions are clearly active elements of the brain's dictionary. The anterior cingulate cortex plays a part in virtually all aspects of language and speech. Real-word knowledge appears to reflect stored conceptual knowledge in regions of the brain traditionally associated with visual perception and motor control. Some aspects of human linguistic ability, such as the basic conceptual structure of words and simple syntax, are phylogenetically primitive and most likely were present in the earliest hominids. Lieberman (2002a, 2002b) further suggests that speech production, complex syntax, and a large vocabulary developed in the course of hominid evolution, and *Homo erectus* most likely talked, had large vocabularies, and commanded fairly complex syntax. Full human speech capability, enhancing the robustness of vocal communication, most likely is a characteristic of anatomically modern humans.

These two authors (Vygotsky and Lieberman), although using rather different approaches, have both postulated that the development of language and complex cognition are related with some motor programs, sequencing, internalizing actions, and the like.

The recent discovery of so-called "mirror neurons" represents a new element in understanding inner speech and action representation. A mirror neuron is a neuron which fires both when an animal performs an action and also when the animal observes the same action performed by another animal. In humans, brain activity consistent with mirror neurons has been found in the premotor cortex and the inferior parietal cortex (Rizzolatti & Craighero, 2004; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). In monkeys, the rostral part of ventral premotor cortex (area F5) contains neurons that discharge, both when the monkey grasps or manipulates objects and when it observes the experimenter performing similar actions. These neurons (mirror neurons) appear to represent a system that matches observed events to similar, internally generated actions.

Transcranial magnetic stimulation and positron emission tomography (PET) experiments suggest that a mirror system for gesture recognition also exists in humans and includes Broca's area (Rizzolatti & Arbib, 1998). The discovery of mirror neurons in the Broca's area might have immense consequences for understanding the organization and evolution of mankind cognition (Arbib, 2006; Craighero, Metta, Sandini, & Fadiga, 2007). An obvious implication of mirror neurons is that they can participate in the internal representation of actions. Neuroimaging data have showed that interactions involving Broca's area and other cortical areas are weakest when listening to spoken language accompanied by meaningful speech-associated gestures (hence, reducing semantic ambiguity), and strongest when spoken language is accompanied by self-grooming hand movements or by no hand movements at all suggesting that Broca's area may be involved in action recognition (Skipper, Goldin-Meadow, Nusbaum, & Small, 2007). PET studies have associated the neural correlates of inner speech with activity of the Broca's area (McGuire et al., 1996).

5. Is there anything special in the prefrontal cortex?

For some time it has been assumed that the prefrontal cortex is significantly larger in humans than in other primates (e.g., Blinkov & Glezer, 1968). This difference in volume was assumed to represent a major reason to account for differences in complex forms of cognition (executive functions) observed in humans.

Nonetheless, such an assumption turned out to be incorrect. Measures of prefrontal lobe volumes have not found differences between mankind and non-human primates. Semendeferi, Damasio, Frank, and Van Hoesen (1997, 2002) measured the volume of the frontal lobe as a whole and of its main sectors (including cortex and immediately underlying white matter) in humans, chimpanzees, gorillas, orangutans, gibbons, and macaques using three-dimensional reconstructions of magnetic resonance (MR) scans of the brain. Although the absolute volume of the brain and the frontal lobe was found to be largest in humans, the relative size of the frontal lobe was similar across hominoids: macaque (28.1%), gibbon (31.1%), orangutan (35.3%), gorilla (32.4%), chimpanzee (35.9%), and human (36.7%). Most significantly, it was found that humans do not have a larger frontal lobe than expected from a primate brain of mankind size. Furthermore, the relative size of the sectors of the frontal lobe (dorsal, mesial, and orbital) was similar across the primate species studied. Semendeferi and colleagues suggested that the special cognitive abilities attributed to a frontal advantage may be due to differences in individual cortical areas and to a richer interconnectivity, none of which required an increase in the overall relative size of the frontal lobe during hominid evolution.

Schoenemann, Sheehan, and Glotzer (2005) found that a major difference between humans and other primates was the white matter volume. Using MRI from 11 primate species, the authors measured gray, white, and total volumes for both prefrontal and the entire cerebrum on each specimen. In relative terms, prefrontal white matter was found to have the largest difference between human and non-human, whereas gray matter showed no significant difference. Increased brain interconnectivity may represent a major characteristic of the human brain. As a note of caution, it is important to keep in mind that subjects used in this study were contemporary people, living in city environments, with a high level of education, etc., not humans living in those conditions existing 150,000 years ago. Stimulation can be rather different not only qualitatively but even probably quantitatively, potentially impacting on brain interconnectivity.

