

The Executive Functions and Self-Regulation: An Evolutionary Neuropsychological Perspective

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Neuropsychology has customarily taken a molecular and myopic view of executive functioning, concentrating largely on those proximal processes of which it may be comprised. Although commendable as a starting point, such an approach can never answer the question, "Why executive functioning?" The present paper encourages neuropsychologists to contemplate the longer-term, functional nature of the executive functions (EFs), using an evolutionary perspective. For purely illustrative purposes, a previously developed model of the EFs is briefly presented and is then examined from an evolutionary perspective. That model views the EFs as forms of behavior-to-the-self that evolved from overt (public) to covert (private) responses as a means of self-regulation. That was necessary given the interpersonal competition that arises within this group-living species. The EFs serve to shift the control of behavior from the immediate context, social others, and the temporal now to self-regulation by internal representations regarding the hypothetical social future. The EFs seem to meet the requirements of a biological adaptation, being an improbable complex design for a purpose that exists universally in humans. Discovering the adaptive problems that the EFs evolved to solve offers an invaluable research agenda for neuropsychology lest that agenda be resolved first by other scientific disciplines. Some adaptive problems that the EFs may have evolved to solve are then considered, among them being social exchange (reciprocal altruism or selfish cooperation), imitation and vicarious learning as types of experiential theft, mimetic skill (private behavioral rehearsal) and gestural communication, and social self-defense against such theft and interpersonal manipulation. Although clearly speculative at the moment, these proposals demonstrate the merit of considering the larger adaptive problems that the EFs evolved to solve. Taking the evolutionary stance toward the EFs would achieve not only greater insight into their nature, but also into their assessment and into those larger adaptive capacities that may be diminished through injury or developmental impairment toward that system.

KEY WORDS: executive functions; evolution; self-regulation; adaptation.

The present paper attempts to illustrate the utility of considering the nature of the executive functions (EFs) from an evolutionary perspective and to encourage neuropsychologists to adopt such a frame of reference in future attempts to understand the nature of the EFs. It will draw upon a previously developed model of the EFs, using a behavioral basis for their description rather than the information-processing or cognitive-psychology perspective that is more widely cited in the current literature. In

doing so, this paper considers several possible adaptive purposes that the executive system may have evolved to solve. Of course, definitive solutions to the adaptive riddle of the EFs are not proposed here. Instead, this paper merely seeks to illustrate the substantial heuristic value that could accrue if neuropsychology approached this riddle from the perspective of biological evolution.

The current stance of viewing the human brain and its EFs from the metaphor of a computer, as in information-processing approaches to cognitive psychology, is insufficient to the task of explaining why the EFs exist. The tale it tells of the nature of the EFs is boring and of limited utility. That is because it is devoid of an evolutionary context and the plot and motives that context provides for

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understanding why adaptations exist in particular species. If that seems provocative, it is intentional, for this paper aims to provoke a necessary discussion about the evolutionary significance of the EFs. Science is a form of storytelling and all good scientific tales that deal with adaptations in living organisms must eventually come to include their evolutionary history and context if they are to be not only interesting and insightful but also fully useful to science and the public it serves. Without reference to that context, the complete meaning or purpose(s) of the EFs cannot be known. Computer metaphors for executive functioning cannot address that purpose largely because computers do not have to replicate themselves across generations while fending off predators, outwitting competitors, attracting mates, investing in their offspring, and solving the adaptive problems that arise in doing so. Phonological loops and visual-spatial sketchpads do not have to find and compete for energy sources and mates in order to reproduce the recipes of themselves into the next generation. Moreover, information-processing metaphors for executive functioning fail to incorporate any notions of self-control, a sense of the future, or the larger, more distal social purposes likely to be associated with the executive system. In short, computers do not come with self-interested motives or biological imperatives preinstalled; human brains do. And so do the EFs provided by that brain. Those adaptive motives are essential to consider in fully answering the great EF question, “Why executive functioning?” Such motives may be quite revealing of the larger adaptive purposes of the EFs, of what is truly diminished by their impairment, of how they might better be clinically assessed, and of what they involve when those functions are being neuroimaged.

The goals of this paper therefore are (1) to define the EFs and the self-regulation they provide; (2) to provide a brief overview of a previously developed model of the EFs; and (3) then to show how it may suggest the adaptive purposes for which the EFs may have evolved, and in doing so to illustrate the valuable implications that arise from taking the evolutionary stance toward the discovery of these adaptive purposes. Taking that evolutionary perspective can be of some value even if definitive answers to those adaptive purposes cannot be offered at this time. It can serve as a source of hypotheses about the EFs and keep neuropsychologists’ attention on the larger EF question, “Why do the EFs exist?”

These goals are admittedly ambitious. But the rampant ambiguity and confusion currently surrounding the nature of the EFs in neuropsychology demand a bold attempt at clarification and synthesis. Whether this paper succeeds or not in doing so, it at least seeks to provoke further discussion among neuropsychologists on the adaptive

purposes of the EFs and the value of an evolutionary stance in that discussion. In contrast, a cursory review of the present empirical literature on the EFs would only suggest that they evolved so as to arrange concentric rings on spindles, to persist in detecting Xs from Os, to recite digits backward, or to sort patterns on cards by various categories. These, however, are only tests of the most simplified and particularized processes that may be involved in executive functioning. Helpful as they may have been, those tests reveal only the most proximal answers to the “what” question but give us no clue to the “why” question—Why is there executive functioning? The processes those measures assess are but a means to some end, and should not be confused with the end itself. No matter how informative such proximal studies are of how executive functioning occurs, they fail to explicate the genetically self-interested motives that an evolutionary analysis implies for all biological adaptations (Dawkins, 1974, 1995, 1997; Williams, 1966/1996).

Not to take the evolutionary stance in neuropsychology concerning the EFs (or other brain functions for that matter) will surely result in its conceptual territory being overtaken by the rapidly encroaching fields of evolutionary psychology and sociobiology that have not been hesitant to address such issues. Neuropsychologists would be left as outsiders to the advancement of understanding of the very field of science they have staked out as being their own—the understanding of brain–behavior relationships. And deservedly so if they persist in taking a narrow view of the functions of the human brain as if it were only an information processor. A fleshy version of a Turing machine it may be, but ultimately it is a Turing machine with a sexual agenda whose very existence hinges on its contributions, however indirect, to reproductive or inclusive fitness (Gazzaniga, 1998; Tooby and Cosmides, 1992). Adaptations arise to solve the adaptive problems that occur along the way in achieving these forms of fitness; the executive system as an adaptation can be no exception. The EF system is an adaptation because it fulfills the specifications for one: it is universal in humans, complex, improbable, and has the earmarks of having been designed for a purpose (functionality).

Evolution is the only credible explanation of the means by which such adaptations arise. The great evolutionist Theodosius Dobzhansky proclaimed that nothing in biology makes sense except in the light of evolution (see Plotkin, 1998, p. 1). Given that neuropsychology is a subfield of biology as much as it is of psychology, Dobzhansky’s admonition is just as pertinent to attempts by neuropsychologists to understand the EFs. Evolution offers the only means to answer the question “Why executive functioning?” The alternative explanation, known

as the standard social science model (SSSM), views such complex executive functioning and its associated social behavior as chiefly a cultural product achieved largely through social or operant learning. Such a model is grossly inadequate for the EFs (see Pinker, 1997; Tooby and Cosmides, 1992, for a discussion of the limitations of the SSSM for an understanding of cognitive mechanisms in psychology). Ever-accumulating evidence seems to show that the developmental emergence of the executive system is inexplicable when viewed purely or largely as a product of social learning and culture (Barkley, 1997b). This has proven to be the case with other neuropsychological functions, such as locomotion, language and symbolization, and perceptual preferences in mate selection. It has also proven informative for understanding perceptual biases, gender differences in spatial functioning, male jealousy and mate protection, and developmental psychology, among others (Buss *et al.*, 1998; Crawford and Krebs, 1998; Deacon, 1997; Geary and Bjorklund, 2000; Pinker, 1995, 1997; Plotkin, 1998; Tooby and Cosmides, 1992).

The intention here is not to spin purely entertaining “just-so” stories of human psychological adaptations, as Gould has criticized some psychologists for doing (1991, 1997). Instead more precise, relatively operational, and potentially testable propositions are sought that can be used to construct scientific hypotheses concerning the nature and purpose(s) of the executive system. Science is, itself, a form of storytelling. But it is a precise, testable, self-correcting, and thereby useful way of doing so (Buss *et al.*, 1998). Evolutionary psychologists, sociobiologists, and philosophers have long speculated on the evolutionary origins and adaptive functions of consciousness and the mind itself (Baldwin, 1895; Campbell, 1960; Dennett, 1995; Donald, 1991, 1993; Humphrey, 1984; James, 1890/1992; Lumsden and Wilson, 1982; Plotkin and Odling-Smee, 1981; Wilson, 1998; see Richards, 1987, for an historical review). So also have neuropsychologists (Vygotsky and Luria, 1994). As Popper (1968, 1972) argued, such efforts at theory-development in science constitute a Darwinian process in their own right—a cultural form of evolution in which scientific theories compete with each other and so become successively better adapted to explaining, predicting, and potentially controlling environmental phenomena. The present paper thus constitutes merely a further step in this long line of explanatory descent with modification concerning the nature of the EFs.

This paper differs considerably in several important respects from the author’s earlier work on the nature of the EFs (Barkley, 1997a, 1997b). Those earlier efforts were aimed primarily at the explication and empirical justification of a new theory of the EFs; no evolutionary perspective was offered as to why they came to exist. Such

effort had as its larger purpose to provide a greater understanding of the neuropsychological disorder of attention deficit hyperactivity disorder (ADHD). The present paper briefly reiterates this theory to acquaint the unfamiliar reader with this model and its assumptions so as to illustrate how it may fit into an evolutionary perspective on the EFs. From this perspective, a deeper understanding may be attained both of the nature and adaptive purpose(s) of the executive system. That may lead to a better appreciation of how best to broaden or amend the clinical assessment of the EFs and of the impact in adaptive functioning that deficits in this system may produce as a consequence of injury or of developmental aberrations.

DEFINING INHIBITION, SELF-CONTROL, AND EXECUTIVE FUNCTION

The terms behavioral or response inhibition, self-control or self-regulation, and especially executive function are frequently used in the literature of neuropsychology, often without providing any definition of the terms. That literature is typified by descriptions of various activities thought to be involved in EF while the construct itself goes undefined. For instance, the term executive function has been used to encompass the actions of planning, inhibiting responses, strategy development and use, flexible sequencing of actions, maintenance of behavioral set, resistance to interference, and so forth (Denckla, 1996; Morris, 1996; Spreen *et al.*, 1995). Others simply concluded that the EFs are what the frontal lobes do (Stuss and Benson, 1986). Denckla (1994) defined executive functioning by its components: interference control; effortful and flexible organization; and strategic planning or anticipatory, goal-directed preparedness to act. Dennis (1991) did likewise, recognizing the components of regulatory (mental attention), executive (planning), and social discourse (productive verbal interaction with others). And so did Spreen and colleagues in their description of the EFs as inhibition, planning, organized search, self-monitoring, and flexibility of thought and action (Spreen *et al.*, 1995). Might the underlying theme of the EFs be this future orientation as conjectured by Denckla (1994) and which the philosopher Dennett (1995) has called “the intentional stance?” Or is it the temporal ordering of events (Shimamura *et al.*, 1990) or their hierarchical staging into arrangements of goal–subgoal components (Goel and Grafman, 1995)? Could those arrangements simply be parts of a larger capacity for the formation of social scripts, as Sirigu and colleagues suggested (Sirigu *et al.*, 1995)? Such scripts involve the generation of the sequential steps needed to complete a social goal, such as shopping for

groceries, planning a wedding, and so forth. As Sirigu *et al.* (1995) found, these scripts are impaired in frontal-lobe injured patients. Yet all such efforts to describe the EFs seem to fall short of the mark. They merely beg the question of what underlying theme binds these descriptions together. What is the essence of the EF construct so that we may know one from a nonexecutive function?

The situation in clinical neuropsychology is even worse. There examinations of executive functioning seem to select batteries of tests for three simple reasons: (1) other neuropsychologists, particularly one's mentors, previously used them and said they measured the EFs; (2) scientific papers in clinical journals used them and said they were measures of EFs; and (3) these measures are often poorly performed by patients with injuries to the frontal lobes. This constitutes avoidance of conceptual responsibility that is unhelpful in attempting to fully understand the functional integrity of the EFs in clinical populations. To say that the Wisconsin Card Sort Test, the Tower of Hanoi, Digit Span Tasks, continuous performance tests, the Paced Auditory Serial Additions Task, Self-Ordered Pointing Tasks, the Stroop Color-Word Association Task, the Kaufman Hand Movements Task, the F-A-S Verbal Fluency Test, or other so-called EF tests assess executive functioning is simply circularity of reasoning. The construct is being reified by its measure. This merely sidesteps the issue of what comprises the essential ingredients of executive functioning that would guide clinical decisions as to how they should be assessed. Moreover, no matter how forced their interpretations may be in clinical reports, extant EF measures tell precious little about what is ultimately lost in adaptive functionality in those patients suffering injury to their executive system. This is painfully evident in the low-order correlations of EF tasks with ratings by patients and others of their apparent executive functioning in natural settings. The shared variance between such measurement approaches is often below 10% (Burgess *et al.*, 1998).

Brazen as this may seem, this paper at least defines the EFs. It does so using behavioral terms because this at least permits them to be operationally defined, more easily understood, and potentially more easily examined in research. It also makes them more capable of identification in humans and other primates through the available anthropological evidence concerning earlier hominids and their artifacts. Understanding the evolutionary origins of the EFs in human ancestors and other related species is critical because evolution acts gradually in shaping new adaptations out of old ones; small changes add up over time. This principle of gradualism does not mean that evolution is necessarily slow. Only that the development of an

adaptation occurs by small steps, not huge leaps (Dawkins, 1997). The evolutionary rate can vary as a function of context such that small steps can accumulate quickly or slowly. But, regardless of rate of change, the transitions in the emergence of an adaptation occur through small degrees of change. How then do we account for the transition from the rudimentary appearance of some EFs evident in a few other primates (e.g., nonverbal working memory in rhesus monkeys and chimpanzees) to the complex executive system ascribed to humans? Operationalizing terms into their manifest behavioral equivalents may clarify their possible path of gradual evolution and their adaptive purpose(s). It surely leads to predictions that can be more easily testable and falsifiable. Specifying the EFs more precisely could, as well, offer a better understanding of what functional activities are evident in neuroimaging studies of the EFs.

Response inhibition has been used to refer to three somewhat distinct processes:

1. inhibiting the initial prepotent response to an event so as to create a delay in responding;
2. interrupting an ongoing response that is proving ineffective thereby permitting a delay in the decision to continue responding (a sensitivity to error); and
3. protecting the self-directed (executive) responses that will occur within the delay as well as the goal-directed behavior they generate from disruption by competing events and responses (interference control or resistance to distraction; Barkley, 1997a,b; Fuster, 1997).

The first of these is, arguably, the most important, for without a delay in the prepotent response, the remaining goal-directed actions are pointless, if they can occur at all (Barkley, 1997b; Bronowski, 1967/1977). Note that it is not just the response that is delayed, but the decision about the response (Bronowski, 1967/1977, 1976). The prepotent response is that response for which immediate reinforcement (positive or negative) is available within a particular context or which has been previously associated with that response in that context (Barkley, 1997a). Both forms of reinforcement—positive and negative—must be considered in defining a response as being prepotent. Although some forms of impulsive behavior function to achieve an immediate reward, others serve to escape or avoid immediate aversive, punitive, or otherwise undesirable events (negative reinforcement). Such escape/avoidance responses are just as much a part of immediate gratification as are responses that result in immediate reward. Both forms of prepotent response will require inhibition if executive functioning and self-regulation are to occur and be effective.

Self-control is a response (or series of responses) by the individual that functions to alter the probability of their subsequent response to an event and thereby changes the likelihood of a later consequence related to that event (Barkley, 1997a,b; Kanfer and Karoly, 1972; Mischel *et al.*, 1989; Skinner, 1953). Some considered self-control to be the choice of a delayed, larger reward over a more immediate, smaller one (Ainslie, 1974, 1975; Burns and Powers, 1975; Logue, 1988; Mischel, 1983; Navarick, 1986). But this ignores the self-directed actions in which the individual must engage to value the delayed over the immediate reward and to pursue that delayed consequence. Neuropsychology tends to view impulsiveness as a problem or deficit, yet for most species that have a nervous system that learns from contingencies of reinforcement, there actually is no “problem” of impulsiveness—it is their default state. The “problem” posed by impulsiveness is relatively unique to humans, and so then are likely to be those adaptive neuropsychological mechanisms that have evolved to solve it. This asks the question of what social problem impulsiveness created for humans for which inhibition and self-regulation evolved to solve it.

