

From Movement to Thought: Executive Function, Embodied Cognition, and the Cerebellum

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Abstract This paper posits that the brain evolved for the control of action rather than for the development of cognition per se. We note that the terms commonly used to describe brain–behavior relationships define, and in many ways limit, how we conceptualize and investigate them and may therefore constrain the questions we ask and the utility of the “answers” we generate. Many constructs are so nonspecific and over-inclusive as to be scientifically meaningless. “Executive function” is one such term in common usage. As the construct is increasingly focal in neuroscience research, defining it clearly is critical. We propose a definition that places executive function within a model of continuous sensorimotor interaction with the environment. We posit that control of behavior is the essence of “executive function,” and we explore the evolutionary advantage conferred by being able to anticipate and control behavior with both implicit and explicit mechanisms. We focus on the cerebellum's critical role in these control processes. We then hypothesize about the ways in which procedural (skill) learning contributes to the acquisition of declarative (semantic) knowledge. We hypothesize how these systems might interact in the process of grounding knowledge in sensorimotor anticipation, thereby directly linking movement to thought and “embodied cognition.” We close with a discussion of ways in which the cerebellum instructs frontal systems how to think

ahead by providing anticipatory control mechanisms, and we briefly review this model's potential applications.

Keywords Cerebellum · Executive function · Embodied cognition · Frontal systems · Forward models · Inverse models

Introduction

Studies considering the contributions of various brain regions to adaptive behavior frequently conceptualize the systems governing brain–behavior relationships within separate and distinct domains. Clinical neuroscience, for example, often views behaviors as differentiated between cognitive, attention/executive, language, visuospatial, learning and memory, and sensory and motor domains. However, these distinctions are artificial, and they obscure the fact that the brain operates as an integrated whole. Moreover, the longer we compartmentalize brain function in this modular way, the more habitual this way of thinking becomes. The constructs reify and we may not realize how much they constrain our investigations and our ability to apply research findings to advance understanding of brain–behavior relationships [1]. This is not only of theoretical importance, but it is also of practical significance because it also limits our approaches to treating patients.

The prevailing models that guide understanding of behavior and cognition within certain clinical fields such as neuropsychology, psychiatry, neurology, and occupational and physical therapy are “top down” or cortico-centric in nature. In emphasizing cortical function, these fields fail to consider the substantial roles that subcortical structures play, which other branches of neuroscience have increasingly recognized as critical to adaptation [2–4].

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The INS Dictionary of Neuropsychology defines “cognition” as, “the mental processes associated with attention, perception, thinking, learning, and memory” [5]. This definition is so all-encompassing as to render it practically meaningless. Of what practical value is a term such as “cognition” if it must be operationally defined in each and every instance it is applied [1]? Such a broad definition of “cognition” encompasses the concept of executive function, while at the same time, the term “executive function” (EF) is defined in different ways by the clinical fields that apply it. Even neuropsychiatry and neuropsychology are unable to agree upon the key elements that comprise this obviously multiple component function (see definitions provided by Lezak, Gualtieri, and Dubois et al. [6–8]). We are defining EF as *the functions an organism employs to act independently in its own best interest as a whole, at any point in time, for the purpose of survival*, as initially proposed by Miller [9].

While there are no universally agreed upon definitions for “cognition” or “executive function,” both have historically been conceptualized as falling under the direct influence of conscious voluntary control. More recently, efforts have been made to include emotional and motivational functions within conceptualizations of EF [10, 11]. The prefrontal cortex (PFC) has been described as participating in two separate but related categories of EF. “Metacognitive” EFs include problem solving, planning, concept formation, strategy development and implementation, and controlling attention and working memory; these functions depend upon the integrity of the dorsolateral prefrontal cortex (DLPFC). “Emotional/motivational” EFs include coordinating cognition with motivation and affect in order to fulfill biological needs in relation to the conditions at the time; these functions depend upon medial frontal and orbitofrontal areas. They are believed to be phylogenetically older and perhaps more primitive EFs, but they nevertheless remain essential to successful, autonomous adaptation [11]. These concepts are very similar to the concepts of “cold” and “hot” EF, which are dependent upon the functions of the cognitively based DLPFC and the more medial PFC cortices, respectively [12].