It can be tentatively concluded that it is questionable that the size of the prefrontal cortex can account for the human executive functions. Some other factors have to be considered, such as connectivity (increased stimulation?).

6. Executive functions in pre-historical man

Some recent studies have approached the question of the evolution of the prefrontal cortex and executive functions (Risberg, 2006; Roth & Dicke, 2005; Winterer & Goldman, 2003). It is usually accepted that *Homo sapiens sapiens* appeared about 150,000 years ago, and during this time, his brain evolution has been minimal (Wood, 1992). It means, the humans existing since about 150,000 years ago had basically the very same neurological organization of contemporary individuals, including the biological foundations for the so-called executive functions.

How were executive functions used by pre-historical man? Of course, we cannot be sure, but some few papers have approached this question (e.g., Bednarik, 1994, 2003; Coolidge & Wynn, 2001, 2005; Sugarman, 2002; Wayne, 2006).

Coolidge and Wynn (2001) raised the question of how executive functions (supposedly, one of the key evolutionary acquisitions that led to the development of modern thinking) were demonstrated by prehistoric people. Coolidge and Wynn assumed that it is possible to match many of the features of executive function with activities reconstructed from archaeological evidence. The potential application of several components of executive function (such as sequential memory, task inhibition, and organization and planning) is analyzed by the authors: (1) Sequential memory: it can be speculated in the Palaeolithic Lithic reduction sequences, but even sophisticated procedures like Levallois can be explained without resort to closely linked sequences of action. The production and use of barbed bone projectile points is another potential marker. The final product depends much more closely on a set sequence of actions. It is a true multi-step technology. (2) 'Tasks of inhibition', in which immediate gratification and action are delayed, are harder to identify archaeologically. Agriculture requires such inhibition. Facilities such as traps, that capture remotely, are technologies of inhibition and were probably present in the European Mesolithic. Palaeolithic examples are less convincing. Coolidge and Wynn (2001, 2005) consider that nothing of Middle Palaeolithic foraging, however, would require tasks of inhibition (indeed, they conclude that *nothing in the archaeological record of Palaeolithic appears to require executive function*). (3) 'Organization and planning' is another basic executive function ability that likely was required for activities such as migration and colonization.

Coolidge and Wynn's (2001) review of the archaeological evidence finds no convincing demonstration for executive functions among the traces left by Neanderthals. The authors conclude that the archaeological records support the hypothesis that executive function was a late and critical acquisition in human cognitive evolution. In a very ingenious study, Stout and Chaminade (2007) using positron emission tomography (PET) recorded the brain activity from six inexperienced subjects learning to make stone tools of the kind found in the earliest archaeological records. The authors found that tool making is associated with the activation of diverse parieto-frontal perceptual-motor systems, but no activation was observed in dorsolateral prefrontal cortex. They concluded that human capacities for sensorimotor adaptation, rather than abstract conceptualization and planning, were central factors in the initial stages of human technological evolution, such as making stone tools. Nonetheless, complex cognitive processes (i.e., metacognitive executive functions) seem to be crucial for further development and survival of *H. sapiens*. The key factor for *H. sapiens* late evolution seems to be the mental ability to plan and strategize, which allowed them to find innovative solutions to the many changing environmental problems which they were exposed (Coolidge & Wynn, 2008). This may be one reason to account why *H. sapiens* survived while *Homo neanderthalensis* disappeared. Changing environmental conditions (e.g., global climates changes) may require flexible survival strategies. It has been conjectured that during the past history changing physical environment conditions resulted in a selection that gave human ancestors adaptive versatility to endure increasing environmental instability (Bonnefille, Potts, Chalié, Jolly, & Peyron, 2004; Potts, 1996, 2004).

Mithen (1994, 1996) has proposed the accessibility of mental modules as the impetus for mankind culture at the time of the Middle/Upper Palaeolithic transition, about 60,000 to about 30,000 years ago. He identified these mental modules as general intelligence, social intelligence, natural history intelligence, technical intelligence, and language. Probably, language was the most important one, increasing communication, and facilitating the transmission of knowledge, potentially resulting in an increased probability of survival and reproduction.