What then are the EFs? Neuropsychologists seem to view them as unobservable “cognitive” or mentalistic events largely mediated by the prefrontal cortex. This view is incorrect for two reasons. First, as asserted here, the EFs are not mental in some impossibly undetectable sense that they take place in a mind somewhere. *The EFs are composed of the major classes of behavior toward oneself used in self-regulation.* An executive act is any act toward oneself that functions to modify one’s own behavior so as to change the future outcomes for that individual. Such actions may be covert but need not be so to be classified as “executive.” The term covert here merely means that the outward, publicly observable (musculo-skeletal) manifestations of such behavior have been made very difficult to detect by others over the course of human evolution. But those actions still occur and they can still be thought of as forms of behavior. And second, developments in the technology of neuroimaging and the fine-grained recording of shifts in muscle potential suggest that this covert behavior-to-the-self is now capable of successful measurement (D’Esposito *et al.*, 1997; Livesay *et al.*, 1996; Livesay and Samaras, 1998; Ryding *et al.*, 1996).

The conceptual linkage of inhibition with self-regulation and of both of these constructs with executive functioning is now obvious. Response inhibition is a prerequisite to self-regulation. The EFs are the general forms or classes of self-directed actions that humans use in self-regulation. The EFs and the self-regulation they effect produce a net overall maximization of social consequences when considering both the immediate and

delayed outcomes of certain response alternatives. Self-regulation and the EFs that comprise it, in short, function to alter the future and so are instrumental to purposive, intentional behavior. And, as shall become evident later, that future is a social one. This view of the EFs resembles that of Lezak (1995) as “those capacities that enable a person to engage successfully in independent, purposive, self-serving behavior” (p. 42) or that of Denckla (1994), noted earlier, as attention and intention toward the future. Regrettably, neither author specifies the nature of those EF capacities with any precision.

Self-control is nearly impossible if there is not some means by which the individual is capable of perceiving and valuing future over immediate outcomes. A long-term outcome may have a greater reward value than a short-term reward if both were to exist at the same point in time. But arranged temporally as they are, the reward value of the long-term outcome will be discounted as a function of the length of the temporal delay involved (Mazur, 1993). Humans demonstrate a remarkable shift over the first three decades of life toward a greater preference for delayed versus immediate rewards (Green *et al.*, 1996). They discount future outcomes less steeply with age in comparison to younger individuals. All this requires some neuropsychological capacity to sense the future; that is, to construct hypothetical futures, particularly for social consequences. It also simultaneously involves the weighing of alternative responses and their temporally proximal and distal outcomes—a calculation of risk/benefit ratios over time. Some neuropsychological mechanism must have evolved that permitted this relatively rapid construction of hypothetical social futures while simultaneously engaging in a temporally discounting economic analysis of immediate versus delayed outcomes. Without such an evolved mental mechanism, self-control would not occur. As shall be shown now, the first EF to develop in children provides the capacity for just such a cross-temporal spreadsheet.

A MODEL OF THE EXECUTIVE FUNCTIONS

The details of this model of executive functions can be found in previous publications (Barkley, 1997a,b) along with the evidence that seems to support their existence. That evidence comes from developmental psychology, neuropsychological studies into the underlying factors or dimensions of executive function test batteries, and neuroimaging research on the apparent localization of these executive functions within the prefrontal lobes. It also comes from a substantial amount of research on executive functioning in children and adults with ADHD, a disorder

of inhibition believed to originate in the prefrontal-striatal-cerebellar network (Castellanos *et al.*, 1996; Filipek *et al.*, 1997).

Bronowski (1967) first proposed the initial structure of this model in his discussion of the unique properties of human language that he attributed to the prefrontal cortex. I further elaborated this framework by drawing heavily from Fuster's insights into the functioning of the prefrontal cortex (Fuster, 1995, 1997). To this, I added the work of Goldman-Rakic (1995) on working memory, and also that of Damasio (1994, 1995) on the somatic marker system and the rapid economic (motivational) analysis of hypothetical outcomes it affords. The model of EFs offered here is thereby a hybrid one.

From an evolutionary perspective, any theory of the executive functions will need to be framed with as few components as possible (to meet the principle of parsimony) and with some attention to the principle of gradualism. As noted earlier, that principle requires that any evolutionary explanation of an adaptation shed some light on the small changes likely to have occurred to give rise to that adaptation in its present form. No prior theory of EFs conforms to this principle of gradualism. The present one does so by suggesting how the EFs may have arisen from those psychological abilities seen in primates closely related to humans over the course of hominid evolution that led to humans. Metaphorical models of working memory or other EFs based on the computer, such as Baddeley's (Baddeley, 1986; Baddeley and Hitch, 1994), cannot do this, given that they are, after all, metaphors and are ahistoric. They also tacitly treat the EFs as unique, arising only in humans and being qualitatively discontinuous from those mental capacities evident in primates. Biology, anthropology, and neurology in contrast do not treat such adaptations as discontinuities in their bottom-up analyses of human behavioral and mental abilities. They seek to identify points of continuity across related species (Donald, 1991). Neuropsychology can ill-afford to do otherwise in its efforts at theorizing on the executive functions.

The evolution of a set of special mental faculties that comprise the executive system provides the foundation for the human capacity for vicarious learning and culture, as Darwin (1871/1992) seemed to have recognized. Any account of the EFs must in some way constitute the bridge between operant learning as occurs in related primate species and culture as it occurs in humans. That is because culture does not automatically spring from mere trial-and-error learning by consequences. The neuropsychological functions that create the capacity for culture (Durham, 1991) are very much akin to those capacities attributed to executive functioning—inhibition, self-awareness, self-

regulation, imitation and vicarious learning, symbolization, and generativity (mental simulation for behavioral innovation).

The present EF model fits more easily than others do within an evolutionary framework because (a) it has relatively few components, (b) lends itself to gradualist interpretations of their origins, and (c) offers a potential bridge between operant learning and the capacity for culture shown in humans. That bridge is the executive system and the vicarious learning it affords. As Campbell (1960) argued, all means by which organisms acquire information about the environment are evolutionary in form. This is known as universal Darwinism (Richards, 1987). At one level is the widely recognized biological (genetic) form of evolution (Ridley, 1997). This gave rise to a capacity for behavioral evolution, characterized by operant conditioning (Skinner, 1981, 1984) with the advent of nervous systems that learn from consequences. But somehow humans then progressed to having another form of evolution, that being a capacity for culture (Durham, 1991). The bridge from operant to cultural evolution is not an obvious one, however. The missing link between the levels of behavioral and cultural evolution can be understood as an ideational (mental) one (Lumsden and Wilson, 1982). According to the EF model here, it will be found to consist of covert operant learning-to-the-self. Such private simulation of settings, behaviors, and their outcomes is created from the EFs, given that they represent covert behavior toward the self. Hence there is a linkage now evident among the levels of evolution, from genetic→behavioral→ideational→cultural with the basis for the ideational level of evolution proposed here as being the executive system.

The EF model is graphically depicted in Fig. 1. Space here permits only a very brief summary of it; far greater detail is provided elsewhere (Barkley, 1997b). In this model, response inhibition is considered as an EF because it is a form of self-directed behavior that alters the probability of a later action; in this case, the prepotent response itself. Inhibition sets the occasion for the occurrence of the EFs and provides the protection from interference those EFs will require so as to construct hypothetical futures and direct behavior toward them. Despite being relatively distinct, the inhibitory function and the other four EFs are interactive in their natural state and share a common purpose. That purpose is to "internalize" or make private certain self-directed behavior so as to anticipate and prepare for change (time) and the future, especially the social future. Why such self-directed behaviors had to become covert in form will be discussed later. For now, suffice to say that the ultimate utility function of this EF system is to maximize the net long-term versus short-term social outcomes for the individual.

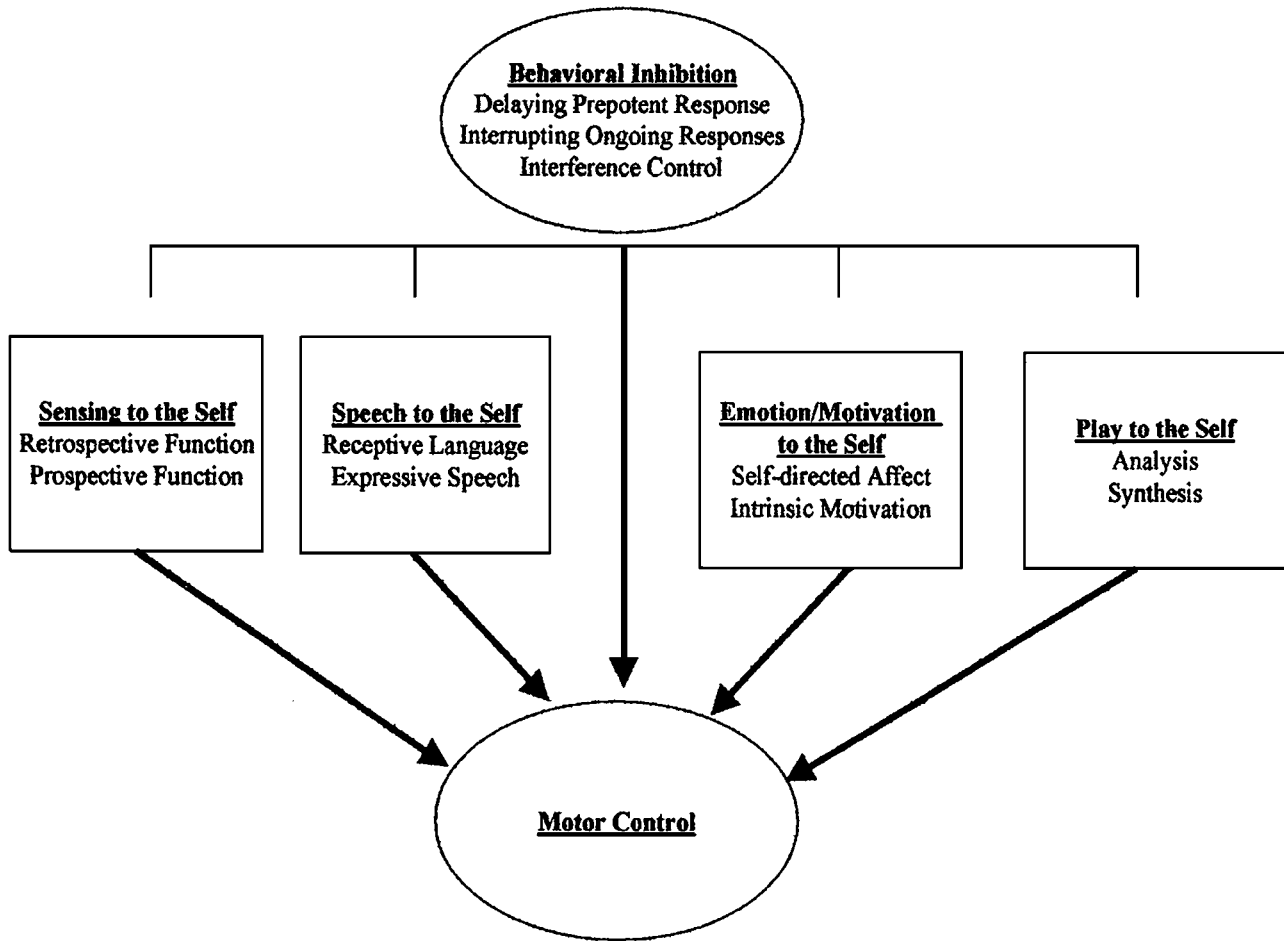


Fig. 1. Conceptual model linking behavioral inhibition to four major executive functions (boxes) and the behavioral (motor) control provided by those executive functions. Each executive function is a form of covert behavior to the self with its overt manifestations largely suppressed.

The four EFs are believed to develop via a common process. All represent private, covert forms of behavior that at one time in early child development (and in human evolution) were entirely publicly observable and were directed toward others and the external world at large. With maturation, this outer-directed behavior becomes turned on the self as a means to control one's own behavior. Such self-behaving then becomes increasingly less observable to others as the suppression of the public musculo-skeletal aspects of the behavior progresses. This progressively greater capacity to suppress the publicly observable aspects of behavior is what is meant here by the terms "covert, privatized, or internalized." In this sense, all of the executive functions follow the same general sequence of stages as the internalization of speech (Diaz and Berk, 1992; Vygotsky, 1978, 1987; Vygotsky and Luria, 1994).

Nonverbal Working Memory (Covert Self-Directed Sensing)

The first EF is nonverbal working memory. It is akin to Baddeley's visual-spatial sketchpad in his information-processing rendition of working memory (Baddeley, 1986). It originates in the privatization of sensory-motor actions—it is sensing to the self (literally, resensing to the self). The most important of the senses to humans are vision and audition and so this EF may be chiefly composed of visual imagery and covert audition—covert seeing and hearing to the self.

This EF has both retrospective (sensory or resensing) and prospective (preparatory motor) elements (Fuster, 1997; Goldman-Rakic, 1995) and requires interference control for its effective performance. Here then arises the mental module for sensing the hypothetical future

from the experienced past. This serves to generate the private or mental representations (images, auditions, etc.) that bridge the cross-temporal elements within a contingency arrangement (event- response-outcome) that is so crucial for self-control toward the future. As neuroimaging technology can now show, during nonverbal working memory tasks, neural activation occurs in the same associative sensory cortex that was used in the initial perceptual analysis of the original external event (D'Esposito *et al.*, 1997).

Peirce (1897/1955), and later Deacon (1997) and Donald (1993), noted that such private sensory-motor representations are prerequisites for symbolization. They constitute mental icons and those icons can be linked with others to form indexical relations (e.g., smell smoke→ iconic smoke→ iconic fire→ escape). Symbols can then arise as means of linking such indexical relations to each other (Deacon, 1997). Both private sensory representations (nonverbal working memory) and symbolization (language and verbal working memory) are among the prerequisites for culture (Deacon, 1997; Donald, 1993; Durham, 1991; Lumsden and Wilson, 1982). Humans must have evolved a capacity for resensing to the self while inhibiting the motor execution that would ordinarily be associated with that resensed event. This likely constituted the first step toward culture in human ancestors because it is the basis for imitative behavior, and it is through imitation that culture is transmitted (Blackmore, 1999; Donald, 1993). Imitation also provides for the development of tool manufacture as well as social communication via gesture. Nonverbal working memory is a requirement for imitation because it provides the mental template (sensory-motor representation) from which the actual imitative act will be constructed and executed (Barkley, 1997b). Interestingly, this resensing of one's past experiences is also likely to be the origin of *autonoetic awareness*, or the awareness of self across time (Barkley, 1997b; Kopp, 1982; Wheeler *et al.*, 1997).

Verbal Working Memory (Covert Self-Directed Speech)

The second EF is verbal working memory. It is similar to Baddeley's construct of the same name. This EF originates in the developmental internalization of speech. The individual is capable of activating the central or cortical aspects of speech without engaging the actual motor execution of that speech. Such self-speech permits self-description and reflection, self-instruction, self-questioning and problem-solving, as well as the invention of rules and meta-rules to be applied to oneself (Diaz and Berk, 1992).

Self-Regulation of Affect/Motivation/Arousal (Covert Self-Directed Emotion)

This EF may occur initially as a mere consequence of the first two (private sensing and speech). Those EFs involve covertly re-presenting forms of visual and verbal information to oneself. These mentally represented events have associated affective and motivational properties or valences, which Damasio (1994, 1995) called somatic markers. Initially those affective and motivational valences may have publicly visible counterparts—emotional displays—as when we laugh out loud in response to a mentally visualized incident. Eventually, though, these affective displays are kept private or covert in form. Hence originates the third EF of privatizing affect and its motivational properties. In brief, it is feeling (emoting/motivating) to the self. This model argues that this EF forms the wellspring of intrinsic motivation (willpower) so necessary to support future-directed behavior.