The neuroanatomical systems that are cited in support of these proposals are consistent with conceptualizations of the limbic system as consisting of a phylogenetically older orbitofrontal division and a newer hippocampal division [13]. The phylogenetically older division makes executive decisions that are intuitive, based upon processes and “hunches” of which we are not consciously aware. Instrumental learning, in which the basal ganglia play such an important role, is clearly implicated in this system [14, 15]. The newer hippocampal division presumably provides the context in which decisions and plans are made on the basis of conscious control. This is the substrate for goal-

directed thinking, which is considered to be under the influence of conscious awareness. However, EF is not only associated with thinking but with “visceral” functions as well. This is a critical point. Cortico-centric models of behavior seem to assume that “intention” and “goal-directed” behaviors are primarily, if not solely, the products of deliberation and conscious thought that are mediated exclusively by the neocortex and specifically by the prefrontal lobes. However, as models of behavior evolve that integrate the role of subcortical structures in these processes, our understanding of “cognition” and “EF” is expanding to include the ways in which aspects of these functions operate outside of conscious awareness.

Serial-Order Processing, Conscious Cognitive Control, Executive Functions, and Continuous Sensorimotor Interaction

Action (or movement) and goal-directed behavior are inherent in the concepts and definitions of cognition and EF. Conscious cognitive control of action and goal-directed behavior have been emphasized in these conceptualizations, while functions that underlie human conscious and non-conscious processing have not been included. Were conscious control necessary for executive function, one would imagine that executive function would be unique to humans, but it is not. Other animals clearly demonstrate “EF” in their behavior. Non-human primates use tools. This means they plan, which in turn means they have some form of “EF” [16, 17]. In fact, Ramnani [18] has recently reviewed the prefrontal-cerebellar and posterior parietal-cerebellar connectional profiles in non-human primates, which appear to represent the anatomic underpinning for “EF.” This neuroanatomy includes many aspects of the circuitry that we propose supports EF, embodied cognition, and the influence of cerebellar control models in human sensorimotor learning. Additionally, other animals without language capability can imagine and compare different navigational pathways before embarking on them in practice, and they can select from certain short-term and long-term goals, while they also predict and avoid certain dangers [19].

Such findings portray that EF cannot possibly be unique to human conscious cognitive control and cannot be solely dependent upon declarative knowledge and language processes. So how do animals engage in these behavioral selections that are consistent with conceptualizations of EF as applied to humans? Pezzulo [20] has attempted to address this question theoretically by proposing that all knowledge for behavior, for all organisms, is derived from sensorimotor anticipation. His conceptualization is based upon three ideas. First, any organism's knowledge and representational ability is derived from *sensorimotor inter-*

action. This idea is similar to early stages of Piaget's developmental theory. In psychological, non-neuroscience literature, it is often referred to as “embodied cognition” [21, 22]. Second, he asserts that the reuse of sensorimotor learning mechanisms throughout the course of evolution is sufficient to account for the development of procedural and declarative knowledge. In this model, the anticipatory mechanisms that are used in the control and execution of behavior generate *procedural knowledge*. At the same time, the re-enactment of these situated behaviors and actions through mental simulation or imagination *can produce declarative knowledge*. Third, these functions or processes allow for internal manipulation that can generate “EF.” This is the result of imagining the results of prior activities, which he describes as *internalized situated action*.

Pezzulo's theoretical position is compelling, but it is not systematically superimposed upon a functional neuroanatomy. This paper will consider the neuroanatomic underpinnings of the ways in which sensorimotor interaction supports procedural and semantic, declarative knowledge. This viewpoint will provide biologic consistency along the phylogenetic scale in an attempt to understand “cognition” as action control or “EF.” The current paper will focus on the specific role of the cerebellum at the expense of critically examining the important roles played by other brain regions, which have been described in great detail elsewhere [23–26].