It could be speculated that at the beginning of human history, transmitting knowledge from generation to generation was limited. Although some forms of learning can be transmitted by modeling or imitation (vicarious learning or social learning or modeling) (e.g., Bandura, 1977) language development represented a powerful instrument to accumulate and transmit knowledge about the world. The crucial point in the origins of executive functions becomes the possibility to conceptualize the environment (concepts are represented in words) and to transmit and progressively accumulate this knowledge about the world.

7. Metacognitive executive functions as a cultural product

There is no convincing evidence that Paleolithic individuals used executive functions (Coolidge & Wynn, 2001), understood as "the ability for planning...etc." (first interpretation of prefrontal abilities: metacognitive executive functions). For thousands of years, prefrontal abilities were in consequence exclusively used to fulfill basic impulses following socially acceptable strategies (e.g., hierarchy in the group) (second interpretation of prefrontal abilities: emotional/motivational executive functions).

Which were the milestones for cultural development and how did metacognitive executive functions appear? It could be speculated that some crucial inventions fueled the development of cultural evolution (Vygotsky, 1934/1962). For instance, kind of cognitive fluidity has been postulated as a basic requisite for executing complex human activities (Gardner, 1983). The most important candidate for this crucial invention that fueled the development of cultural evolution is language. Language allows the transmission of knowledge and facilitates survival and reproduction. Without language, children can learn from parents by imitation, but imitation is limited to some elementary activities, such as making a simple stone ax. Language represents a major instrument of internal representation of the world and thinking (Vygotsky, 1934/1978). Language development obviously was a slow process taking thousands of years, but the most critical element of human language is the use of grammar, likely appearing some 10,000–100,000 years ago (Ardila, 2006). Probably, *H. neanderthalensis* did not have a grammatical language and according to archeological evidence, did not use executive functions (Coolidge & Wynn, 2008). Language grammar likely developed from action internalization (Ardila, 2006).

Written language represents an extension of oral language. Written language appeared only some 6000–8000 years ago and its diffusion has been so slow that even nowadays about 20% of the world population is illiterate (UNESCO, 2000). Performance in psychometric executive function tests has been observed to be very significantly correlated with subjects' educational level (e.g., Ardila, Ostrosky-Solis, Rosselli, & Gomez, 2000; Ardila, Rosselli, & Rosas, 1989; Ardila & Rosselli, 2007b; Ostrosky, Ardila, Rosselli, Lopez-Arango, & Uriel-Mendoza, 1998; Reis & Castro-Caldas, 1997; Rosselli, Ardila, & Rosas, 1990). For instance, Gomez-Perez and Ostrosky-Solis (2006) observed that whereas tests related to memory are sensitive to aging, those related to executive functioning are mostly sensitive to education. It can be argued that illiterates possess basic executive functions (e.g., ability to internally represent actions) but they lack an important instrument to organize executive functions: written language.

8. Tentative conclusions

The analysis of executive functions represents one of the most intensively studied neuroscience questions during the last decade. The emphasis in reasoning, abstracting skills, behavioral control, anticipating the consequences of behavior, and similar abilities, has contributed to the frequently found false idea that human behavior is guided by rationality. Human history blatantly contradicts this idea.

This misinterpretation of mankind behavior is linked to the assumptions that the human brain is unique and "superior" to the brain of other species. We refer to our species as the "wise man" (*H. sapiens*). Analyzing executive functions, it may be concluded that two different types of executive functions could be separated: metacognitive and emotional/motivational, depending on different brain systems. It could be argued that only the first one should be referred to as executive functions; usually, however, they are considered together in most definitions of executive functions, assuming a certain unity.

Contemporary testing of executive functions has focused on abstracting, problem solving, and similar metacognitive abilities. These metacognitive abilities seem to be useful in solving external and emotionally neutral problems. When social situations and biological drives are involved, the ability to rationally solve problems seems to decrease in a significant way. In this regard, contemporary testing of executive functions has limited ecological validity.

Archeological analysis has discovered only some—if any, evidence of metacognitive executive functions in prehistorical man. We have to conclude that metacognitive abilities represent a recent acquisition, not obviously dependent on recent biological changes. The development of some cultural instruments, potentially resulting in a new type of evolution has been suggested. Language as an instrument not only to conceptualize the immediate experience, but for its transmission of knowledge, has been proposed as the major cultural instrument for metacognition. Language complexity has historically increased with the development of written language. No question, some other cultural instruments have also contributed to the development of metacognitive abilities; for instance, mathematics, drawing, and technology (from the wheel to computers). From the point of view of the brain, metacognitive executive functions are not necessarily correlated with a further brain development; increased neural interconnectivity may potentially support the increased complexization of executive functions found in contemporary *H. sapiens*.