Reconstitution (Covert Self-Directed Play)

And finally, the fourth EF is self-directed play, or reconstitution. Fluency, flexibility, and generativity are some other terms by which this EF is known in neuropsychology. This EF serves to generate a diversity of new combinations of behavioral units out of old ones through a two-step process, that being analysis and synthesis. In analysis, old behavior patterns are broken down into smaller sequences or units. These units are then recombined (synthesized) into new sequences that can be tested against the requirements of the problem to be solved (Corballis, 1989; Fuster, 1987, 1997). It is hypothesized here to arise from the internalization of play (both sensory-motor and symbolic) and serves to create novel future-directed actions. Such novel actions will be needed when obstacles to a goal are encountered (problems) in order to overcome them and successfully attain the goal. The generation of such novel responses has been shown to be especially problematic for patients with frontal-lobe injuries (Godefroy and Rosseaux, 1997). It has been blamed on their inability to form and sustain mental referents from instructions so as to manipulate them to discover a means to achieve a goal. And that, it is argued, is simply covert play to one's self.

This EF may be subdivided further into verbal and nonverbal components comparable to the working memory system on which it likely depends. Fluency tasks are one means of assessing this function. Recent neuroimaging studies suggest that verbal and nonverbal (design) fluency are mediated by separate (left vs. right) regions of the dorsolateral frontal cortex (Lee *et al.*, 1997; Stuss *et al.*,

1998). That would imply that a bivariate subdivision of this EF might be useful. However, prior factor analytic studies of EF measures have found only a single dimension representing both verbal and nonverbal fluency (Levin *et al.*, 1996).

Verifying the Nature of Executive Functioning

To briefly summarize, the internalization of sensory-motor action, self-speech, and emotion/motivation along with the internalization of play (reconstitution) provide an exceptionally powerful set of mind tools that greatly facilitate adaptive functioning. In a sense, these EFs permit the private simulation of actions within specific settings that can be tested out mentally for their probable consequences (somatic markers) before a response is selected for eventual execution. This, as Karl Popper noted, allows our ideas to die in our place (see Dennett, 1995). It constitutes a form of mental trial and error learning that is devoid of real world consequences for one's mistakes.

One obvious result of redefining the EFs in this way as being relatively covert behavior-to-the-self is that it is testable. When individuals are engaged in each of these forms of private behavior it may be possible to detect subtle yet measurable aspects of the originally public form of that behavior. This could be done by using very sensitive instruments that can detect fine changes in muscle tension or even movement associated with the covert form of the behavior involved. Livesay and colleagues have done this to show that some changes in muscle tension and even micromovements of the oral-musculature occur during covert verbal thought. And changes in muscle tension in the limbs have been found to occur during acts of visual imagery of imagined manipulative activity (Livesay *et al.*, 1996; Livesay and Samaras, 1998). This prediction also could be tested through neuroimaging studies. Those studies might show that the same or similar zones of cortical activation are involved in both the public and private forms of behavior. Except that in the private form the primary sensory cortex would not be activated and the primary motor zone associated with the public behavior would need to be suppressed to preclude the actual public execution of the response. Ryding *et al.* (1996) appear to have demonstrated this very finding in their neuroimaging studies of covert self-speech or verbal thought and D'Esposito *et al.* (1997) have done so for visual imagery. Perhaps this explains the relatively recent discovery that the cerebellum is related in some ways to "cognition" and the planning and execution of motor actions once attributed to just the prefrontal cortex (Diamond, 2000; Houk and Wise, 1995). Not only is the cerebellum important in the execution of overt behavior, but it may be just as important in this form

of covert behavior to the self that comprises nonverbal working memory.

This rendering of executive function as covert behavior-to-the-self leads to a further prediction—we should expect that the private forms of the behavior suffer from many of the same constraints, flaws, and qualities as do their public counterparts. For instance, the fact that the author is largely color-blind to pastel reds and greens would have little or no meaning for a cognitive psychological view of nonverbal working memory, such as that proposed by Baddeley (1986). Yet it would have substantial meaning here as a prediction that the author's capacity for visual imagery (nonverbal working memory) would be equally deficient in these color hues. Such a prediction has some support in research on visual imagery (Kosslyn, 1994). The same would be true of mentally simulated motor actions that would be afflicted with the same deficits, flaws, and limitations as are the publicly observable movements on which they are based. This seems to be the case for children with developmental motor coordination disorder (Maruff *et al.*, 1999). Such deficits are imminently understandable from the perspective of the present EF theory but make little or no sense when viewed from the information processing/computer metaphor of the EFs. And so too would comparable deficits and constraints be predicted to occur in private speech, private emotion/motivation, and private play (reconstitution) if deficits existed in their public counterparts.

Moreover, the present perspective on the executive system further argues that an individual could not engage in both the public and private action simultaneously, given that many of the same brain regions are employed in both. A moment's reflection will show this to be true for speech. One cannot speak covertly to oneself and publicly to others at the same time. This should be so for the other EFs as well. By adulthood, then, humans have two means of behaving—a public one and a covert one. Behaviors proposed for execution are initially tested out in their covert form and then one is selected for public execution (Bronowski, 1967). It is the covert form that is impaired by injuries to the frontal lobes, often to the detriment of the effective use of the public form as well.

A third prediction from this model is that of a stage-wise hierarchy in the development of these EFs, each requiring the previous one to emerge before it can begin to do so during maturation. So crucial may be nonverbal working memory (sensing to the self) to human development and survival that it seems to arise within the first few months of life. By age 12–24 months it comes to far exceed that of our closest living primate relative (Diamond *et al.*, 1994; Hofstader and Reznick, 1996; Kopp, 1982; Zelazo *et al.*, 1995). Thereafter may come the internalization of

self-speech and then that of emotion/motivation, eventually leading to that of reconstitution. This sequence is admittedly speculative. Some type of staging in the development of EFs, however, has been suggested in cross-sectional studies of age-related differences in batteries of EF tasks (Hale *et al.*, 1997; Levin *et al.*, 1996; Passler *et al.*, 1985; Welsh *et al.*, 1991). None of these were longitudinal designs, however, and so these studies cannot speak directly to the slope, rate, and specific staging of the developmental trajectories the EFs may take.

A BRIEF OVERVIEW OF EVOLUTION

Before speculating on the evolutionary significance of the EFs, it may help to very briefly review the evolutionary process itself for those unfamiliar with it. Readers should pursue the excellent text by Ridley (1996) for a detailed discussion of modern evolutionary theory and the books by Dawkins (1974, 1982, 1987, 1996), Williams (1966/1996), and Zahavi and Zahavi (1997) for additional considerations. Evolution is an algorithm. It involves a set of five essential steps that, where found to exist together, result in the accumulation of information about the environment by entities that replicate themselves. Familiar to many is the biological level of evolution, but one should not overlook the likelihood that other levels of information evolution now exist on this planet, as noted earlier (e.g., behavioral, ideational, and cultural). The five steps in the algorithm of evolution are set forth in Table I, and include (1) replication, (2) retention, (3) variation, (4) selection, and (5) bifurcation. The first requirement is that of a copying process. Entities must be able to make replicates. Genes made of DNA fulfill this requirement in biological evolution.

Second, the copying process must yield replicates that have high yet imperfect fidelity to the parental copy. This is the concept of inheritance in which offspring largely resemble their parents. In biology, DNA provides this substrate of inheritance by which information in the parental copy is passed along with high fidelity to offspring.

The third step in the evolutionary algorithm is that there be some means by which errors arise in the copying process. This produces variation among members of the next generation of copies. In biological evolution, this variation arises largely through mutations in DNA.

The next step is that of selection by the environment. Some variants are not likely to survive as well or to replicate as well in a given environmental context, given the features of that context. These features impose constraints on the replicating entities by their very existence. For

instance, in biological evolution the temperature or oxygen content of the specific environment may impose such constraints. As a consequence, across replications there will occur a process of differential replacement. The proportion of variants in the offspring population will not be the same as in parental generations such that some variants increase in frequency while others decrease across generations. Although termed survival of the fittest, it is more accurately viewed as a process of environmental culling or removal of variants from the population. Those removed are those least suited to surviving and replicating in that given context. In this process of descent with modification, the mixture of variants in the population changes across generations.

Finally, for a new species to arise from the ancestral one, there must be some bifurcation that occurs in the environment. That is, the context affecting these replicating entities splits such that one subgroup is now exposed to environmental constraints that are different from those affecting the original group. Over time, the subgroup exposed to the new environment will tend to diverge in the nature and proportion of its variants because the new environment imposes constraints (selective filters) that are different from those of the old one. In biological evolution, this often occurs when one subgroup migrates to a new environment or when a geologic upheaval splits the original population and results in a new environment for one subgroup and not another. The differences in environmental constraints may now impose different selective effects such that the two groups begin to diverge over time in the nature of their variants. Eventually, a new species may now arise over time from the original one.

This five-step evolutionary algorithm is programmable in computer software. The outcomes it produces are simpler yet hauntingly similar in many respects to those outcomes found in nature (Dawkins, 1987). Such an algorithm gives rise to a number of rather surprising attributes (also listed in Table I), such as the coexistence of selfishness with cooperation, simplicity with complexity, random variation with adaptation, and efficiency with waste.

One of the major debates in evolutionary theory over the past 34 years has been over the issue of the level at which this evolutionary process acts (Dawkins, 1976; Ridley, 1996; Williams, 1966/1996). Is it at the level of individuals within species, of groups within species, or of the genes within the individuals themselves? Although not entirely settled, most scientists seem to agree with selfish gene theory—evolution acts at the level of the genes because they are the replicating entities (Dawkins, 1976; Ridley, 1996). Individuals technically do not replicate and pass themselves on to the next generation, but the genes within them, particularly in their germ plasm, do so.

Table I. The Steps in and Attributes of the Evolution Algorithm*The algorithm that is evolution*

For any system of information to evolve, as in genetic evolution, it must involve at least five processes:

1. **Retention (heredity):** a means by which information is encoded and preserved (a storage substrate, such as DNA),
2. **Replication:** a means by which those entities make copies of themselves with high though imperfect fidelity, as in gene reproduction;
3. **Mutation:** a means by which errors or variation are continually introduced into the pool of replicating entities, as in radiation induced mutations in DNA;
4. **Selection:** a relatively consistent (recurring) feature of the environment across generations that affects the differential removal of some variants of the replicators more than others across replications, as in the physical constraints of the environment (e.g., temperature, light, oxygen, water, etc.) as well as the other species of replicators that may exist in that environment;
5. **Bifurcation:** a division of the population into at least two groups due to a change in the environment and so a change in its attendant selection pressures. Those changes affect one subgroup of the original population more than they do the other subgroup. For instance, through migration to new environments, climatically induced isolation, geologic upheaval, and so forth.

Attributes of the evolution algorithm

1. **Self-interested (selfish):** The replicating entities are simply those that are good at getting themselves replicated.
2. **Cooperative:** Over time, some replicating entities will come to combine in ways that may enhance the likelihood of further replication as a group more than as individuals.
3. **Progressive:** Such combinations as may arise in #2 result in more complex replicators.
4. **Purposeless:** The replicating entities do not progress in their complexity to a preordained goal but merely progress in complexity.
5. **Adaptive:** Over time, as a result of recurring features of the environment, characteristics of the replicators will arise by chance (sources that are uncorrelated with the selective mechanisms) that enhance the differential survival and replication of some replicators over others. This gives the appearance of the replicator being suited or adapted to its environment but it is the environment that selected it to be so.
6. **Useless:** The replicators exist solely because they are good at causing the environment to replicate them. Consequently, some replicators and combinations of them will arise that have no adaptive function or value other than being good at replicating. These can be considered “junk” replicators.
7. **Efficient:** The adaptations that arise in replicators are the result of a cost/benefit balance such that the increased costs of having the adaptation are outweighed by the indirect benefits to increased survival and replication of the replicators.
8. **Wasteful:** Most mutations that occur in the replicators are disadvantageous to their survival and replication resulting in their differential removal from the next generation.
9. **Cumulative:** On rare occasions mutations arise that offer some advantage to the replication of the replicator over others without that advantage resulting eventually in its differential replacement of other entities across generations in the population. These infrequent yet helpful mutations accumulate over time making the later replicators appear increasingly better suited to their environment.

Source: See Campbell (1960); Dawkins (1976, 1987, 1996); Durham (1991); Ridley (1996, 2000).

Although clearly it is individual organisms that are now being culled from the population through the effects of selection, those organisms are but the vehicles for the genes inside of them. And the culling is actually at the level of genes via the gene vehicles (individuals) they build. At the beginnings of life on this planet, this process of culling likely took place directly on the replicators themselves before selfishly cooperative suites teamed up to create protective outer shells or vehicles (Maynard Smith and Szathmary, 1999; Ridley, 2000). It is not the individual who replicates himself/herself but the genes within the individual and so the genes are treated as the level at which evolution works over time. This gene's eye view of evolution must be kept in mind because it implies that genes and to a great extent the individuals that house them are essentially self-interested entities. Their self-interest is reflected in the fact that the best replicators are good at getting themselves replicated into the next generation. Adaptations that arise in the process should largely be viewed as being for

the good of the genes and not necessarily for the good of the individual, the group, or the species. Although typically what is good for the genes is typically what is good for the individual housing them, this is not always the case. Cooperation can arise among genes so as to form cells, among cells so as to form individuals, among individuals so as to form groups, and even among collections of groups. But it does so because the benefits for the genes involved in this cooperative process are greater than the costs of such cooperation in terms of the survival and replication of those genes. This perspective forces us to always first examine the possible self-interested motives that lie behind adaptations, including psychological ones, before considering the benefits those adaptations may have for any groups formed by those individual members of that species.

With this review in mind, attention can now be turned to the question of whether the EFs can be considered to be evolved psychological adaptations. And, if so, then

attention can be given to those problems they may have evolved to solve for humans.

ADAPTATION DEFINED

Deutsch (1997) defined an adaptation in terms of information: "An entity is adapted to its niche if it embodies knowledge that causes the niche to keep that knowledge in existence" (p. 181). A more detailed definition of an adaptation from the field of evolutionary psychology comes from Tooby and Cosmides (1994, pp. 61, 62):

Stripped of complications and qualifications, an adaptation is: (1) a system of inherited and reliably developing properties that recurs among members of a species that (2) became incorporated into the species' standard design because during the period of their incorporation, (3) they were coordinated with a set of statistically recurrent structural properties outside the adaptation (either in the environment or in the other parts of the organism), (4) in such a way that the causal interaction of the two (in the context of the rest of the properties of the organism) produced functional outcomes that were ultimately tributary to propagation with sufficient frequency (i.e., it solved an adaptation problem for the organism).

Although technically precise, this definition is hardly stripped of complication. Yet within it are the means to create an adaptational test kit that has the following basic requirements (see also Pinker, 1997; Ridley, 1996; Williams, 1966/1996): (1) *universality*; (2) *complexity*; (3) *improbability*; and (4) *functional design*. First, one must ask if the supposed adaptation is universal across human populations, countries, and cultures? In short, is it part of the species' design? This would seem to be the case for the EFs in humans (and the prefrontal cortex that largely mediates them). Although there seems little published research that specifically addresses the cross-cultural nature of the EFs, to the author's knowledge no population has yet been reported not to have them. It would be surprising to learn otherwise. We may draw this inference as well from the fact that virtually every population studied for their language employs a past and future tense in their language (Pinker, 1994). Such temporal terms are highly unlikely unless each user has some cognitive capacity for a sense of past and future (the hindsight and foresight of nonverbal working memory) that serve as the referents for these tenses in language (Bronowski, 1967/1997). As with past and future tense, every human language seems to make some reference to the other EFs as well (e.g. visual imagery, private audition, internal speech, mental simulation or pretending). If the EFs did not exist, then such references would be meaningless. For the moment, then, there is little reason to doubt the universality of the EFs.

The second test for an adaptation is whether it shows complexity. Is there a pattern or intricacy to the adaptation that cannot simply be attributed to the byproducts of known laws of physics or chemistry at those levels of analysis without the need to posit some function at the biological level? For instance, does the adaptation involve multiple working parts that serve a purpose? The eye is often used as an example of an adaptation in biology, given its multiple interacting parts that seem to function seamlessly together. Its existence and complexity cannot merely be attributed to being a byproduct of physical or chemical processes. The capacity for language represents another example (Pinker, 1994; Pinker and Bloom, 1992). It is a complex ability comprising multiple parts that appear to work well together. There is no question that the EFs constitute a complex psychological device. An inspection of Fig. 1 makes this point clear. Nor have any prior neuropsychologists commenting on the EFs ever claimed otherwise. Indeed, part of the problem of defining an EF may well have derived from this complexity. Yet it is a complexity that appears to work relatively fluidly, effortlessly, and successfully in normal humans. Hindsight (retrospection) and foresight (prospection) and the other internal sensings-to-the-self, as well as covert self-speech, private feelings, and mental play are complex processes that interact beautifully and seamlessly to form the human executive system as well as the thinking and self-regulation that system provides.

