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Executive Functions of the Frontal Lobes and the Evolutionary Ascendancy of *Homo Sapiens*

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A core question of cognitive archaeology is the evolution of modern thinking. In this article, it is argued that a cluster of specific cognitive abilities, 'executive functions', was one of the key evolutionary acquisitions that led to the development of modern thinking. A review of the history of executive functions is presented as well as current opinions as to their nature and genetic basis. Examples are also presented from the cognitive archaeological record that may be representative of executive functions in the evolution of modern thought.

One of the core questions of cognitive archaeology concerns the evolution of modern thought. When did modern thinking appear, and what were the circumstances of this evolutionary breakthrough? Some features of the human mind appear to be very old; spatial cognition, for example, appears to have been essentially modern prior to the end of the Acheulean several hundred thousand years ago (Wynn 1989). Yet culture was not modern, lacking many elements of complexity that characterize the modern world. There is a general consensus among palaeoanthropologists that humans possessed modern cognitive abilities by the time of the European Upper Palaeolithic, largely because all of the familiar elements of modern culture were in place, including ritual and art. Explaining this development has not been as easy. Richard Klein, for example, has recently suggested that the key was the 'neural capacity for language or for "symboling"', which resulted from a rapid 'biological' change within the last 100,000 years (Klein 2000). This is congruent with Davidson & Noble's argument for the origins of language (Davidson & Noble 1989; Noble & Davidson 1996). Other scholars have invoked cognitive abilities. Donald (1991) has suggested that externally stored symbols were the key, Mithen (1996) has emphasized the evolution of 'cognitive fluidity', and Shepard (1997) has posited evolution of abilities of internal representation that enable mental rehearsal. While all are reasonable hypotheses, based largely on general understandings of the modern mind, they are comparatively weak evolutionary models, because they lack any identifiable inherited component. In the argument that follows, we suggest that a specific cognitive ability, 'executive function', was one of the key evolutionary acquisitions and indeed may even have been the crucial development that led to modern thinking.

On September 13, 1848, an apparently responsible, capable, and virile 25-year-old man, Phineas Gage, the foreman of a railroad construction crew, accidentally dropped a 13¹/₄ pound iron tamping rod on a dynamite charge. The tamping rod was driven by the explosion through the left side of his face and out the top of the frontal portion of his cranium. He was taken to his nearby hotel, which was to serve as his hospital room until 32 days later, when he was able to leave his bed. At this point, it was noted that Phineas was eating well, sleeping well, and his long-term memories appeared to be intact. Seventy-four days after the accident, Phineas was able to return to his home about 30 miles away, but there were discernable differences in Phineas' behaviour, not related to his health, general intelligence, or memory. The original contractors who had hired him considered the 'change in his mind' so great that they refused to rehire him. Phineas told his attending physician, J.M. Harlow (1868), that he could not decide whether to work or to travel. There were reports that Phineas was roaming the streets, purchasing items, although he did not appear to have his usual concern about price. About this same time, Harlow noted that Phineas' mind seemed 'childish' and that he would make plans and change them capriciously and then abandon them quickly. More importantly, Harlow wrote:

> Previous to his injury, though untrained in the schools, he possessed a well-balanced mind, and was looked upon by those who knew him as a shrewd, smart business man, very energetic and persistent in executing all his plans of operation. In this regard his mind was so radically changed, so decidedly that his friends and acquaintances said he was 'no longer Gage'. (Harlow 1868, 340)

In the literature, the quote 'no longer Gage' has more often become associated with Phineas' personality changes: his postmorbid use of profanity as well as depression, irritability, and capriciousness. Clearly, though, it seems that Harlow was associating Phineas' most important change with the loss of his once shrewd business acumen and his former ability in 'executing all of his plans of operation'. It must have been these latter abilities that originally made him so valuable as a foreman. Significantly, Harlow's description may have been the first in the written literature for the frontal lobe metaphor: that they serve as a kind of executive, making decisions, forming goals, planning, organizing, devising strategies for attaining goals, and changing and devising new strategies when initial plans fail. The Russian neuropsychologist Luria (1966) wrote extensively about these executive functions of the frontal lobes or the prefrontal cortices. Luria noted that patients with frontal lobe damage frequently have their speech, motor abilities, and sensations intact, yet their complex psychological activities are tremendously impaired. He observed that they were often unable to carry out complex, purposive, and goal-directed actions. Furthermore, he found that they could not accurately evaluate the success or failure of their behaviours, especially in terms of using the information to change their future behaviour. Luria found these patients unconcerned with their failures, hesitant, indecisive, and indifferent to the loss of their critical awareness of their own behaviours. Lezak (1982), a contemporary American neuropsychologist, wrote that the executive functions of the frontal lobes were:

> . . . the heart of all socially useful, personally enhancing, constructive, and creative abilities . . . Impairment or loss of these functions compromises a person's capacity to maintain an independent, constructively self-serving, and socially productive life no matter how well he can see and hear, walk and talk, and perform tests. (Lezak 1982, 281)