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References

Arbib, M. A. (2006). Aphasia, apraxia and the evolution of the language-ready brain. *Aphasiology, 20*, 1125–1155.

Anderson, V. (2001). Assessing executive functions in children: Biological, psychological, and developmental considerations. *Developmental Neurorehabilitation, 4*, 119–136.

Anderson, S. W., Bechara, A., Damasio, H., Tranel, D., & Damasio, A. R. (1999). Impairment in social and moral behaviour related to early damage in human prefrontal cortex. *Nature Neuroscience, 2*, 1032–1037.

Ardila, A. (2006). Orígenes del lenguaje: un análisis desde la perspectiva de las afasias. *Revista de Neurología, 43*, 690–698.

Ardila, A., Ostrosky-Solis, F., Rosselli, M., & Gomez, C. (2000). Age related cognitive decline during normal aging: The complex effect of education. *Archives of Clinical Neuropsychology, 15*, 495–514.

Ardila, A., Rosselli, M., & Rosas, P. (1989). Neuropsychological assessment in illiterates: Visuospatial and memory abilities. *Brain and Cognition, 11*, 147–166.

Ardila, A., & Rosselli, M. (2007a). *Neuropsicologia clinica*. Mexico: Manual Moderno.

Ardila, A., & Rosselli, M. (2007b). Illiterates and cognition: The impact of education. In B. Uzzell, M. Pontón, & A. Ardila (Eds.), *International handbook of cross-cultural neuropsychology* (pp. 181–198). Mahwah, NJ: Lawrence Erlbaum Associates.

Ardila, A., & Surloff, C. (2007). *Dysexecutive syndromes*. San Diego: Medlink: Neurology.

Baddeley, A. (1986). *Working memory*. Oxford: Oxford University Press.

Baldo, J. V., Schwartz, S., Wilkins, D., & Dronkers, N. F. (2006). Role of frontal versus temporal cortex in verbal fluency as revealed by voxel-based lesion symptom mapping. *Journal of the International Neuropsychological Society, 12*, 896–900.

Bandura, A. (1977). *Social learning theory*. New Jersey: Prentice Hall.

Barbas, H. (2006). Organization of the principal pathways of prefrontal lateral, medial, and orbitofrontal cortices primates and implications for their collaborative interaction in executive functions. In J. Risberg & J. Grafman (Eds.). *The frontal lobes. Development, function and pathology* (pp. 21–68). Cambridge: Cambridge University Press.

Barkley, R. A. (1997). *ADHD and the nature of self-control*. New York: Guilford Press.

Bechara, A., Damasio, H., & Damasio, A. R. (2000). Emotion, decision making and the orbitofrontal cortex. *Cerebral Cortex, 10*, 295–307.

Bednarik, R. G. (1994). Art origins. *Anthropos, 89*, 169–180.

Bednarik, R. G. (2003). The earliest evidence of palaeoart. *Rock Art Research, 20*, 89–135.

Beer, J. S., John, O. P., Scabini, D., & Knight, R. T. (2006). Orbitofrontal cortex and social behavior: Integrating self-monitoring and emotion-cognition interactions. *Journal of Cognitive Neuroscience, 18*, 871–879.

Benton, A. L., Hamsher, K., & Sivan, A. B. (1994). *Multilingual aphasia examination* (3rd ed.). Iowa City, IA: AJA Associates.

Berg, E. A. (1948). A simple objective technique for measuring flexibility in thinking. *Journal of General Psychology, 39*, 15–22.

Blair, R. J. (2004). The roles of orbital frontal cortex in the modulation of antisocial behavior. *Brain and Cognition, 55*, 198–208.

Blinkov, S. M., & Glezer, I. I. (1968). *Das Zentralnervensystem in Zahlen und Tabellen*. Jena: Fischer.

Bonnefille, R., Potts, R., Chalié, F., Jolly, D., & Peyron, O. (2004). High-resolution vegetation and climate change associated with Pliocene Australopithecus afarensis. *Proceedings of the National Academy of Sciences of the United States of America, 101*, 12125–12129.

Coolidge, F. L., & Wynn, T. (2001). Executive functions of the frontal lobes and the evolutionary ascendancy of *Homo sapiens*. *Cambridge Archaeological Journal, 11*, 255–260.

Coolidge, F. L., & Wynn, T. (2005). Working memory, its executive functions, and the emergence of modern thinking. *Cambridge Archaeological Journal, 15*, 5–26.