The third requirement of improbability is related to this issue of complexity. It simply means that the adaptation would not have arisen by chance alone. One has to consider the likelihood that a mere random occurrence could have assembled the parts into the complex whole of the adaptation. It seems most unlikely that a capacity for visual imagery (and the other private sensings to the self that forge the nonverbal working memory function) could have arisen by mere accidental arrangement. After all, this could hardly have been the case for the eye and visual system on which visual imagery and imagination are based. And so it would seem to be just as improbable that a capacity for visual imagery and imagination would arise by chance either. The same can be said of covert-speech, the capacity for covert emotions, or that of covert play, not to mention the general process of self-directing and then internalizing or privatizing the public behaviors on which the EFs are based. The chance that such an assemblage could have arisen by accident alone seems infinitesimal.

The final requirement is that the alleged adaptation appears to have been designed for a purpose. Note that the meaning of design here is one of functionality, not one of intention. Evolution and the adaptations it produces have no intentions. But the evolutionary process is very

good at producing functional designs. An adaptation does something useful for the organism. It solves some adaptive problem. Contrary to popular belief, adaptations do not typically result in some direct or immediate improvement in the number of offspring produced by an organism. Instead, adaptations solve problems for organisms and, in so doing, *indirectly* result in an improvement in the differential survival and reproduction of those organisms and especially their genes (Symons, 1992; Williams, 1966/1996). An adaptation is a “system of properties crafted by natural selection to solve a specific problem posed by the regularities of the physical, chemical, developmental, ecological, demographic, social, and informational environments encountered by the ancestral populations during the course of a specie’s or population’s evolution” (Tooby and Cosmides, 1992, p. 62). Does the executive system seem to be designed for some purpose? It would appear so, given that its loss due to brain injury or to impaired development, as in ADHD, results in relatively devastating behavioral and social impairments for those so afflicted (Barkley, 1998; Fuster, 1997; Stuss and Benson, 1986).

What might that adaptive purpose be? Evident from the earlier discussion is that a major purpose of the executive system is self-control, given that the EFs are the types of self-directed behavior humans use to self-regulate their social conduct for future ends. What adaptive problem might have created the selection pressures necessary for an organism to develop self-regulation? This question cannot be answered with any certainty at this time. But even a consideration of a few possibilities would serve to move the discussion along so as to get closer to a more fully integrated and satisfying account of why this EF system exists. And it also might provide deeper insights into the problems of daily living likely to occur in clinical patients whose executive function/self-regulation (EF/SR) mechanism(s) have become dysfunctional for various reasons. This “asking of functional questions and placing the phenomenon in a functional context often prompts important new insights about its organization, opening up new lines of investigation and bringing to light previously unobserved aspects and dimensions of the phenomenon” (Tooby and Cosmides, 1992, p. 10).

The approach neuropsychologists can take to this problem was outlined nicely by Tooby and Cosmides (1992) and later by Buss *et al.* (1998; see also Holcomb, 1998). It is relatively immune to the customary criticism of being merely post hoc storytelling, or the invention of Just-So stories. That is because the evolutionary approach to psychological adaptations proposes its hypotheses so as to address the following key questions (Buss *et al.*, 1998, p. 543): “(a) Is the evolutionary psychological hypothesis formulated in a precise and internally consistent manner?

(b) Does the hypothesis coordinate with known causal processes in evolutionary biology, much like hypotheses in cosmology must coordinate with known laws of physics? (c) Can new specific empirical predictions about behavior or psychology be derived from the hypothesis for which data are currently lacking? (d) Can the hypothesis more parsimoniously account for known empirical findings, and overall, is it more evidentially compelling than are competing hypotheses? And (e) is the proposed psychological mechanism computationally capable of solving the hypothesized problem?” This is simply a restatement of the key requirements that would be demanded of any scientific hypothesis and it applies as much to neuropsychology as it does to evolutionary psychology or biology. The approach can proceed bidirectionally, from the known mechanism to the nature of the adaptive problem it was designed to solve, as is being done here. Or it can proceed from a known adaptive problem to hypotheses about the design of psychological mechanisms that ought to exist to solve that problem, as illustrated by Cosmides and Tooby (1992) in their analysis of social exchange and cheater-detection mechanisms.

POSSIBLE ADAPTIVE PROBLEMS ADDRESSED BY THE EF/SR SYSTEM

In considering the larger human adaptive problems that an EF/SR system might solve, it is necessary to keep in mind the ancestral environment in which the system evolved (the environment of evolutionary adaptation or EEA; Tooby and Cosmides, 1992). For it is in that environment that the problem(s) existed and for which the EF/SR system evolved to address. That environment is not the contemporary one but the environment of roughly 1.5 million and 100,000 years ago (Donald, 1991; Tooby and Cosmides, 1992). Yet the recurring features of that EEA relevant to the adaptation under consideration may still be present today despite massive changes in other irrelevant aspects of the environment (Crawford, 1998). For instance, despite marked changes in culture and technology, humans still live as groups that involve nonkin with whom they engage in reciprocal altruism or social exchange.

In the EEA, who or what were human ancestors in competition with that would pose a problem requiring an EF/SR system? The answer must be either parasites or peers, for humans had few other predators that offered them serious competition or selection pressures during the EEA (Pleistocene) or in that earlier period of evolution of their closest *Homo* ancestor, *Homo erectus* (1.5 million years; Donald, 1993; Cosmides and Tooby, 1992; Ridley,

1993). And it is during those periods that we must be content to look to explain the relatively rapid evolutionary expansion of the prefrontal cortex and hence the EF/SR system it provides (Deacon, 1997; Donald, 1993). That rapid expansion, as Donald noted (1991), seems to have occurred in at least two stages that correspond to those two major transitions in human evolution; the emergence of *Homo erectus* and the subsequent emergence of the Cro-Magnon people.

It seems very difficult to argue that the rapid evolution of the executive system solved any problems related to human parasites. The human immune system seems to have evolved for combating that particular problem and, indeed, so may have been the much earlier evolution of sexual forms of reproduction (Ridley, 1996). Nor does it seem that the EF/SR system should have arisen to deal with problems posed by the physical (nonsocial) world itself. That is because the principle of convergence in evolution would imply that executive systems, like eyes, should be found to have evolved in many other species on many independent occasions when those species were subjected to similar or identical environmental selection pressures. Clearly the EF/SR system does not seem to have arisen on multiple occasions independently in other species. Thus while the EF/SR system may seem to come in handy for dealing with aspects of the physical world (Tower of London or Hanoi type tasks, for instance), it would be difficult to argue that this system evolved for those reasons alone. Nor does it seem logical that this EF/SR system evolved to detect Xs from Os on a continuous performance test, or for detecting a pattern in card sorting, helpful as the EF/SR system is to performing those tests. The capacities assessed by those tests may be important to the larger purpose of an EF/SR system, but they clearly are not that purpose.

The problem to be solved more likely was posed by the particular environmental niche in which human ancestors lived in the EEA, the way that they lived in it, and perhaps the way they continue to live today. That niche and lifestyle were and continue to be obviously social ones. And that would imply that the problem or problems to be solved by the EF/SR system were of a social nature—a point made 20 years ago by Diamond (1980) in his analysis of executive functioning and the prefrontal lobes. The selection pressures for the evolution of this system most likely arose from competition with one's fellow humans. What problems did humans pose for each other for which the EF/SR system might have evolved as a response?

Group hunting might be a first and obvious conjecture because such migratory hunting by bands of hunter-gatherer-scavengers for extended periods was most likely part of the human EEA when the EF/SR system arose. Group hunting might well benefit from a system that grants

its owner greater hindsight/foresight, a general sense of time and timing, a capacity for cross-temporal organization, patience and persistence, planning, problem-solving, and the multistep orchestration of a peer group in a coordinated effort to kill a large animal. If this were so, however, one might expect to find that EF/SR systems would have evolved in other species that engage in group hunting, such as wolves, hyenas, lions, killer whales, and other predatory mammals. Again, that is suggested by the principle of convergence in evolutionary theory. Species exposed to the same or similar environmental selection pressures tend to have similar (though not necessarily identical) adaptations. This does not seem to have been the case for executive functioning as it exists in humans. There seems to be little evidence that these other hunting species engage in self-regulation toward the future to the extent humans do. Moreover, the practice of group hunting as done by humans requires imitation, communication, and tool use as prerequisites. Thus it was unlikely to have been the initial reason for which the EF/SR system arose.

Hunting also seems to have fallen largely to males implying that one ought to find substantial sex differences in humans in the extent and functioning of the EF/SR system. That does not seem to be the case either. Thus, whatever problem it was that this system arose to solve, it probably was not particularly exclusive to the activities of one sex more than the other one. This does not rule out the possibility, however, that the EFs may show subtle sex differences as a consequence of two possibilities. First, differences could arise in the way the general adaptive problem is specifically imposed upon the two sexes. And second, sex differences may have existed previously in the public forms of behavior that make up the EFs and that arose for other reasons. Those differences would then come to exist in the private forms of those behaviors when turned on the self and internalized to form the EF. For instance, if females mature earlier and are more adept at language than males, then they may also be more adept at verbal working memory than males, given that the latter is merely the former internalized. In any case, it would seem that the adaptive problem would not be the exclusive domain of one sex over the other, given that as best as can be currently determined both sexes possess a comparable EF/SR system.

If not for group hunting by males, then what problem did the EF/SR system evolve to solve? Is there something about the larger social environment in which such hunting occurred that is a more general characteristic of human social activities of which hunting is but one instance? This might shed some light on the adaptive problem solved by the EF/SR system? Whatever this general feature of human life may be, given the principle of gradualism in

evolution, it will need to be something that is evident in rudimentary form in those primate species most closely related to humans. Those species seem to have, at least in a more primitive form, elements of an EF/SR system, such as nonverbal working memory, and the prefrontal cortex that houses it. That similarity has allowed for the study of the nonverbal working memory system in some primates (Fuster, 1997; D'Esposito *et al.*, 1997; Goldman-Rakic, 1995) that has shed considerable light on its functioning in humans.

To understand this adaptive problem, the executive system may need to be thought of as having evolved in at least two or more stages perhaps paralleling the two major transitions to the modern enlarged prefrontal cortex, as Donald (1991) noted. Those stages may represent nonverbal and verbal working memory, or private sensing to the self and speaking to the self. Consequently, the initial adaptive problem may not necessarily have been one that required complex, private self-speech to begin to address it. Indeed, the first stage in this transition (nonverbal) may well have given some impetus to the second (verbal). A third much more recent stage might then be the evolution of reconstitution, or internalized play. Perhaps that corresponds to the emergence of rapid cultural evolution some 35,000–50,000 years ago (Diamond, 1999). This might make sense given that this EF is thought to serve as the engine of private goal-directed innovation in the present EF model. Important here is not the speculations about the timing but the fact that the evolution of the EFs is likely to have arisen in stages, each giving impetus to the next.

The EF model described earlier also implies yet another feature of the adaptive problem this paper is attempting to unearth. Whatever that problem may be, solving it seems to require that the individual act in opposition to their own immediate urges (impulses) and self-interests and to the compelling features of the immediate context that may elicit those impulses. This requirement of oppositionality makes sense for at least two reasons: (1) the inhibition of and the delay in such prepotent (immediately reinforcing) responses to contextually compelling stimuli represents the first step in this EF/SR model and (2) this resistance to immediate self-interests and contextually compelling stimuli is often greatly diminished in people with injuries to the prefrontal cortex. It would seem then that the adaptive problem to be solved required that a competing source of stimuli arise that would elicit responding that is in opposition to the moment. As discussed earlier, that source of alternative stimuli is argued here as being private (mental) representations (re-sensations) to the self.

There appear to be at least five major activities for which humans might be in need of inhibition (delayed responding) and an associated nonverbal working memory

system: (1) reciprocal altruism (delayed social exchange) and its associated formation of social coalitions, (2) imitation, (3) tool use, (4) mimetic skill and communication, and (5) self-defense and innovation against social manipulation. There may be a common thread among them. Reciprocal altruism involves tit-for-tat, or doing for another what that other person has done for you. It is but a small step from that behavior to generalized imitation, or doing what others do (Blackmore, 1999). Tool use also requires imitation. And so does mimetic skill and gestural communication (Donald, 1991). Once imitation and mimetic communication arose, however, it would be possible for people to manipulate others to their own social ends via these social tools. This would necessitate that a means for self-defense against such social manipulation would need to evolve. Self-regulation generally, and private speech specifically, could provide that means. The thread interweaving them all would seem to be the capacity for social exchange and, related to it, imitation. For that reason, social exchange and imitation (vicarious learning) deserve pride of place for the moment in any discussion of the evolution of executive functioning.

This particular way of staging these capacities also implies that one should find the largest set of group living species that engage in social exchange but have not yet evolved generalized imitation. There should be a smaller set of species that have evolved social exchange and even primitive imitation but not tool utilization, and an even smaller subset that have evolved rudimentary forms of all five of these capacities (Ridley, 1997). Such a progression also intimates why only humans (and their ancestors) have such a highly developed EF/SR system—they may have been among the few or only species that ventured down this evolutionary path, beginning with group living involving kin and nonkin that presaged reciprocal altruism.

Reciprocal Altruism (Social Exchange) and Coalition Formation

Among human universal social attributes, reciprocal altruism with nonkin (others with whom one does not share genetic self-interest) stands out as among our most unique behavioral features relative to other species. Humans exchange goods or services now for other ones later despite having no common genetic self-interests with those with whom they engage in such exchanges. They do it nearly all the time, forming the backbone of human economic systems (Ridley, 1997). Although Williams (1966/1996) prefers the less emotive term *social donors* for those engaged in this practice to Haldane's term of *altruism*, the point is the same. Genetically unrelated humans live within a social group and frequently exchange

benefits and costs now for benefits and costs later. The exchanges are reciprocated and those reciprocations are delayed in time. Such a delayed exchange of costs and benefits between nonkin constitutes a promise or a social contract. Darwin (see Williams, 1966/1996, p. 94) was apparently well aware of the fact that a group-living species might well come to evolve a form of social exchange (what he termed as “the lowly motive”). He also appreciated that such exchange was an important factor to consider in understanding the evolution of not only human mental functions but friendship and culture as well.

Reciprocal exchange, particularly when it is delayed, constitutes a prime candidate for the initial adaptive function of the prefrontal cortex. It requires both inhibition and a representational memory system for sensing past and future—the foundation of self-control, as discussed above. Just as with any other form of adaptation, the mental mechanisms affording self-control exact a biological cost to the individual. That cost must be outweighed by some benefit and such benefit need not be for the good of the species or even the group in order to evolve. It must be for the good of the individual and specifically the individual’s genes. Yet humans voluntarily subject themselves to periods of self-deprivation (as in sharing or even dieting), deferred gratification (such as saving, investing, and education), and even aversiveness (as in getting inoculations against diseases). From the standpoint of selfish gene theory and its related kin selection theory (Ridley, 1997), these actions make little sense in the context of the moment. According to those theories, individuals should seek as much benefit and advantage now for themselves and their genetic relatives if only for the fact that others will do so if they do not leaving them at a disadvantage. Such personal greed is certainly evident in humans and can result in a sort of Tragedy of the Commons whereby publicly held resources are depleted by self-interested individuals even if the long-term depletion of the asset is not in those individual’s best interests (Ridley, 1997). In such instances, acts of self-control are losing strategies. The costs of reciprocal altruism and self-control can be substantial and the individual employing it can be easily cheated out of or out-competed for the immediate resources. The existence of reciprocal altruism requires that there be some advantage to the self-interested motives of those individuals involved in those exchanges.