More recently, Welsh & Pennington (1988) have defined executive functions as the ability to maintain an appropriate problem-solving set for the attainment of a future goal. Pennington & Ozonoff (1996) view the domain of executive functions as distinct from cognitive domains such as sensation, perception, language, working memory, and long-term memory. They see it as overlapping with such domains as attention, reasoning, and problem-solving 'but not perfectly' (Pennington & Ozonoff 1996, 54). They also add interference control, inhibition, and integration across space and time as other aspects of executive function. Their central view of executive function is:

> a context-specific action selection, especially in the face of strongly competing, but context-inappropriate, responses. Another central idea is maximal constraint satisfaction in action selection, which requires the integration of constraints from a variety of other domains, such as perception, memory, affect, and motivation. Hence, much complex behavior requires executive function, especially much human social behavior. (Pennington & Ozonoff 1996, 54)

The ability to integrate across space and time (or 'sequential memory function') is, no doubt, another salient feature of the executive functions. Successful planning for goal attainment would require the ability to sequence a series of activities in their proper order. Current neuropsychological assessment of executive functions invariably includes measures of planning, sequential memory, and temporal order memory (e.g. Lezak 1995). It is also important to note that the frontal lobes or prefrontal cortices have greater interconnectivity with subcortical regions of the brain than any of the other lobes of the cortex. The frontal lobes have extensive and reciprocal connections to the thalamus, basal ganglia, limbic system, and also posterior portions of the cortex (e.g. Luria 1973; Damasio 1994). Thus, the neural substrate of the frontal lobes also makes it an ideal candidate as a domain, which has greater access to other domains and functions of the brain than any other domain.

Could it be that executive functions of the frontal lobes are the key to modern cognition? Necessary to our present argument would be evidence that executive functions are heritable, and here there are two lines of evidence, direct and indirect. The indirect evidence lies in Pennington & Ozonoff's (1996) hypothesis that executive function deficits are the core or primary dysfunction in children with Attention-Deficit/Hyperactivity Disorder (ADHD). Their empirical research with ADHD children provides a strong and frequent association with executive function deficits, such as consistent deficits in sequential memory, tasks of inhibition, and measures of organization and planning. They argue that the overall pattern of these deficits is such that executive function deficits may be considered the primary and defining cognitive problem in ADHD, and there is substantial evidence for the heritability of ADHD. It has been shown from twin studies that the variability in ADHD may be about 70 per cent to 80 per cent heritable (Eaves *et al.* 1993; Stevenson 1992).

The direct evidence comes from a recent study (Coolidge *et al.* 2000) of 224 monozygotic and dizygotic twins whose parents rated their executive function deficits on a standardized rating scale across varying situations. Through univariate and multivariate (structural equation modelling) statistical analyses, they found that the variability in executive functions scores appeared to be about 80 per cent heritable. The pattern of heritability appeared to be additive rather than nonadditive, and like general intelligence, then, not attributable to a single dominant gene or recessive genes but to many alleles at different loci which add up to a strong effect on variation in executive functioning.

Because executive function details specific abilities (manifested as deficits in ADHD individuals) that are linked and highly heritable, it is a good candidate for articulation with the archaeological record. As is always the case, the archaeological record provides evidence of varying resolution and explanatory power. Despite this inherent noise (Klein 2000), it is possible to match many of the features of executive function with activities reconstructable from archaeological evidence. Because the evidence for modern thinking has been reviewed on several occasions recently (Klein 2000; Mithen 1996; Noble & Davidson 1996), we will be selective in our examples.

'Sequential memory' is an essential ability for any task requiring complex linkage of steps. Certainly, many modern technical activities depend on this ability, and it is easy to recognize comparable complexity as far back as the Neolithic (ceramic manufacture and loom weaving, for example). Such complexity is harder to identify in the Palaeolithic. Lithic reduction sequences are tempting targets, but even sophisticated procedures like Levallois can be explained without resort to closely-linked sequences of action (Schlanger 1996). The production and use of barbed bone projectile points is a better marker. Here the final product depends much more closely on a set sequence of actions. It is a true multi-step technology (Knecht 1993). The Congolese site of Katanda has yielded barbed bone points dated by ESR to perhaps 100,000 years ago (Brooks *et al.* 1995), though Klein (2000) favours a more conservative date of 50,000 years ago for this evidence.

'Tasks of inhibition', in which immediate gratification and action are delayed, are harder to identify archaeologically but not impossible. Agriculture, especially cultivation, planting, storage, herd culling, and so on, requires such inhibition. Indeed, this may be the key cognitive prerequisite for food producing subsistence posited by Sherratt (1997). Facilities (Oswalt 1976) such as traps, that capture remotely, are technologies of inhibition and were arguably present in the European Mesolithic. Again, Palaeolithic examples are less convincing. Intercept hunting of reindeer is one possibility, which would push evidence back to the Upper Palaeolithic. Nothing that we know of Middle Palaeolithic foraging, however, would require tasks of inhibition (indeed, nothing in the archaeological record of Neanderthals appears to require executive function).