Coolidge, F. L., & Wynn, T. (2008). A stone-age meeting of minds neandertals became extinct while *Homo sapiens* prospered. A marked contrast in mental capacities may account for these different fates. American Scientist Online, 96, <http://www.americanscientist.org/template/AssetDetail/assetid/56450;jsessionid=aaa8s-19FU6GQB/>. Accessed 6.02.08.

Craighero, L., Metta, G., Sandini, G., & Fadiga, L. (2007). The mirror-neurons system: Data and models. *Progress in Brain Research, 164*, 39–59.

Cummings, J. L. (1993). Frontal-subcortical circuits and human behavior. *Archives of Neurology, 50*, 873–880.

Damasio, A. R. (1994). *Descartes' error*. New York: Putnam.

Damasio, A., & Anderson, S. W. (1993). The frontal lobes. In K. M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology* (4th ed.). New York: Oxford University Press.

De Frias, C., Dixon, R., & Strauss, E. (2006). Structure of four executive functioning tests in healthy older adults. *Neuropsychology, 20*, 206–214.

Delis, D., Kaplan, E., & Kramer, N. (2001). *Delis–Kaplan executive function system*. Psychological Assessment Resources, Inc..

Denckla, M. B. (1994). Measurement of executive function. In G. R. Lyon (Ed.), *Frames of reference for the assessment of learning disabilities: New views on measurement issues* (pp. 117–142). Baltimore, MD: Paul H. Brooks.

Denckla, M. B. (1996). A theory and model of executive function: A neuropsychological perspective. In G. R. Lyon & N. A. Krasnegor (Eds.). *Attention, memory and executive function* (pp. 263–277). Baltimore, MD: Paul H. Brooks.

Dobzhansky, T. (1973). Nothing in biology makes sense except in the light of evolution. *The American Biology Teacher, 35*, 125–129.

Duncan, J., Emslie, H., Williams, P., Johnson, R., & Freer, C. (1996). Intelligence and the frontal lobes: The organization of goal-directed behavior. *Cognitive Psychology, 30*, 257–303.

Elliott, R. (2003). Executive functions and their disorders. *British Medical Bulletin, 65*, 49–59.

Eslinger, P. J., & Damasio, A. R. (1985). Severe disturbance of higher cognition after bilateral frontal lobe ablation: Patient EVR. *Neurology, 35*, 1731–1741.

Feuchtwanger, E. (1923). *Die Funktionen des Stirnhirns*. Berlin: Springer.

Fincham, J. M., Carter, C. S., van Veen, V., Stenger, V. A., & Anderson, J. R. (2002). Neural mechanisms of planning: A computational analysis using event-related fMRI. *Proceedings of the National Academy of Sciences of the United States of America, 99*, 3346–3351.

Friedman, N. P., Miyake, A., Corley, R. P., Young, S. E., DeFries, J. C., & Hewitt, J. K. (2006). Not all executive functions are related to intelligence. *Psychological Science, 17*, 172–179.

Fuster, J. M. (1989). *The prefrontal cortex*. New York: Raven Press.

Fuster, J. M. (1997a). *The prefrontal cortex—Anatomy physiology, and neuropsychology of the frontal lobe*. Philadelphia: Lippincott-Raven.

Fuster, J. M. (1997b). *The prefrontal cortex: Anatomy, physiology, and neuropsychology of the frontal lobe* (3rd ed.). New York: Lippincott, Williams & Wilkins.

Fuster, J. M. (2001). The prefrontal cortex—An update: Time is of the essence. *Neuron, 30*, 319–333.

Fuster, J. M. (2002). Frontal lobe and cognitive development. *Journal of Neurocytology, 31*, 373–385.

Gardner, H. (1983). *Frames of mind: The theory of multiple intelligences*. New York: Basic Books.

Godefroy, O., Cabaret, M., Petit-Chenal, V., Pruvo, J. P., & Rousseaux, M. (1999). Control functions of the frontal lobes. Modularity of the central-supervisory system? *Cortex, 35*, 1–20.

Goldberg, E. (2001). *The executive brain*. New York: Oxford University Press.

Goldstein, K. (1944). The mental changes due to frontal lobe damage. *Journal of Psychology, 17*, 187–208.

Gomez-Perez, E., & Ostrosky-Solis, F. (2006). Attention and memory evaluation across the life span: Heterogeneous effects of age and education. *Journal of Clinical and Experimental Neuropsychology, 28*, 477–494.