Delayed reciprocal exchange requires a capacity to perceive long-term sequences of events and their outcomes for one’s self and for others with whom one is trading. Even rudimentary, little delayed forms of reciprocal exchange would begin to create selection pressures for the evolution of an increasingly longer sense of past and future (nonverbal working memory) so as to evaluate those long-term consequences of the trade. It has been suggested that

in the EEA of prehistoric humans, such as the grasslands of central Africa, food sources and other resources showed cyclical patterns of availability, as they do even today (Ridley, 1997). Periods of plenty were punctuated by periods of famine. Under such conditions of large swings in resource availability, sharing and its associated reciprocal exchange would have brought great advantage to individuals living in groups as a means of mediating or modulating the personal risks and costs associated with these cycles of feast and famine. Under such circumstances, it would pay those who had been lucky in hunting or scavenging to give up some of their excess bounty to others in exchange for the same sort of reciprocation later when those others were more fortunate and the previously successful hunters were not. Like a group insurance pool today, individuals would chip in resources they did not require at the moment to those who needed them in exchange for the same treatment later in their own time of need—a sort of Golden Rule would result. A group of selfish cooperators would evolve provided that the consequences for cheating on the contracts were made sufficiently harsh by the group so as to make renegeing on those exchanges costly (Ridley, 1997). Indeed, in some modern hunter-gatherer groups, such as Eskimos, it seems that on some occasions those successful hunters failing to share when their turn came could lose their life (Dugatkin, 1999; Ridley, 1997). Under periods of extreme resource variability, reciprocal exchange is a good adaptive strategy to use to solve the problem; a strategy converged upon by other species such as vampire bats (reciprocal blood sharing) and some birds and mammals (reciprocal grooming) in more rudimentary forms (Ridley, 1997; Williams, 1966/1996).

Cosmides and Tooby (1992) have reasoned that in a species like humans who have come to live in social groups and who engage in high rates of social exchange over hundreds of thousands of years, there should come to evolve a set of mental mechanisms, modules, or algorithms that permit and facilitate exchanges. One such module or algorithm they have studied extensively is that for the detection of cheaters in such social exchanges. They have reasoned that the costs of being cheated in a social exchange are of a sufficiently serious magnitude as to create selection pressures for cheater detection. That would result in an increase in means of precluding detection and so on in a form of arms race. That is of less concern to this discussion than are the requirements Cosmides and Tooby (1992) posit for the mental mechanism that would be needed for a species to engage in social exchange involving time delays in their reciprocation. Both evolutionary theory and the principles of game theory that have been employed in the study of evolved social behavior impose certain requirements on the nature of any mental mechanism that supports

reciprocal exchange (for a detailed discussion of these constraints, see Cosmides and Tooby, 1992). Important to the present analysis is their stipulation that the “mental organ” that must have evolved to mediate social exchange would need to include the following procedures, steps, or algorithms—algorithms that sound very much like executive functioning (Cosmides and Tooby, 1992, p. 177):

- A sensitivity to cues as to when an exchange is being offered and reciprocation expected
- A capacity to estimate the costs/benefits of various actions, goods, etc. to oneself
- A capacity to estimate costs/benefits of actions, goods, etc. to others
- A capacity to estimate the probability that these actions, etc. will occur in the absence of social exchange
- An algorithm for comparing these estimates to one another
- A set of decision rules that cause one to reject the exchange when the costs to oneself exceed the benefits of the exchange
- A capacity to capture the intercontingent nature of the exchange
- An algorithm for translating the exchange into value assignments for each participant
- A capacity to detect cheaters and to cause one to punish them
- A capacity to store information about the history of one’s past exchanges with others so as to know when to cooperate, defect, or punish defection
- The capacity to recognize different individuals so as to do all of the above

There would be no need for a capacity to detect indiscriminate altruists because there should not be any and if there are any they pose no threat and only benefits to oneself (Cosmides and Tooby, 1992).

Unmentioned by these authors is that social exchange also would necessitate mental modules for (1) the inhibition of prepotent (immediate self-interested) responses, (2) hindsight and forethought (working memory), (3) the temporal discounting of consequences as a function of time to the reciprocated exchange (a time-linked somatic marker system), and (4) generativity, or a means of inventing new sequences of such social exchanges, as in bargaining. In essence, social exchange requires a sort of mental spreadsheet that calculates temporal sequences of exchange for which the executive system seems ideally designed. Where social exchanges occur frequently between two selfish cooperators, those exchanges can become the foundation for building not only friendships but also social coalitions for cooperating with or acting

against other individuals and coalitions. The executive functions would seem to be well-designed mental modules for mediating this adaptive strategy of social exchange and coalition formation. If so, it implies that one of the major detrimental effects of frontal lobe injuries for daily adaptive functioning is the diminution or even loss of the capacity for effective social exchange and its attendant coalition formation in daily social life. Those deficits are obvious to any neuropsychologist who has ever worked clinically with frontally impaired individuals.

Imitation (Vicarious) Learning

Although often not mentioned in neuropsychological discussions of prefrontal lobe functions, particularly those of nonverbal working memory, the capacity to engage in imitation, particularly delayed imitation, is probably one of its most important capacities for a group living social species such as humans. Many species, as Darwin (1871/1992) noted, are capable of mimicry or even immediate imitation of particular acts. For many reasons, immediate mimicry or imitation is a good adaptive strategy and other species have converged on it. Delayed imitation, however, especially in generalized form is a notably human achievement (Donald, 1991, 1993). Our species has an early developing instinct, nay nearly a compulsion, to do it (Meltzoff, 1988).

Imitation, especially delayed imitation, clearly depends on three cognitive capacities: (1) the inhibition of prepotent responses, (2) an evolved mental mechanism for carrying past sensory perceptions of others’ behavior forward in time across a delay interval, and (3) a capacity to construct motor responses on the basis of those mentally reperceived actions of others. The latter two requirements are obviously the retrospective and prospective aspects of the nonverbal working memory system. Initially, it seems likely that the initial delay between the act and its imitation was undoubtedly brief, perhaps owing to the initially fleeting after-images that occurred from primary sensory impressions. Regardless of how it originated, the capacity to inhibit prepotent responses and to carry forward in time past perceptions (retrospection) that create the template for the later imitative motor act (prospection) form the foundation of self-regulation, as noted earlier. The more highly developed the nonverbal working memory capacity, the lengthier and more hierarchically complex the sequence of actions that can be held in mind for later imitation and the longer the delay over which it can be carried into the future. And the greater would be the demand for response inhibition during the period when such imitative responses are being programmed and eventually executed. The more complex the sequence, the more its

syntax and timing must also be held in mind. The holding of a sequence of events in mind may also form the beginnings of a subjective or psychological sense of time (Davies, 1995; Michon, 1985).

Imitation involves the reproduction of another person's behavior following its observation. Vicarious learning is a more advanced form of imitation. It involves not just imitation (doing what gained reinforcement for others) but inverse imitation; not doing what another person does (avoiding what actions led to aversive, painful, or even mortal outcomes for others). Note the requirement for oppositional action involved in vicarious learning. The amount of social learning that occurs in humans through imitation and vicarious learning is substantial, to say the least. It is undoubtedly far more than the learning that could occur by operant conditioning or by trial-and-error learning alone. Imitation develops very early in childhood; in fact, rudiments of it are present in infancy by 9 months of age (Meltzoff, 1988). Its development seems to parallel the development of representational memory, especially visual imagery (Kopp, 1982; Meltzoff, 1988).

There is no other species that comes close to the human capacity for this form of learning. Evolutionary theory demands that explanations for such adaptations initially be considered from a self-interested perspective (the good of the individual or of their genes) before giving credence to explanations at the group level (for the good of others; Dawkins, 1976, 1997; Ridley, 1993, 1997; Williams, 1966/1996). From that self-interested perspective, vicarious learning constitutes a form of *experiential theft* that is clearly in the imitator's self-interests. Through imitation and vicarious learning, the individual profits from the experiences that others may have with real-world contingencies without the costs, penalties, pitfalls, morbidity, and mortality that can be associated with those contingencies. The vicarious learner gains a considerable adaptive advantage in a group living species because they appropriate the experience of another person for their own with minimal costs. From that vantage, imitation and vicarious learning are incredibly useful self-interested adaptations.

The power to imitate and the associated working memory module it requires may well have begun as social exchange that, with a small change, became immediate imitation or mimicry of the acts of others, as is seen in some other primates on occasion. It then could have evolved to permit ever-more delayed and complicated replications of others' behavior through a gradual expansion in working memory capacity. Although such imitation is clearly beneficial to the individual, this tendency to copy would need to be tempered by some means so as to select only for imitation of those behaviors of others that were successful (e.g.,

reinforced). This suggests that what must be mentally represented is not just the actions of others that will be eventually imitated, but the entire contingency arrangement in which those actions occurred. This includes the precipitating events, the responses, and the outcomes of those responses. The notion is similar though not identical to Grafman's (1995; Sirigu *et al.*, 1995) concept of scripts. But unlike Grafman, this author believes that it is the whole contingency, not just the responses or their sequence, that forms the icon or mental representation. To do so, that mental representation must have a tripartate structure—sensory events, motor responses, and the consequences of those responses. Those iconic (mental) consequences constitute somatic markers (emotional/motivational valences) associated with the mentally represented sensory-motor actions. They are derived from prior learning. Iconic consequences would elicit a milder form of the same affective reaction as would their real counterparts, thereby coming to comprise an appraisal mechanism, as Damasio suggests (1995). For instance, we not only wince at observing the failures of others but, to a lesser degree, at our later mentally reenvisioning of those same failures. This makes the somatic marker system the ideal candidate for determining what gets imitated and what does not.

Embedded within the notion of a tripartate structure of mental representations is not simply the capacity to copy what others do, as if it were pure mimicry or some matching-to-sample exercise. It also contains the ability to do the opposite of what the other person did—that is to suppress in one's repertoire the unsuccessful, harmful, or punished actions of others that were witnessed. Merely observing the negative outcomes of the actions of others would be enough to alter their subsequent probability of occurrence in the repertoire of the potential imitator. As noted earlier, some executive function tasks, such as those involving tower building, require just such a process of doing the opposite of what is in evidence in the sensory fields if the problem of the task is to be solved. The person envisions actions that fail and does the opposite. Such a system could conceivably constitute the basis for all observational or vicarious learning.

Unquestionably, imitation and vicarious learning have evolved to become a major pedagogical force in human development and evolution deserving great weight in any theory of the origins of nonverbal working memory. The actions of others, when visually imagined by another at a later time in a similar context creates not just a template for later imitation but a form of nonverbal rule-governed behavior (Barkley, 1997b). Such rule governance of behavior via imitation breaks the stranglehold of motor behavior by the immediate environment by shifting that control to covert representations of earlier witnessed

experiences of others (Donald, 1993). It also would give rise to the following hallmarks of rule-governed motor responding (Cerutti, 1989; Hayes, 1987; Skinner, 1969): (1) reduced variability in responding; (2) diminished influence of immediate contingencies on behavioral control and the spurious conditioning that may cause; (3) greater persistence in responding under conditions of very low rates of reinforcement and during delays in reinforcement; (4) more dispassionate responding; and (5) the appearance of conscious, intentional, purposive, or deliberate action. The guidance of behavior by internal representations gives the appearance of willfulness or volition and may well be the origin of these attributes in humans, as has long been noted (Bastian, 1892; James, 1890/1992).

A further advantage to imitation is that it could result in a marked reduction in the likelihood of childhood injury and death. Children who could imitate their parents no longer simply learn by their own trial-and-error experiences, some of which could be lethal. Indeed, that advantage to children alone could serve to explain the origins of imitation and pedagogy and the prefrontal lobes that subserve such vicarious learning (Williams, 1966/1996). Current evidence suggests that Williams might be correct. Children having ADHD, especially if they are oppositional-defiant (aggressive), are among the most injury prone groups in childhood. And children who have had accidental injuries have a high probability of having ADHD or “externalizing” behavior problems as preexisting conditions (see Barkley, 1998, pp. 121–124).

As others have argued (Donald, 1993; Durham, 1991), this capacity to imitate is also the basic foundation for the beginnings of culture. Culture is yet another form of evolution—the replication of social information, or memes (Dawkins, 1976), across members of a population. Like viruses, then, units of cultural information can spread easily among members of a group of selfish imitators and even between such imitative social groups that periodically interact with each other (Blackmore, 1999). It is this replication from one individual to the next that forms the basis of cultural evolution. And it is the iconic consequences (somatic markers) associated with mental representations of those acts that comprise the selection mechanism, determining whether any act is repeated further (spreads) or not (Durham, 1991).

If one is to live in a group, as humans and their ancestors early on evolved to do, it would seem to be a great adaptive advantage to acquire the benefits of others’ experiences without having to experience those contingencies oneself. However, if imitation got started it would have evolved rapidly given the inherent competition for resources and reproductive opportunities among peers in a social group. That intraspecies competition creates a

tremendous selection pressure toward increasingly greater capabilities to learn through vicarious means across generations of humans. This effect of within-species competition as a force for natural selection has been called the Red Queen Effect (Ridley, 1993). It is so named for the Red Queen in *Alice and Wonderland* who always stayed in the same place no matter how fast she ran. For no matter how well one imitated the actions of others, such competition would insure that even better imitators would be present in the next generation. This would foster selection pressures for increasingly better vicarious learning up to the point where its biological costs outweighed any further increase in the benefits. Intraspecies selection pressures are capable of producing a relatively rapid evolution of a trait within a species in comparison to between species forms of competition (Ridley, 1996). Via this process, individuals competing among themselves for resources and matings may have gained a competitive advantage through imitative learning thus fostering the preferential reproduction of individuals capable of better imitation and so on (Blackmore, 1999). And if that attribute of vicariously learning may have come to be preferred in the selection of a mate by either or both sexes, the selection pressures would be further magnified thus accelerating the evolution toward greater imitation and vicarious learning. Vicarious learning is a form of intelligence and there is little doubt that intelligence is an important characteristic in modern mate preferences in both sexes of humans (Buss, 1992, 1998).

Mimesis and Gestural Communication

The advent of imitation specifically and vicarious learning generally as a consequence of the nonverbal working memory system might have led to the capacity for replication of one’s own behavior as well. The individual who imitates others already has the capacity to witness and later imitate their own behavior creating vicarious learning from the self to the self. When self-replication of behavior occurs across multiple trials, no matter the initial origin of the imitated act, it is a form of behavioral rehearsal or practice. It could easily result in the further refinement of the voluntary movements of an action. And that could be repeatedly replayed and edited under conscious or voluntary control culminating in a product of this modeling that is “an implementable self-image” (Donald, 1993, p. 740).

Donald (1991) believes that the first of three stages in the evolution of the modern mind was this development of repeatable, imitative action or *mimesis*. “Mimetic skill or mimesis rests on the ability to produce conscious,

self-initiated, representational acts that are intentional but not linguistic” (p. 168). Simple acts of immediate imitation or behavioral mimicry as well as conditioned responses are not included in this definition because mimetic acts are defined by their representational function. Donald (1991) states that mimicry is an attempt at literal, exact, and immediate copying and can be found in many animals, such as parrots. Imitation is less literal being an effort to copy the way another does things but not necessarily exactly as they did them. It is the way the action is done and not the precise actions themselves that are being copied. Mimesis involves mimicry and imitation toward a further end, that of reenacting and re-presenting an event or relationship. Donald posited that mimesis incorporates the *invention* of intentional representations. It also involves a delay in the imitated or reenacted event. Should an audience be present, such reenacted responses may have a communicative function but that is not their original one. In mimesis, the person can re-present the event to themselves for the purposes of rehearsal and refinement of skills—a means of delayed reimitation of actions for the sake of self-improvement that would be adaptive in its own right apart from any communicative advantages it offered.

The mental module underlying mimesis is thought to be supra-modal in that it can employ a variety of modalities and forms of action, such as facial expressions, tones of voice, manual signs and gestures, whole body movements, and postures. As Donald noted, long sequences of such acts can serve to express many aspects of the perceived world. Mimesis might thereby come to serve a relatively effective if rudimentary form of presymbolic communication or language. The game of charades is a classic example of mimetic skill. [It would be informative to test frontal lobe injured patients or those with ADHD for their facility in this game.] Such skill could come to have major advantages as a form of pedagogy, as noted earlier, resulting in reductions in child morbidity and mortality.

Donald (1991, pp. 168–173) emphasized six properties of mimetic skill: (1) *Intentionality*: the reenactment is purposive or goal-oriented and is understood to be so by others for whom it is being reenacted. (2) *Generativity*: the re-presentation of prior actions involves the ability to parse or analyze one’s motor actions into units that can then be recombined into new sequences in various ways that serve to represent events. (3) *Communicativity*: Although not originating as a means of communication, mimesis nevertheless has an inherent value as a form of communication. It is capable of being interpreted by others possessing sufficient capacity for event perception. (4) *Reference*: The mimetic act refers to something else

and so can be distinguished from its referent, just as children come to distinguish play-acting an event from the real event itself. (5) *Unlimited objects*: The representations that can be modeled by mimetic skill comprise an unlimited number of perceptual events. Although mimesis is concrete and episode-bound, the number of perceptual events it can be used to convey is limitless. And finally, there is (6) *autocueing*: Actions that are mimetic are capable of being reproduced on the basis of internal, self-generated cues allowing the voluntary recollection of mimetic representations without external cues needing to be present. Mimesis clearly implies the need for a nonverbal working memory system to support it (Donald, 1991). Even more than imitation, mimesis provides a means for the development of a culture that comprises mutually reciprocated mimetic interactions, rituals, customs, games, skills, and other representations as well as pedagogy, conformity and coordination, shared social knowledge, and innovations in these cultural activities and their products.