'Organization and planning' have often been cited by archaeologists (e.g. Roebroeks *et al.* 1988), though most often as a synonym for foresight. The kind of planning that requires executive function is a matter of organizing and coordinating actions (hence its linkage to inhibition and sequential memory). As such, the transport of a flint core for even several score kilometres need not require executive function, but some activities known for the Palaeolithic did, most notably the colonization of the Sahul (New Guinea, Australia, and Tasmania). Davidson & Noble (1992) and Klein (2000) have emphasized the significance of this event as a marker for modern behaviour. Even conservative interpretations place the colonization at least 40,000 years ago, and some believe it happened as early as 60,000 years ago. The colonization of the Sahul required use of watercraft and a journey over the horizon (the Australian landmass is not visible from Timor, the farthest eastern extension of the Sunda shelf), and it seems unlikely that such a colonization was unplanned. Davidson & Noble argue that the key was conceptual thought based on words and language. We suggest that it required executive function. Watercraft themselves are a multi-step technology requiring sophisticated sequential memory, and their use requires the kinds of organization and planning clearly beyond the abilities of Phineas Gage after his accident. This question of planning has often arisen in discussions of Neanderthals, and some authors have suggested that anatomically modern humans had a distinct advantage in this domain (Klein 2000; Tattersall & Matternes 2000). Our review of the archaeological evidence finds no convincing evidence for executive function among the traces left by Neanderthals. Of course, the same can be said for the archaeological traces of early anatomically modern humans in southern Africa. Indeed, the advent of complex modern culture, enabled we suggest by executive function, was not marked by any skeletal change. It was a neural rewiring linked to a relatively simple change at the genetic level. This trait was probably not possessed by Neanderthals (at least initially; the status of late Neanderthals and the Châtelperronian is provocative but outside the scope of this article).

The archaeological record, then, supports the hypothesis that executive function was a late and critical acquisition in human cognitive evolution. This is in keeping with current and related models and hypotheses that bolster the likelihood that executive functions played a major role in the increase in the reproductive fitness of *Homo sapiens*. Mithen (1994; and more recently, Mithen 1996) has touted the accessibility of mental modules as the impetus for a 'big bang' of human 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. As for the exact nature of his 'accessibility' mechanism, he cited the work of Gardner (1983). Gardner believed that the modern mind managed to function 'smoothly, even seamlessly in order to execute complex human activities', and he labelled this linking as 'cognitive fluidity'. Others shared Gardner's view of the mind as consisting of relatively separate domains slowly or suddenly linked together.

Shepard (1997) postulated that natural selection favoured a perceptual and representational system able to provide implicit knowledge of the pervasive and enduring properties of the environment and that natural selection also favoured a heightened degree of voluntary access to this representational system. This access, he proposed, facilitated the accurate mental simulation of varying actions, allowing the evaluation of the success or failure of these actions without taking a physical risk. Shepard thought that the mere accumulation of facts (as in Mithen's natural history intelligence or technical intelligence) would not result in advances in scientific human knowledge but its advancement would require 'thought experiments'. He also postulated that every real experiment might have been preceded by thought experiments that increased the probability of the success of the real experiment.

Dawkins (1989) has also proposed that natural selection would have favoured the reproductive success of those organisms capable of simulation. He describes systems highly similar to those of executive functions and replete with the executive functions metaphor. For example:

> Survival machines that can simulate the future are one jump ahead of survival machines who can only learn on the basis of overt trial and error. The trouble with overt trial is that it takes time and energy. The trouble with overt error is that it is often fatal. Simulation is both safer and faster. (Dawkins 1989, 59)

> . . . consciousness . . . can be thought of as the culmination of an evolutionary trend towards the emancipation of survival machines as executive decision-takers from their ultimate masters, the genes. Not only are brains in charge of the day-to-day running of survival machine-affairs, they have also acquired the ability to predict the future and act accordingly. (Dawkins 1989, 59)

> Genes are the primary policy-makers; brains are the executives. But as brains became more highly developed, they took over more and more of the actual policy decisions, using tricks like learning and simulation in doing so. (Dawkins 1989, 60)

In summary, we see that there are numerous lines of overlapping evidence and speculations that support the executive functions metaphor in the fully modern human mind, such as mental accessibility, cognitive fluidity, thought experiments, and simulation. It may be counter-argued that the concept of executive functions is simply a metaphor, primarily based upon adult brain-damaged or neurologically-impaired patients, or often with unknown or unclear neurological impairment, but whose patterns of neuropsychological dysfunction are nonetheless consistent with patients with demonstrated damage. For a more extensive review of the limitations of the executive functions metaphor, Pennington & Ozonoff's (1996) review may be consulted. Yet as Kuhn (1979) has noted, metaphors go far beyond a simple pedagogical device and lie at the heart of theory-production. The direct evidence for the heritability of executive functions also has the inherent limitations including the validity of parental assessment and the lack of standardized definitions for the breadth of executive functions or the symptomatic manifestations of their deficits. Despite these and other criticisms, the human mind is clearly the product of evolutionary processes. The delineation of all of these forces will remain fertile ground for cognitive archaeologists far into the future.

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