Grafman, J. (2006). Human prefrontal cortex: Processes and representations. In J. Risberg & J. Grafman (Eds.). *The frontal lobes. Development, function and pathology* (pp. 69–91). Cambridge: Cambridge University Press.

Happaney, K., Zelazo, P. D., & Stuss, D. T. (2004). Development of orbitofrontal function: Current themes and future directions. *Brain and Cognition, 55*, 1–10.

Harlow, J. M. (1868). Recovery from the passage of an iron bar through the head. *Massachusetts Medical Society Publications, 2*, 327–346.

Heaton, R. (1981). *Wisconsin card sorting test: Manual*. Odessa: Psychological Assessment Resources, Inc..

Hernandez-Mueller, S., Mulas, F., & Mattos, L. (2005). The contribution of the cerebellum to cognitive processes. *Revista de Neurología, 40*(Suppl. 1), S57–S64.

Hobson, P., & Leeds, L. (2001). Executive functioning in older people. *Reviews in Clinical Gerontology, 11*, 361–372.

Jacobs, R., Harvey, A. S., & Anderson, V. (2007). Executive function following focal frontal lobe lesions: Impact of timing of lesion on outcome. *Cortex, 43*, 792–805.

Kimberg, D., D'Esposito, M., & Farah, M. (1997). Cognitive functions in the prefrontal cortex—Working memory and executive control. *Current Directions in Psychological Science, 6*, 185–192.

Kotik-Friedgut, B., & Ardila, A. (2004). Systemic-dynamic Lurian theory and contemporary cross-cultural neuropsychology. In T. Akhutina, L. Moskovich, & T. Dorothy (Eds.), *A.R. Luria and contemporary psychology*. New York: Nova Science Publishers.

Laiacona, M., De Santis, A., Barbarotto, R., Basso, A., Spagnoli, D., & Capitani, E. (1989). Neuropsychological follow-up of patients operated for aneurysms of anterior communicating artery. *Cortex, 25*, 261–273.

Lafleche, G., & Albert, M. (1995). Executive function deficits in mild Alzheimer's disease. *Neuropsychology, 9*, 313–320.

Lehto, J. (1996). Are executive function tests dependent on working memory capacity? *Quarterly Journal of Experimental Psychology, 49*, 29–50.

Leung, H. C., & Cai, W. (2007). Common and differential ventrolateral prefrontal activity during inhibition of hand and eye movements. *Journal of Neurosciences, 27*, 9893–9900.

Levin, H. S., Eisenberg, H. M., & Benton, A. L. (1991). *Frontal lobe function and dysfunction*. New York: Oxford University Press.

Lie, C. H., Specht, K., Marshall, J. C., & Fink, G. R. (2006). fMRI to decompose the neural processes underlying the Wisconsin card sorting test. *Neuroimage, 30*, 1038–1049.

Lezak, M. D. (1983). *Neuropsychological assessment* (2nd ed.). New York: Oxford University Press.

Lezak, M. D., Howieson, D. B., Loring, D. W., & Hannay, J. (2004). *Neuropsychological assessment*. New York: Oxford.

Lieberman, P. (2002a). *Human language and our reptilian brain*. Cambridge, MA: Harvard University Press.

Lieberman, P. (2002b). On the nature and evolution of the neural bases of human language. *Yearbook of Physical Anthropology, 45*, 36–62.

Luria, A. R. (1966). *Human brain and psychological processes*. New York: Harper & Row.

Luria, A. R. (1969). Frontal lobe syndromes. In P. J. Vinken & G. W. Bruyn (Eds.). *Handbook of clinical neurology* (Vol. 2, pp. 725–757). Amsterdam: North Holland.

Luria, A. R. (1973). *Working brain*. London: Penguin books.

Luria, A. R. (1980). *Higher cortical functions in man* (2nd ed.). New York: Basic.

Manes, F., Sahakian, B., Clark, L., Rogers, R., Antoun, N., Aitken, M., et al. (2002). Decision-making processes following damage to the prefrontal cortex. *Brain, 125*, 624–639.

McGuire, P. K., Silbersweig, D. A., Murray, R. M., David, A. S., Frackowiak, R. S. J., & Frith, C. D. (1996). Functional anatomy of inner speech and auditory verbal imagery. *Psychological Medicine, 26*, 38–39.

Matsumura, M., Sadato, N., Kochiyama, T., Nakamura, S., Naito, E., Matsunami, K., et al. (2004). Role of the cerebellum in implicit motor skill learning: A PET study. *Brain Research Bulletin, 63*, 471–483.