The gradual progression of mimetic self-rehearsal from being public to becoming private via the process of internalization would provide a powerful cognitive tool for covertly improving upon one’s actions through mental rehearsal; a process of covert behavioral evolution within the individual, or ideational Darwinism. Indeed, professional athletes today are coached to employ such mental rehearsals of behavioral actions to achieve refinements in their motor movements without having to actually engage in the repetitive motor actions themselves. Pilots in training have also been found to benefit from such covert visual-motor rehearsal (Prather, 1973). The subsequent performance of many actions can be vastly improved as a function of such covert simulation.

But why would there be a need to evolve such covert rehearsal? Why did it not remain simply overt rehearsal? The answer, given the self-interested perspective of evolution, is most likely that it evolved to shield one’s actions and intentions from other experiential thieves. In the short-term, behaviors may be performed in covert form as a means to anticipate, innovate, and thereby outwit peers who are one’s competitors. It would also serve to keep one’s own behavior and innovations from being stolen (imitated) by those competitors, at least initially, until they could be publicly performed at the critical time in a social situation. The selection pressure that drove the evolution of mental representations, imitation, vicarious learning, and mimesis was probably a consequence of intraspecies competition, or a Red Queen Effect, as others have conjectured (Blackmore, 1999; Donald, 1991; Humphrey, 1984). If so, it would also lead to selection pressures to privatize one’s behavioral actions and their rehearsal, at least temporarily, until the time was right for their execution. This

would be especially so if what is being rehearsed is an action designed to influence others and particularly to use against them.

As noted earlier, the capacity to covertly represent a perceived event by resensing it in its absence, as by a visual reimagining of that stimulus event, creates episodic memory (Donald, 1991). It is a form of mental icon of that event (Deacon, 1997). And that form of iconic memory may provide the necessary stepping stone toward the eventual evolution of mimesis that may then have contributed to the human capacity for symbolization (Donald, 1991; Deacon, 1997). As was previously noted, two or more icons can come to form an indexical relation. Any relationship (such as a logical one) of two or more such indexical relations can come to be designated by an arbitrary marker that thereby becomes a symbol (Deacon, 1997, pp. 78–86; Peirce, 1897/1955). But even without such speculation about symbolic development and its contribution to linguistic communication, the capacity to imitate would have afforded an ability to engage in gestural (mimetic) communications that could be replicated and understood by others (Donald, 1991, 1993). As demonstrated in brain injured patients, that capacity for gestural communication remains intact despite a loss in the capacity for expressive language. This implies that mimesis is associated with distinct neural mechanisms from those mediating language that likely evolved separately from and probably prior to language. Indeed, as Donald (1991), Deacon (1997), Peirce (1897/1955), and Darwin (1871/1992) before them concluded, nonverbal thinking, imitation, mimesis, and tool use may all have been necessary prerequisites to the development of language itself.

To summarize, the beginnings of the power to imitate and vicariously learn within a species would create a cascading of consequences within a social group thereby potentially fostering other related capacities founded on that power to imitate. Among them would be mimetic skill and gestural communication, the privatizing of behavioral rehearsals from which comes a form of behavioral simulation (intrapersonal behavioral evolution), a sense of time and of self, and possibly the beginnings of iconic/indexical (presymbolic) reasoning. An evolved capacity for imitating others in a social group thus seems to be a strikingly advantageous adaptational development that may have had far reaching evolutionary consequences. Might this account for the origins of the nonverbal working memory system? It is certainly a compelling and provocative possibility. But there is another advantage to imitation that should not go overlooked and that could easily have created further selection pressures for a nonverbal working memory module—that advantage is the use of tools.

Tool Utilization

Much has been made over the use of tools as a major force in human evolution and so it may have been. Little has been said, however, of the cognitive modules that would be required for tool use to occur. Undoubtedly, tool construction and use requires the capacity for mental representation (working memory) because that representation is used to guide the subsequent construction of the tool or its subsequent use. Although an external copy of a tool may serve initially as this representational function, an internal representation of it would be more versatile, transportable, and hence useful. Other species use tools, at least in an elementary and highly particularized capacity (Donald, 1991). One might expect that they would have some rudimentary working memory capacity so as to do so. But delayed tool use and complex tool construction for later purposes are uniquely human and so should be the mental modules that support these practices. Humans create tools in advance of a future specific instance where the use of such tools would be helpful. And they transport those tools from where the tools are made to where they may best be later employed. The nature of the neuropsychological mechanisms that would have been needed to support these cultural developments and their dispersal among members of a social group deserve some future research consideration in neuropsychology. Lacking the power to imitate another, the fortuitous discovery by one individual of the use of an object for a purpose other than its original function (a tool) would not have been dispersed to others of the group. It would have passed out of existence from the social group with the death of that individual or any later loss of this talent by that individual via memory decay or behavioral extinction. That tool would not have spread to others, and so a culture of tool users would be impossible.

Tool use demands a cognitive capacity to imitate. Nonverbal working memory is the prerequisite mental module for such imitation. Imitating others' behavior conveys numerous benefits to the imitator apart from whether what one imitates is the other's use of a tool. Those benefits may have been the initial selection advantage for developing imitation. But having evolved, the further evolutionary development of imitative capacity could have been substantially boosted by the additional advantage it offered for tool utilization. In a social group of experiential thieves, it only requires that one discover the use for a tool to have that use be quickly stolen or co-opted by other selfish imitators. Likewise for any individually discovered refinements or innovations in that use or in that tool's design, thus promulgating an evolutionary "tools race" among competing imitators within a social group.

The internalization or privatization of imitative rehearsals and the refinements in performance that might result from those covert simulations could then have become a further source for innovation in tool use and construction (Donald, 1991).

It is tantalizing to ponder the possible relationship between utilization behavior as seen in frontal-lobe-injured patients (Lhermitte, 1983; Lhermitte *et al.*, 1985) and this possible evolutionary scenario for imitation, mimesis, and tool usage, particularly the covert or private simulations of those actions. In utilization behavior, frontally injured patients immediately begin to demonstrate the use of various objects (often tools) presented to them, regardless of the social inappropriateness of doing so in that context. For instance, when presented with a telephone or an umbrella, the patient immediately picks up the phone and begins to dial it or, in the case of the umbrella, opens it. The uses of these tools as demonstrated by the patient are appropriate but that use in that context is inappropriate to that social situation. Such public displays of tool usage suggest that certain aspects of the prefrontal lobes inhibit these public displays though probably still permitting their covert execution. Damage to the prefrontal cortex releases that inhibition such that the entry of the tool into the visual field of the patient immediately elicits its public utilization rather than its more appropriate private one. Cases such as these might suggest that humans have evolved a near compulsion to imitate and demonstrate the utilization of tools, the public displays of which have come to be suppressed when they are in conflict with the larger purpose or demands of a social situation.

Self-Defense From Social Influence

Many hypotheses have been proposed about the origins of language or the more general trait of symbolization in humans (see Darwin, 1871/1992; Deacon, 1997; Donald, 1991; Pinker, 1994, 1997; for a few). Most of them are predicated on the existence of imitation, tool utilization, mimesis, and nonverbal mental representations (covert sensory-motor action to the self) as prerequisites for symbolization. That is because mental representations provide the referents that grant symbols their semantic content. Both Deacon (1997) and Donald (1991) argued that language is just a special case of a more general ability to symbolize. It is that capacity for symbolization, they argue, that must be appreciated and requires explanation as an adaptation, and not language *per se*. The generative power (reconstitution) of the executive system, then, is not just confined to language or visual-spatial designs but extends to the innovation, formation, and recombination of symbols into new arrangements. This implies that along

with diminished fluency in language and design manufacture documented in those with frontal-lobe injuries may come a diminished capacity for symbol formation, innovation, and recombination and their guidance of behavior toward the future. This larger, more general capacity for symbolization of which language is a specific case would be one of the latest-evolved psychological abilities in humans. It had to await the emergence of prerequisite executive capacities that create mental representations, their reconstitution, and the governance of behavior by those representations.

One perspective overlooked in earlier analyses of the purpose of symbolization, which may have some value in appreciating the evolution of speech (and of vocal calls, emotional displays, and mimetic skill before it) and later self-speech, is Dawkins' (1982) concept of the extended phenotype. In essence, Dawkins' point is that many biologists, and especially psychologists, interpret the concept of a phenotype far too narrowly. They see the phenotype as representing only the physical characteristics of the individual that are bounded by the skin. This may be chiefly the result of how high school biology classes teach genetics and the concept of genotypes and phenotypes, concentrating as they often do exclusively on physical attributes of an organism. But the actions of that organism may be as much a part of its phenotype as is its coloration and body configuration. To the extent that genes indirectly influence behavior and those influences are now or were once heritable to any degree, that behavior and its ecological ramifications are part of the individual's phenotype. Dawkins' (1982) example of the effect of the beaver on the countryside, for instance, involves more than just the building of a home from trees and branches. It also involves the destruction of tree life near the water's edge, the creation of dams, the subsequent alteration of water life, the downstream availability of water and its ecological impact, and even the microclimate of that surrounding region. These effects on the environment can be considered to be just as much a part of the phenotype of the beaver as its fur color, paddle-like tail, and dentition. In Dawkins' view, there is no outward ecological limit to the effects a genotype can produce and hence no such limit to its phenotype either.

Moving closer to the aims of this paper, Dawkins also considers the effects of birdsong on other members of a bird's particular species. The adaptive function of that song may be to attract a mate for purposes of reproduction. That song is or was at one time heritable. (The emphasis on both past and present tense here is simply to indicate that traits may be heritable earlier in their evolution. But natural selection consumes heritable variation, such that selection can potentially drive heritability to near zero once the trait is universal and well established in that species design.)

The social influence of the song can be considered to act like a drug on another member of the species. And like a drug, the song's function is to alter the nervous system of surrounding members of the opposite sex of that species so as to make them more inclined to investigate its source and to reproduce with its owner. These effects of birdsong on other members of the species are just as much a part of the bird's phenotype as is its feather coloration or beak configuration.

To the author's knowledge, human language has not been looked upon from this vantage yet like bird song it clearly evolved as a form of social influence. And it certainly provides a veritable lingua pharmacopeia for attempting to alter the nervous systems of one's peers so as to influence their mental representations and eventually their behavior for the ultimate self-interests of the speaker. If that analogy to medication is at all correct, then one should see evidence of the evolution of defensive tactics that serve, at least in part, to diminish that influence upon oneself by the speech of others. It is interesting to ponder what defenses could be mounted against the symbolic pharmacology of one's peers—perhaps more language in response. Persuasion and counterpersuasion in verbal exchange; the classic “war of words;” language as both a drug and its antidote.

Yet it is also possible that self-control might also provide that defense, for (as defined earlier) it serves to free up the individual from momentary control by the context (which is largely social) so as to maximize the longer-term self-interests of the individual. Scientific thinking may also be a more highly developed and codified form of such self-defense. Should language and self-regulation have both offensive and defensive qualities as conjectured here, then a linguistic and self-regulatory Red Queen effect or arms race might well have been set in motion by intraspecies competition and mate selection preferences for these attributes. Again, this could account for their recent and rapid evolution in human history.

Language is an instinct (Pinker, 1994). It is heritable, making it part of the human extended phenotype. So seem to be the executive functions that may have served as its evolutionary prerequisites (inhibition, nonverbal working memory, internalized emotion, and reconstitution). Those executive functions and their social products of reciprocal altruism, imitation, tool use, and mimesis are all thereby a part of the universal human phenotype. One can also consider as part of the phenotype the druglike influences that gestural (mimetic) and symbolic communication have on the brains of others. This concept of the extended phenotype, anchored as it is in the gene's eye view of adaptations and their functions, may offer substantial heuristic insights into human social conduct and, specifically, human execu-

tive functioning. From this perspective, the human phenotype might be thought of as comprising group-living, selfish, imitative, tool-using cooperators (social exchangers) with an instinct for self-regulation, a penchant for social influence and self-defense via self-speech, and a capacity for self-innovation. All of it may be in the service of striving to maximize the individual's long-term economic and reproductive (inclusive) fitness. Admittedly, this self-interested, gene's eye view, is not a pretty picture. Yet it is a potentially useful one in approaching the study of the adaptive purposes of the EFs. Such a view may offer more insight into the EF/SR system than do current views of human neuropsychological functions as ahistoric, unmotivated, non-self-interested, neutered circuit boards.

The specific origin of language and the more general capacity for symbolization does not concern the aims of this paper. There is little doubt that a capacity for symbolization or language would greatly clarify, refine, economize, and expand upon the solutions to the possible adaptive problems for which imitation, mimesis, tool use, and especially social exchange may have arisen to solve. Social communication does not require symbolization, as Donald's (1991) theory of mimetic evolution clearly demonstrates, and as the lack of speech in the deaf and some aphasics attests. But it would be substantially benefited from language for social communication. Likewise, so would pedagogy (Williams, 1966/1996), rule-governed behavior (Hayes, 1987), and social exchange (Cosmides and Tooby, 1992). This could be why humans are the only species to evolve symbolization. They were the only group-living species that entered the evolutionary path toward social exchange, then delayed imitation, followed by tool use and mimesis along with the EFs those capacities required. It may have been upon those earlier adaptations that language was eventually built (evolved). Any or all of these might have created the selection pressures for symbolic language as a substitute for or elaboration upon these earlier-evolved adaptations. Like them, its evolution would have been driven by the selection pressures of intraspecies competition and sexual selection preferences in a group-living species (Blackmore, 1999; Deacon, 1997; Donald, 1991; Pinker, 1997; Ridley, 1997).

More to the aim of this section, why then did *private* speech evolve? Why turn language on the self and make it covert in form? The explanation may well be for the very same reasons that other EFs became private in humans. Because sensorimotor behavior-to-the-self had already become self-directed and then privatized or internalized to form nonverbal working memory, why would not language follow suit? Evolution respects a neat trick when it finds one. Such sensorimotor acts of self-control, of which self-directed speech is clearly an example (Diaz

and Berk, 1992; Vygotsky and Luria, 1994), may initially have been publicly executed earlier in human evolutionary history. But they would be forced to become covert in form because of intraspecies competition from fellow imitators, as noted earlier. It is surely wiser to practice in private what one intends to mimetically rehearse, refine, and later do with or toward others before its public debut so as not to have it stolen, co-opted, or countermanded by one's competitors. So it also may be wiser to rehearse covertly what one wishes to communicate symbolically toward those competitors before shooting off one's mouth. Speech toward others is a means to influence their behavior (drug their nervous systems?) favorably toward the speaker and ultimately in the service of the speaker's own self-interests. It uses others as social tools. To the extent that such attempts at social influence are drafted, rehearsed, and refined covertly for maximal social effect before their emission, so much the better will the individual be in a competitive environment. The development of self-speech may have originated for this purpose of private rehearsal or simulation. Yet it also would be a means for self-defense and self-improvement. It is a means of using the self as a tool for problem solving through the description and interrogation of one's own past, as Vygotsky and Luria (1994) suggested. Its move toward becoming covert over development may, once again, have been for the advantages accompanying secrecy of one's actions from one's imitating peers.

CLINICAL AND RESEARCH IMPLICATIONS

In taking an evolutionary stance in neuropsychology toward the executive system, much is to be gained for clinical neuropsychology. Efforts to understand the adaptive problems solved by the executive system (and the prefrontal cortex) and the genetically self-interested motives behind them can provide much greater insight into what is diminished or lost in those with acquired or developmental impairments of that system. It can therefore offer a more accurate and naturalistic appraisal of the purposes of that system, argued here as largely social ones. And it can show the types of ecological problems that are posed for prefrontally injured patients and their families. Already, this framework is providing much insight into the nature of ADHD (Barkley, 1997b). Consider which of the following may be more insightful and instructive about the EFs and their impairments: To say that a prefrontally injured patient cannot build towers of concentric rings or sort cards by categories on demand as well as others? Or to say that the those more proximal problems actually reflect ones that lie in the larger realms of:

- social exchange (reciprocal altruism),
- vicarious learning,
- tool utilization,
- mimetic skill and communication,
- self-regulation for self-defense,
- and the governance of social behavior by mentally represented information?