Medalla, M., Lera, P., Feinberg, M., & Barbas, H. (2007). Specificity in inhibitory systems associated with prefrontal pathways to temporal cortex in primates. *Cerebral Cortex, 17*(Suppl. 1), i136–i150.

Miller, B. L., & Cummings, J. L. (1998). *The human frontal lobes: Functions and disorders*. New York: The Guilford Press.

Miller, P., & Wang, X. J. (2006). Inhibitory control by an integral feedback signal in prefrontal cortex: A model of discrimination between sequential stimuli. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 201–206.

Mitchell, R. L., & Phillips, L. H. (2007). The psychological, neurochemical and functional neuroanatomical mediators of the effects of positive and negative mood on executive functions. *Neuropsychologia, 45*, 617–629.

Mithen, S. (1994). From domain specific to generalized intelligence: A cognitive interpretation of the middle/upper palaeolithic transition. In C. Renfrew & E. B. W. Zubrow (Eds.), *The ancient mind: Elements of cognitive archaeology* (pp. 29–39). Cambridge, UK: Cambridge University Press.

Mithen, S. (1996). *The prehistory of the mind*. London: Thames and Hudson.

Miyake, A., Friedman, N., Emerson, M., Witzki, A., & Howerter, A. (2000). The unity and diversity of executive functions and their contributions to complex ''Frontal Lobe'' tasks: A latent variable analysis. *Cognitive Psychology, 41*, 49–100.

Moll, J., Zahn, R., de Oliveira-Souza, R., Krueger, F., & Grafman, J. (2005). The neural basis of human moral cognition. *Nature Reviews Neuroscience, 6*, 799–809.

Oaksford, M., Morris, F., Grainger, B., & Williams, J. M. G. (1996). Mood, reasoning, and central executive processes. *Journal of Experimental Psychology: Learning, Memory and Cognition, 22*, 477–493.

Osaka, N., Osaka, M., Mondo, H., Morishita, M., Fukuyama, H., & Shibasaki, H. (2004). The neural basis of executive function in working memory: An fMRI study based on individual differences. *NeuroImage, 21*, 623–631.

Ostrosky, F., Ardila, A., Rosselli, M., Lopez-Arango, G., & Uriel-Mendoza, V. (1998). Neuropsychological test performance in illiterates. *Archives of Clinical Neuropsychology, 13*, 645–660.

Parkin, A., & Java, R. (1999). Deterioration of frontal lobe function in normal aging: Influences of fluid intelligence versus perceptual speed. *Neuropsychology, 13*, 539–545.

Pennington, B. F., & Ozonoff, S. (1996). Executive functions and developmental psychopathology. *Journal of Child Psychology and Psychiatry, 37*, 51–87.

Perecman, E. (Ed.). (1987). *The frontal lobes revisited*. New York: The IRBN Press.

Piguet, O., Grayson, G., Browe, A., Tate, H., Lye, T., Creasey, H., et al. (2002). Normal aging and executive functions in ''Old-old'' community dwellers: Poor performance is not an inevitable outcome. *International Psychogeriatric Association, 14*, 139–159.

portal.unesco.org/education/en/ev.php-URL_ID=12874&URL_DO=DO_TOPIC&URL_SECTION=201.html.

Potts, R. (1996). Evolution and climate variability. *Science, 273*, 922–923.

Potts, R. (2004). Paleoenvironmental basis of cognitive evolution in great apes. *American Journal of Primatology, 62*, 209–228.

Pribram, K. H., & Luria, A. R. (Eds.). (1973). *Psychophysiology of the frontal lobes*. New York: Academic Press.

Reis, A., & Castro-Caldas, A. (1997). Illiteracy: A cause for biased cognitive development. *Journal of the International Neuropsychological Society, 5*, 444–450.

Risberg, J. (2006). Evolutionary aspects of the frontal lobes. In J. Risberg & J. Grafman (Eds.). *The frontal lobes. Development, function and pathology* (pp. 1–20). Cambridge: Cambridge University Press.

Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in Neurosciences, 21*, 188–194.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience, 27*, 169–192.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research, 3*, 131–141.

Roberts, A. C., Robbins, T. W., & Weiskrantz, L. (1998). *The prefrontal cortex: Executive and cognitive functions*. Oxford: Oxford University Press.

Roberts, A. C., Robbins, T. W., & Weiskrantz, L. (2002). *The prefrontal cortex: Executive and cognitive functions*. Oxford: Oxford University Press.