This reformulation clearly speaks volumes more about the social devastation accompanying executive deficits than does the view from the computer metaphor. Yet those adaptive functions would not be evident without taking the evolutionary stance toward the executive system in clinical neuropsychology.

Noteworthy is that the aforementioned adaptive purposes incorporate as inherent features much of what is already known about the more proximal processes attributed to executive functioning (e.g., temporal sequencing, planning, rule discovery, flexibility, problem solving, etc.). But it views them as means to a greater social end by placing them in the larger perspective of those self-interested motives that frame the endpoints themselves. The proximal processes revealed in previous EF research include holding information in mind (working memory), response inhibition, flexibility, fluency, the temporal ordering of events and behavioral sequences, social scripts, rule following, and oppositional thinking, among others. The larger social purposes of reciprocal altruism, vicarious learning and experiential theft, gestural and symbolic communication and social manipulation, and the social self-defense these other capacities would have initiated incorporate these more proximal processes. But this would not have been so obvious had an evolutionary perspective not been considered.

For instance, to say that the EFs involve planning or problem solving, as many neuropsychologists often do, says paltry little without further specifying about what and for what adaptive ends such planning or problem solving arose to accomplish. Planning and problem solving are not the ends but the means to some end. Planning, unlike vision, is patently unnecessary for dealing with the physical world we and other species inhabit, as witnessed by the fact that millions of species have survived on this planet without it. The evolutionary framework urges us to look at the precise environmental selection pressures that were uniquely specific to the history of human ancestral species and their niche to discover the function of "planning" or "problem solving." That perspective overwhelmingly points to a social (group living) function for the EFs; it is for social intelligence (Dimond, 1980). The evolutionary approach informs us that planning may well have arisen initially for purposes of social exchange (selfish

cooperation) and coalition formation so as to outwit and thereby outresource others. If so, it may have set off an intraspecies Red Queen effect so as to outthink, outcompete, and outmaximize social resources relative to one's contemporary experiential thieves in the social chess match that group living with nonkin must have created.

Just as important, scientifically framed proposals as to the adaptive purposes of the executive system can also result in the development of better methods of assessing the EFs, both for basic research and clinical evaluation. Conceptualized as forms of private behavior to the self, many of the EFs are likely to be involved in the performance of most measures currently used to assess executive functioning. For instance, the Tower of Hanoi test certainly must involve the capacities for visual imagery, self-speech, and mental play (simulation) such that it cannot reflect upon the integrity of any single one of these EFs but on their interaction so as to solve the design problem. As this illustrates, designing measures that tap purely one EF, particularly that of nonverbal working memory, will prove difficult because subjects are likely to employ self-speech in most of them, contaminating the interpretation of any results (Barkley, 1997b). For now, it may be more helpful to use batteries of tests whose factor structures are previously established as representing the EFs outlined here. Those factors represent the underlying structural or dimensional level that is more likely to be indicative of any particular EF than will any single test (see Barkley, 1997b, for a review of factor analyses of EF batteries). This permits the factor score to be used as a reflection of a particular EF rather than any one measure from that factor.

Efforts to develop better EF measures might also improve the evaluation of the adaptive impact resulting from impairments in the executive system and the prefrontal cortex. Surely this might prove more beneficial to clinical neuropsychology and its consumers than does the current array of methods. Those methods are based largely on narrow cognitive constructs devoid of an adaptive history and of the self-interested motives that drove it. The development of rating scales (for both self-and other-reports of patients) that contained items that reflect the EFs and their larger adaptive purposes might be a first step in this direction (see Burgess *et al.*, 1998, for an attempt at a rating scale of EFs). The re-configuration of laboratory tasks to take into account the social ends for which these EFs evolved also may enhance their sensitivity to impairments that may exist within those EFs. For instance, might there be some benefit to redesigning the Tower of Hanoi or the Wisconsin Card Sort Task so that they focused more on planning and rule detection involving social goals or purposes instead of planning and rule discovery in the abstract? One might find the same result as did Cosmides

and Tooby (1992) in redesigning a test of abstract thinking. They discovered that humans were far better at solving the task when it was framed in a social context and having a social end. Given the hypothesis here that the EFs arose to solve largely social problems in a group-living species, the results of such efforts are likely to prove far more ecologically valid (predictive to naturalistic settings) than is the current armamentarium of EF tasks that are abstract in nature and devoid of their likely social ends. Executive functioning provides for the cross-temporal organization of behavior toward the future (Fuster, 1997). This paper has shown that the future most important to consider here is largely a social one. If so, then both the larger time frames over which reference is made in rating scales (e.g., weeks or months) and the social phrasing of their items may prove much more valid in detecting executive deficits. And they might do so with greater economy than would current abstract tests spanning hours in a clinic.

The model of executive functioning offered here and its associated evolutionary framework may also provide greater utility for rehabilitation planning than might purely abstract and cognitive formulations of the executive system. For instance, the EF/SR model set forth here states that normal individuals have developed a means to guide social behavior by internal representations and motivations and that these originally arose out of external behavior and representations. To assist prefrontally-injured patients, this model points to the need to externalize both the sources of information (representations) one wishes to control behavior in those patients AND those sources of motivation that will support its occurrence (Barkley, 1997b). It also stipulates that such adjustments must occur at the natural "points of performance" of the desired behaviors and not focus so much on the training of skills. For what is lost or diminished in such patients is not so much knowing what to do but doing what one knows WHEN it would have been beneficial to do so. Furthermore, the adaptationist framework for this model might conceivably point to those contexts and social functions in the larger social arena for which some assistance or accommodations must be provided to the executive-impaired individual. Those functions include vicarious learning, reciprocal social exchange and social contracts, rule-governed behavior for personal safety, self-regulation toward the future, protection from nefarious social influence via the linguistic pharmacopeia of others, etc.

And finally, the EF/SR model set forth here along with its adaptationist perspective might well offer advantages to the interpretation of functional neuroimaging studies than might purely cognitive frameworks. If the executive functions are forms of behavior-to-the-self that occur in a covert (internalized) form, the imaging of those

functions may well reveal aspects of subtle motor activities that would not have been evident from purely cognitive formulations of those functions. Those motor aspects will be the vestiges of the forms of public behavior that served as the origins for the EFs. For instance, does activation of the anterior cingulate, striatal, or cerebellar, or a combination of these regions during nonverbal working memory tasks requiring visual imagery and imagined manipulations reflect such covert behavior-to-the-self? The fact noted earlier that shifts in peripheral muscle tension of the oral/speech musculature are detectable during verbal thought suggests so. And so does the subtle shift in muscle potentials in the arm and hand involved in a visually imagined manipulation imply that these seemingly cognitive acts remain subtle forms of behavior-to-the-self. Those covert self-directed behaviors likely activate brain areas on functional neuroimaging that are associated with their vestigial publicly observable counterparts. If so, such a perspective may better serve to interpret those neuroimaged activation patterns, such as the role of the cerebellum in cognition and executive functioning (Diamond, 2000), than would framing the EFs in purely cognitive or computer terms. For no matter how far functional neuroimaging technology advances, the conceptual and explanatory yield will be limited by the psychological constructs, models, and frames of reference employed to describe those functions being imaged.

CONCLUSION

This paper has strongly argued for taking an evolutionary, adaptationist stance toward the origin and nature of executive functioning. It began with the concepts of behavioral inhibition, self-regulation, and executive functioning so as to show their inherent linkages. At its core, response inhibition provides for a delay in the emission of prepotent responses. During that delay, self-directed actions could begin to take place so as to evaluate and modify, as needed, the decision to respond. Such self-directed behavior is the essence of self-regulation. The EFs constitute those four major forms of self-directed actions that humans use for self-regulation toward the future. It is asserted that each EF begins as a form of public behavior directed at others and the external world but becomes self-directed and then private or covert in form over development as forms of self-regulation. Those major EFs are (1) self-directed sensory-motor actions (e.g., visual imagery, etc.), (2) self-directed speech, (3) self-directed emotion/motivation, and (4) self-directed play or reconstruction. The EFs create a shift in the sources of control of behavior across development from the external to in-

ternal, from social others to the self, and from control by the moment to control by time (sequential change) and the future. These shifts function to achieve a net maximization of longer-term over short-term outcomes, many of which are social in nature. This strategy of maximizing longer-term social consequences over near-term ones must have offered an adaptive advantage of some sort that indirectly benefited the individual's reproductive (inclusive) fitness.

This paper has urged neuropsychologists to adopt the governing paradigm of biology—evolution—in their pursuit of the solution to the riddle of the executive functions. In doing so, neuropsychologists must familiarize themselves with the process of natural selection and the constraints that process poses for the formulation of hypotheses on the nature of the executive functions. In particular, greater familiarity with selfish gene theory, the principles of gradualism and convergence, kin selection, game theory and social exchange, and the requirements for viewing an attribute as an adaptation are all to be encouraged. From this perspective, models of the executive system must not only be parsimonious, but they must be operationalized such that their process of gradual evolution from other primates through our hominid ancestors can be made more apparent. And those models must be framed in such a way as to make them not only consilient with existing scientific findings but testable (capable of falsification) as well.

This paper further argued that the relative uniqueness of the executive system to humans implies that there was something about the specific environmental niche which human ancestors occupied that gave rise to the need for the EFs as adaptations to that niche. Attempts to understand the peculiarities, adaptive problems, and selection pressures posed by that niche are likely to provide fruitful insights into the origins and purposes of the EFs and the cross-temporally organized and future-directed behavior they permit. It was proposed that those adaptive problems were largely social ones that may have resulted from the group-living evolutionary pathway that human ancestors found themselves occupying and the selection pressures such group living would have created. In essence human ancestors became group-living selfish cooperators so as to meet certain environmental selection pressures posed by earlier environments.

Among the possible adaptive problems that the executive system may have evolved to solve would be social exchange, imitation and vicarious learning (experiential theft) and the enhanced pedagogy they permitted, tool construction and utilization, mimetic skill and communication, and social self-defense against the pharmacological effects of the communications of others. Out of these

initial capacities may have been born the later adaptive pressures that gave rise to the human penchant for symbolization (language), narrative, and metaphor. Such propositions are admittedly speculative for the moment. They are offered here not to end the debate on the nature and original adaptive purposes of the EFs but to initiate it among neuropsychologists seeking to understand these functions. The crux of the argument made here is that the adaptationist stance toward understanding the EFs will prove more useful in providing a deeper, more integrated conceptualization of those functions than will current preferences for viewing these functions from a purely cognitive stance or its associated computer metaphor. The brain-as-computer framework is of limited value for it is devoid of history, detached from human motives, and sanitized of the general selection pressures to which all life must answer (genetic replication and its attendant adaptive problems). It is decoupled from the specific niche-related adaptive problems with which human ancestors had to contend. Efforts at understanding executive functioning will prove sorely limited by continuing to neglect the role of evolution in its origins. So will efforts to understand other neuropsychological processes besides the EFs. Neuropsychology is as much a subspecialty of biology as of psychology. Evolution is the governing theory of biology. If nothing in biology makes sense except in the light of evolution, then nothing in neuropsychology will ultimately make sense except in that same light. The executive functions are no exception.

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REFERENCES

- Ainslie, G. (1974). Impulse control in pigeons. *Journal of the Experimental Analysis of Behavior* 21: 485–489.
- Ainslie, G. (1975). Specious reward: A behavioral theory of impulsiveness and impulse control. *Psychological Bulletin* 82: 463–496.
- Baddeley, A. D. (1986). *Working memory*, Clarendon Press, London.
- Baddeley, A. D., and Hitch, G. J. (1994). Developments in the concept of working memory. *Neuropsychology* 8: 1485–493.
- Baldwin, J. M. (1895). Consciousness and evolution. *Science* 2: 219–223.
- Barkley, R. A. (1997a). Behavioral inhibition, sustained attention, and executive functions: Constructing a unifying theory of ADHD. *Psychological Bulletin* 121: 65–94.
- Barkley, R. A. (1997b). *ADHD and the Nature of Self-Control*, Guilford, New York.
- Barkley, R. A. (1998). *Attention Deficit Hyperactivity Disorder: A Handbook for Diagnosis and Treatment* (2nd. Ed.), Guilford, New York.
- Bastian, H. C. (1892). On the neural processes underlying attention and volition. *Brain* 15: 1–34.
- Blackmore, S. (1999). *The Mem Machine*, Oxford, New York.
- Bronowski, J. (1967/1977). Human and animal languages. In *A Sense of the Future*, MIT Press, Cambridge, MA, pp. 104–131.
- Bronowski, J. (1976). *The Ascent of Man*, Little-Brown, New York.
- Burgess, P. W., Alderman, N., Evans, J., Emslie, H., and Wilson, B. (1998). The ecological validity of tests of executive function. *Journal of the International Neuropsychological Society* 4: 547–558.
- Burns, D. J., and Powers, R. B. (1975). Choice and self-control in children: A test of Rachlin's model. *Bulletin of the Psychonomic Society* 5: 156–158.
- Buss, D. M. (1992). Mate preference mechanisms: Consequences for partner choice and intrasexual competition. In Barkow, J. H., Cosmides, L., & Tooby, J. (eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, New York: Oxford University Press, pp. 249–266.
- Buss, D. M. (1998). The psychology of mate selection: Exploring the complexity of the strategic repertoire. In Crawford, C., & Krebs, D. L. (eds.), *Handbook of Evolutionary Psychology: Ideas Issues and Applications*, Mahwah, NJ: Lawrence Erlbaum Associates, pp. 405–430.
- Buss, D. M., Haselton, M. G., Shackelford, T. K., Bleske, A. L., and Wakefield, J. C. (1998). Adaptations, exaptations, and spandrels. *American Psychologist* 53: 533–548.
- Campbell, D. T. (1960). Blind variation and selective retention in creative thought as in other knowledge processes. *Psychological Review* 67: 380–400.
- Castellanos, F. X., Giedd, J. N., Marsh, W. L., Hamburger, S. D., Vaituzis, A. C., Dickstein, D. P., Sarfatti, S. E., Vauss, Y. C., Snell, J. W., Lange, N., Kaysen, D., Krain, A. L., Ritchhie, G. F., Rajapakse, J. C., and Rapoport, J. L. (1996). Quantitative brain magnetic resonance imaging in attention-deficit hyperactivity disorder. *Archives of General Psychiatry* 53: 607–616.
- Cerutti, D. T. (1989). Discrimination theory of rule-governed behavior. *Journal of the Experimental Analysis of Behavior* 51: 259–276.
- Corballis, M. C. (1989). Laterality and human evolution. *Psychological Review* 96: 492–505.
- Cosmides, L., and Tooby, J. (1992). Cognitive adaptations for social exchange. In Barkow, J., Cosmides, L., and Tooby, J. (eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, New York, Oxford University Press, pp. 163–228.
- Crawford, C. (1998). Environments and adaptations: Then and now. In Crawford, C., and Krebs, D. L. (eds.), *The Handbook of Evolutionary Psychology: Ideas, Issues, and Applications*, Erlbaum, Mahwah, NJ, pp. 275–302.
- Crawford, C., and Krebs, D. L. (1998). *The Handbook of Evolutionary Psychology: Ideas, Issues, and Applications*, Erlbaum, Mahwah, NJ.
- Damasio, A. R. (1994). *Descartes' Error: Emotion, Reason, and the Human Brain*, Putnam & Sons, New York.
- Damasio, A. R. (1995). On some functions of the human prefrontal cortex. In Grafma, J., Holyoak, K. J., and Boller, F. (eds.), *Annals of the New York Academy of Sciences: Vol. 769. Structure and Functions of the Human Prefrontal Cortex*, New York Academy of Sciences, New York, pp. 241–251.
- Darwin, C. (1871/1992). *The Descent of Man and Selection in Relation to Sex*, Encyclopedia Britannica, Chicago, IL.
- Davies, P. (1995). *About Time: Einstein's Unfinished Revolution*, Simon and Schuster, New York.
- Dawkins, R. (1974). *The Selfish Gene*, Oxford University Press, New York.