Ross, E. D., & Stewart, R. M. (1981). Akinetic mutism from hypothalamic damage: Successful treatment with dopamine agonists. *Neurology, 31*, 1435–1439.

Rosselli, M., Ardila, A., & Rosas, P. (1990). Neuropsychological assessment in illiterates II: Language and praxic abilities. *Brain and Cognition, 12*, 281–296.

Roth, G., & Dicke, U. (2005). Evolution of the brain and intelligence. *Trends in Cognitive Sciences, 9*, 250–257.

Salthouse, T. (1996). The processing-speed theory of adult age differences in cognition. *Psychological Review, 103*, 403–428.

Salthouse, T. (2005). Relations between cognitive abilities and measures of executive functioning. *Neuropsychology, 19*, 532–545.

Salthouse, T., Atkinson, T., & Berish, D. (2003). Executive functioning as a potential mediator of age-related cognitive decline in normal adults. *Journal of Experimental Psychology: General, 132*, 566–594.

Schoenemann, P. T., Sheehan, M. J., & Glotzer, L. D. (2005). Prefrontal white matter volume is disproportionately larger in humans than in other primates. *Nature Neuroscience, 8*, 242–252.

Semendeferi, K., Damasio, H., Frank, R., & Van Hoesen, G. W. (1997). evolution of the frontal lobes: A volumetric analysis based on three-dimensional reconstructions of magnetic resonance scans of human and ape brains. *Journal of Human Evolution, 32*, 375–388.

Semendeferi, K., Lu, A., Schenker, N., & Damasio, H. (2002). Humans and great apes share a large frontal cortex. *Nature Neuroscience, 5*, 272–276.

Shallice, T. (1982). Specific impairments of planning. *Philosophical Transactions of the Royal Society of London Series B, 298*, 199–209.

Simon, H. A. (1975). The functional equivalence of problem solving skills. *Cognitive Psychology, 7*, 268–288.

Skipper, J. I., Goldin-Meadow, S., Nusbaum, H. C., & Small, S. L. (2007). Speech-associated gestures, Broca's area, and the human mirror system. *Brain and Language, 101*, 260–277.

Smith, P. B., Bond, M. H., & Kagitcibas, C. (2006). *Understanding social psychology across cultures: Living and working in a changing world (sage social psychology program)*. New York: Sage Publishers.

Spies, K., Hesse, F. W., & Hummitzsch, C. (1996). Mood and capacity in Baddeley's model of human memory. *Zeitschrift fur Psychologie, 204*, 367–381.

Stout, D., & Chaminade, T. (2007). The evolutionary neuroscience of tool making. *Neuropsychologia, 45*, 1091–1100.

Stroop, J. R. (1935). Studies of inference in serial verbal reactions. *Journal of Experimental Psychology, 18*, 643–662.

Stuss, D. T., & Benson, D. F. (1986). *The frontal lobes*. New York: Raven Press.

Stuss, D. T., & Knight, R. T. (2002). *Principles of frontal lobe function*. New York: Oxford University Press.

Sugarman, R. (2002). Evolution and executive functions: Why our toolboxes are empty? *Revista Española de Neuropsicología, 4*, 351–377.

Victor, M., & Ropper, A. H. (2001). *Adams & Victor's principles of neurology*. New York: McGraw-Hill.

Vygotsky, L. S. (1929). The problem of the cultural development of the child II. *Journal of Genetic Psychology, 36*, 415–432.

Vygotsky, L. S. (1934/1962). *Thought and language*. Cambridge, MA: MIT Press.

Vygotsky, L. S. (1934/1978). *Mind in society*. Cambridge, MA: Harvard University Press.

Vygotsky, L. S. (1987). *Lecture 2. Memory and its development in childhood. The collected works of L.S. Vygotsky* (Vol. 1, pp. 301–310). New York: Kluwer Academic/Plenum Press.

Wayne, C. (2006). The evolutionary origins of volition. In D. Spurrett, H. Kincaid, D. Ross, & L. Stephens (Eds.), *Distributed cognition and the will: Individual volition and social context*. Cambridge: MIT Press, MA.

Winterer, G., & Goldman, D. (2003). Genetics of human prefrontal function. *Brain Research: Brain Research Review, 43*, 134–163.

Wood, B. (1992). Origin and evolution of the genus *Homo*. *Nature, 355*, 783–790.

Yoon, J. H., Hoffman, J. N., & D'Esposito, M. (2007). Segregation of function in the lateral prefrontal cortex during visual object working memory. *Brain Research, 1184*, 217–225.