- Dawkins, R. (1982). *The Extended Phenotype*, Oxford University Press, New York.
- Dawkins, R. (1984). Replicators, consequences, and displacement activities. *The Behavioral and Brain Sciences* 7: 486–487.
- Dawkins, R. (1987). *The Blind Watchmaker: Why the Evidence of Evolution Reveals a Universe Without Design*, W. W. Norton & Co, New York.
- Dawkins, R. (1995). *River Out of Eden*, Oxford University Press, New York.
- Dawkins, R. (1997). *Climbing Mount Improbable*, Oxford University Press, New York.
- Deacon, T. W. (1997). *The Symbolic Species: The Co-evolution of Language and the Brain*, W. W. Norton, New York.
- Denckla, M. B. (1994). Measurement of executive function. In Lyon, G. R. (ed.), *Frames of Reference for the Assessment of Learning Disabilities: New Views on Measurement Issues*, Paul H. Brookes, Baltimore, MD, pp. 117–142.
- Denckla, M. B. (1996). A theory and model of executive function: A neuropsychological perspective. In Lyon, G. R., and Krasnegor, N. A. (eds.), *Attention, Memory, and Executive Function*, Paul H. Brookes, Baltimore, MD, pp. 263–277.
- Dennett, D. (1995). *Darwin's Dangerous Idea: Evolution and the Meanings of Life*, Simon & Schuster, New York.
- Dennis, M. (1991). Frontal lobe function in childhood and adolescence: A heuristic for assessing attention regulation, executive control, and the intentional states important for social discourse. *Developmental Neuropsychology* 7: 327–358.
- D'Esposito, M., Detre, J. A., Alsop, D. C., Shin, R. K., Atlas, S., and Grossman, M. (1995). The neural basis of the central executive system of working memory. *Nature* 378: 279–281.
- D'Esposito, M., Detre, J. A., Aguirre, G. K., Stallcup, M., Alsop, D. C., Tippet, L. L., & Farah, M. J. (1997). A functional MRI study of mental image generation. *Neuropsychologia* 35: 725–730.
- Deutsch, D. (1994). *The Fabric of Reality*, Penguin Books, London.
- Diamond, A. (2000). Close interrelation of motor development and cognitive development and of the cerebellum and prefrontal cortex. *Developmental Psychology* 71: 44–56.
- Diamond, A., Cruttenden, L., and Neiderman, D. (1994). AB with multiple wells: 1. Why are multiple wells sometimes easier than two wells? 2. Memory or memory + inhibition? *Developmental Psychology* 30: 192–205.
- Diamond, J. (1999). *Germes, Guns, and Steel: The Fates of Human Societies*, W. W. Norton & Co, New York.
- Diaz, R. M., and Berk, L. E. (1992). *Private Speech: From Social Interaction to Self-Regulation*, Erlbaum, Mahwah, NJ.
- Diaz, R. M., Neal, C. J., and Amaya-Williams, M. (1990). The social origins of self-regulation. In Moll, L. C. (ed.), *Vygotsky and Education: Instructional Implications and Applications of Sociocultural Psychology*, Cambridge University Press, New York, pp. 127–154.
- Dimond, S. J. (1980). *Neuropsychology: A Textbook of Systems and Psychological Functions of the Human Brain*, Butterworths, London, pp. 390–411.
- Donald, M. (1991). *Origins of the Modern Mind: Three Stages in the Evolution of Culture and Cognition*, Harvard University Press, Cambridge.
- Donald, M. (1993). Precipitous origins of the modern mind: Three stages in the evolution of culture and cognition. *The Behavioral and Brain Sciences* 16: 737–791.
- Dugatkin, L. (1999). *Cheating Monkeys and Citizen Bees: The Nature of Cooperation in Animals and Humans*, The Free Press, New York.
- Durham, W. H. (1991). *Co-evolution: Genes, Culture, and Human Diversity*, Stanford University Press, Stanford.
- Filipek, P. A., Semrud-Clikeman, M., Steingard, R. J., Renshaw, P. F., Kennedy, D. N., and Biederman, J. (1997). Volumetric MRI analysis comparing subjects having attention-deficit hyperactivity disorder with normal controls. *Neurology* 48: 589–601.
- Fuster, J. M. (1995). Memory and Planning: Two temporal perspectives of frontal lobe function. In Jasper, H. H., Riggio, S., and Goldman-Rakic, P. S. (eds.), *Epilepsy and the Functional Anatomy of the Frontal Lobe*, Raven, New York, pp. 9–18.
- Fuster, J. M. (1997). *The Prefrontal Cortex: Anatomy, Physiology, and Neuropsychology of the Frontal Lobe* (3rd Ed.), Lippincott-Raven, Philadelphia.
- Gazzaniga, M. (1998). *The Mind's Past*, University of California Press, Berkeley.
- Geary, D. C., and Bjorklund, D. F. (2000). Evolutionary developmental psychology. *Developmental Psychology* 71: 57–65.
- Godefroy, O., and Rosseaux, M. (1997). Novel decision making in patients with prefrontal or posterior brain damage. *Neurology* 49: 695–701.
- Goel, V., and Grafman, J. (1995). Are the frontal lobes implicated in “planning” functions? Interpreting data from the Tower of Hanoi. *Neuropsychologia* 33: 623–642.
- Goldman-Rakic, P. S. (1995). Architecture of the prefrontal cortex and the central executive. In Grafman, J., Holyoak, K. J., and Boller, F. (eds.), *Annals of the New York Academy of Sciences: Vol. 769. Structure and Functions of the Human Prefrontal Cortex*, New York Academy of Sciences, New York, pp. 71–83.
- Gould, S. J. (1991). Exaptation: A crucial tool for evolutionary psychology. *Journal of Social Issues* 47: 43–65.
- Gould, S. J. (1997). Evolutionary psychology: An exchange. *New York Review of Books*, XLIV, 53–58.
- Grafman, J. (1995). Similarities and distinctions among current models of prefrontal cortical functions. In Grafman, J., Holyoak, K. J., & Boller, F. (eds.), *Structure and Functions of the Human Prefrontal Cortex*, New York: New York Academy of Sciences, pp. 337–368.
- Green, L., Myerson, J., Lichtman, D., Rosen, S., and Fry, A. (1996). Temporal discounting in choice between delayed rewards; The role of age and income. *Psychology and Aging* 11: 79–84.
- Hale, S., Bronik, M. D., and Fry, A. F. (1997). Verbal and spatial working memory in school-age children: Developmental differences in susceptibility to interference. *Developmental Psychology* 33: 364–371.
- Hayes, S. (1987). *Rule-Governed Behavior*, Plenum, New York.
- Hofstadter, M., and Reznick, J. S. (1996). Response modality affects human infant delayed-response performance. *Child Development* 67: 646–658.
- Holcomb, H. R., III (1998). Testing evolutionary hypotheses. In Crawford, C., and Krebs, K. L. (eds.), *The Handbook of Evolutionary Psychology: Ideas, Issues, and Applications*, Erlbaum, Mahwah, NJ, pp. 303–334.
- Houk, J. C., and Wise, S. P. (1995). Distributed modular architectures linking basal ganglia, cerebellum, and cerebral cortex: Their role in planning and controlling action. *Cerebral Cortex* 2: 95–110.
- Humphrey, N. (1984). *Consciousness Regained*, Oxford University Press, Oxford.
- James, H. (1890/1992). *The Principles of Psychology*, Henry Holt, New York (Reprinted by Britannica, Great Books of the Western World).
- Kanfer, F. H., and Karoly, P. (1972). Self-control: A behavioristic excursion into the lion's den. *Behavior Therapy* 3: 398–416.
- Kopp, C. B. (1982). Antecedents of self-regulation: A developmental perspective. *Developmental Psychology* 18: 199–214.
- Kosslyn, S. (1994). *Image and the Brain*, MIT Press, Cambridge.
- Lee, G. P., Strauss, E., Loring, D. W., McCloskey, L., Haworth, J. M., and Lehman, R. A. W. (1997). Sensitivity of figural fluency on the Five-Point Test to focal neurological dysfunction. *The Clinical Neuropsychologist* 11: 59–68.
- Levin, H. S., Fletcher, J. M., Kufera, J. A., Harvard, H., Lilly, M. A., Mendelsohn, D., Bruce, D., and Eisenberg, H. M. (1996). Dimensions of cognition measured by the Tower of London and other cognitive tasks in head-injured children and adolescents. *Developmental Neuropsychology* 12: 17–34.
- Lezak, M. D. (1995). *Neuropsychological Assessment* (3rd Ed.), Oxford University Press, New York.
- Lhermitte, F. (1983). “Utilization Behavior” and its relation to lesions of the frontal lobes. *Brain* 106: 237–255.

- Lhermitte, F., Pillon, B., and Sraru, M. (1985). Human autonomy and the frontal lobes. Part I: Imitation and utilization behavior: A neuropsychological study of 75 patients. *Annals of Neurology* 19: 326–334.
- Livesay, J. R., Liebke, A. W., Samaras, M. R., and Stanley, S. A. (1996). Covert speech behavior during a silent language recitation task. *Perceptual and Motor Skills* 83: 1355–1362.
- Livesay, J. R., and Samaras, M. R. (1998). Covert neuromuscular activity of the dominant forearm during visualization of a motor task. *Perceptual and Motor Skills* 86: 371–374.
- Logue, A. W. (1988). Research on self-control: An integrating framework. *The Behavioral and Brain Sciences* 11: 665–709.
- Lumsden, C. J., and Wilson, E. O. (1982). *Precis of Genes, Mind, and Culture*. *The Behavioral and Brain Sciences* 5: 1–37.
- Maruff, P., Wilson, P., Trebilcock, M., and Currie J. (1999). Abnormalities of imagined motor sequences in children with developmental coordination disorder. *Neuropsychologia* 37: 1317–1324.
- Maynard Smith, J., and Szathmari, E. (1999). *The Origins of Life: From the Birth of Life to the Origin of Language*, Oxford University Press, New York.
- Mazur, J. E. (1993). Predicting the strength of a conditioned reinforcer: Effects of delay and uncertainty. *Current Directions in Psychological Science* 2: 70–74.
- Meltzoff, A. N. (1988). Infant imitation and memory: Nine-month-olds in immediate and deferred tests. *Child Development* 59: 217–225.
- Michon, J. A. (1985). Introduction. In Michon, J., and Jackson, T. (eds.), *Time, Mind, & Behavior*, Springer-Verlag, Berlin, Germany.
- Mischel, W. (1983). Delay of gratification as process and as person variable in development. In Magnusson, D., and Allen, U. L. (eds.), *Human Development: An Interactional Perspective*, Academic Press, New York, pp. 149–166.
- Mischel, W., Shoda, Y., and Rodriguez, M. I. (1989). Delay of gratification in children. *Science* 244: 933–938.
- Morris, R. D. (1996). Relationships and distinctions among the concepts of attention, memory, and executive function: A developmental perspective. In Lyon, G. R., and Krasnegor, N. A. (eds.), *Attention, Memory, and Executive Function*, Paul H. Brookes, Baltimore, pp. 11–16.
- Navarick, D. J. (1986). Human impulsivity and choice: A challenge to traditional operant methodology. *Psychological Record* 36: 343–356.
- Passler, M. A., Isaac, W., and Hynd, G. W. (1985). Neuropsychological development of behavior attributed to frontal lobe functioning in children. *Developmental Neuropsychology* 1: 349–370.
- Peirce, C. S. (1897/1955). Logic as semiotic: The theory of signs. In Buchler, J. (ed.), *The Philosophical Writings of Peirce*, Dover, New York, pp. 98–119.
- Pinker, S. (1995). *The Language Instinct*, Harper Perennial, New York.
- Pinker, S. (1997). *How the Mind Works*, W. W. Norton, New York.
- Pinker, S., and Bloom, P. (1992). Natural language and natural selection. In Barkow, J., Cosmides, L., and Tooby, J. (eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, Oxford University Press, New York, pp. 451–494.
- Plotkin, H. (1998). *Evolution in Mind: An Introduction to Evolutionary Psychology*, Harvard University Press, Cambridge.
- Plotkin, H. C., and Odling-Smee, F. J. (1981). A multi-level model of evolution and its implications for sociobiology. *The Behavioral and Brain Sciences* 4: 225–268.
- Popper, K. (1968). *The Logic of Scientific Discovery*, Harper and Row, New York.
- Popper, K. (1972). *Objective Knowledge: An Evolutionary Approach*, Oxford University Press, Oxford.
- Prather, D. C. (1973). Prompted mental practice as a flight simulator. *Journal of Applied Psychology* 57: 353–355.
- Richards, R. J. (1987). *Darwin and the Emergence of Evolutionary Theories of Mind and Behavior*, University of Chicago Press, Chicago.
- Ridley, M. (1996). *Evolution* (2nd Ed.), Blackwell Science, Cambridge, MA.
- Ridley, M. (1993). *The Red Queen: Sex and the Evolution of Human Nature*, Penguin Books, New York.
- Ridley, M. (1997). *The Origins of Virtue*, New York: Viking.
- Ridley, M. (2000). *Genome: The Autobiography of Human Life in 23 Chapters*, W. W. Norton, New York.
- Ryding, E., Bradvik, B., and Ingvar, D. H. (1996). Silent speech activates prefrontal cortical regions asymmetrically, as well as speech-related areas in the dominant hemisphere. *Brain and Language* 52: 435–451.
- Shimamura, A. P., Janowsky, J. S., and Squire, L. R. (1990). Memory for the temporal order of events in patients with frontal lobe lesions and amnesic patients. *Neuropsychologia* 28: 803–813.
- Sirigu, A., Zalla, T., Pillon, B., Grafman, J., DuBois, B., and Agid, Y. (1995). Planning and script analysis following prefrontal lobe lesions. In Grafman, J., Holyoke, K. J., and Boller, F. (eds.), *Annals of the New York Academy of Sciences: Vol. 769. Structure and Functions of the Human Prefrontal Cortex*, New York Academy of Sciences, New York, pp. 277–288.
- Skinner, B. F. (1953). *Science and Human Behavior*, Macmillan, New York.
- Skinner, B. F. (1969). *Contingencies of Reinforcement: A Theoretical Analysis*, Appleton-Century-Crofts, New York.
- Skinner, B. F. (1981). Selection by consequences. *Science* 213: 501–504.
- Skinner, B. F. (1984). Selection by consequences. *The Behavioral and Brain Sciences* 7: 477–510.
- Spreen, O., Risse, A. H., and Edgell, D. (1995). *Developmental Neuropsychology*, Oxford University Press, New York.
- Stuss, D. T., Alxander, M. A., Hamer, L., Palumbo, C., Dempster, R., Binns, M., Levine, B., and Izkawa, D. (1998). The effects of focal anterior and posterior brain lesions on verbal fluency. *Journal of the International Neuropsychological Society* 4: 265–278.
- Stuss, D. T., and Benson, D. F. (1986). *The Frontal Lobes*, Raven, New York.
- Symons, D. (1992). On the use and misuse of Darwinism in the study of human behavior. In Barkow, J., Cosmides, L., and Tooby J. (eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, Oxford University Press, New York, pp. 137–162.
- Tooby, J., and Cosmides, L. (1992). The psychological foundations of culture. In Barkow, J., Cosmides, L., and Tooby, J. (eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, Oxford University Press, New York, pp. 19–136.
- Vygotsky, L. S. (1978). *Mind in Society*, Harvard University Press, Cambridge, MA.
- Vygotsky, L. S. (1987). Thinking and speech. In Minick, N. (trans.), *The Collected Works of L. S. Vygotsky, Vol. 1: Problems in General Psychology*, Plenum, New York.
- Vygotsky, L. S., and Luria, A. (1994). Tool and symbol in child development. In van der Veer, R., and Valsiner, J. (eds.), *The Vygotsky Reader*, Blackwell Science, Cambridge, MA, pp. 99–174.
- Welsh, M. C., Pennington, B. F., and Grossier, D. B. (1991). A normative-developmental study of executive function: A window on prefrontal function in children. *Developmental Neuropsychology* 7: 131–149.
- Wheeler, M. A., Stuss, D. T., and Tulving, E. (1997). Toward a theory of episodic memory: The frontal lobes and autonoetic consciousness. *Psychological Bulletin* 121: 331–354.
- Williams, G. C. (1966/1996). *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*, Princeton University Press, Princeton.
- Wilson, E. O. (1998). *Consilience: The Unity of Knowledge*, Alfred A. Knopf, New York.
- Zahavi, A., and Zahavi, A. (1997). *The Handicap Principle: A Missing Piece of Darwin's Puzzle*, Oxford University Press, New York.
- Zelazo, P. R., Kearsley, R. B., and Stack, D. M. (1995). Mental representations for visual sequences: Increased speed of central processing from 22 to 32 months. *Intelligence* 20: 41–63.