It has been estimated that much of what we do, perhaps 95% of an adult human's activity or behavior is routine and automatic, outside of voluntary conscious cognitive awareness [27–29]. These are things we do spontaneously, “without thinking,” simply because they need to be done. These behaviors are not merely due to faster processing as compared to controlled processing [30]. Instead, these automatic behaviors are efficient, economical, elegant, initiated without uncertainty or hesitation, and always adaptive in context and adjustable to contextual changes [31]. Such behaviors can be construed as executive functions. Their efficient, automatic quality demonstrates the significant role implicit processes play in EF. This point is critical to understanding our view of EF, its multifaceted nature, and its anatomic underpinnings.

Such automatic behaviors cannot possibly be accounted for by a model of cognitive control that depends upon serial-order processing. Within this traditional (and still popular and clinically applied) model, three processes are central: first, we perceive; next, we “think” to formulate or choose a response; last, we act. This processing model relies upon direct sensorimotor feedback, which is inevitably delayed by numerous factors, including the time necessary for processing sensory information, and the delay for transmission of motor commands from the brain to the muscles [32, 33]. While some behaviors are generated this

way, this means of processing is too time and resource-consuming to account for how smoothly and quickly people are generally able to coordinate and control their bodies and objects within the external world. Seminal papers by Cisek and Kalaska, Shadlen and Movshon, and Singer review neurobiologic data from various disciplines and conclude there is little evidence to support a perception-cognition-action model as a phylogenetically conserved and primary mode of adaptation [34–36].

This consciously driven, top down model's insufficiency for explaining so many of our adaptive behaviors points to the need for an alternate model. A more implicit, bottom-up model that emphasizes the role of subcortical brain structures (e.g., the “bottom” in “bottom up”) and is based upon continuous sensorimotor interaction with the environment fills this need. Such a model provides phylogenetic and biologic continuity across species, in most of whom the brain clearly did not evolve for the primary purpose of cognition or “thinking” [37]. Instead, the brain evolved to meet changing and emerging demands for survival, in the context of continuous interaction with the environment. Therefore, there must have been considerable evolutionary pressure to develop the ability for *anticipation* to guide the physical actions necessary for survival. Evolutionary processes favored the development of predictive or “anticipatory,” and simulative or “imaginative” mechanisms for the purpose of *action control* and not for cognition per se. Both procedural (skill) knowledge and declarative (semantic) knowledge can thus be explained and understood in terms of continuous “on-line” sensorimotor anticipation and “off-line” simulation of (imagination or *thinking about*) potential action. Animals that possessed only mechanisms that allowed them to adjust to behavior as circumstances unfolded could not survive and adapt because their behavior would be limited to *reactive context processing in the moment*, in the here-and now. To survive, they would also have to develop mechanisms for *proactive context processing* to serve *intentional control of goal-directed behavior*. These processes lay at the base and heart of EF.

Bloedel and Bracha posit that there is no duality between motor and “cognitive” functions [38], and we agree. Without movement or action, there is no need for thought. We (and numerous others) argue that for the brain, the primary substantive difference between planning an activity and engaging in its motor counterpart is the *actual execution of that behavior* [4, 39–41]. For example, there is no inherent difference between planning how to rearrange the furniture in one's living room and actually doing it. Thought manipulation controls action. Thought evolved *from* the motor system as a mechanism to facilitate the development of motor programming and action control.

In the following sections of this paper, we emphasize that the cerebellum plays a critical role in sensorimotor

behavior. As such, it lays at the foundation of executive function as defined as an organism's acting independently in its own best interest as a whole, for the purpose of survival [9]. We argue that the cerebellum appears to train frontal systems about how to execute motor behavior in various settings and contexts by anticipating outcomes or sensory/knowledge feedback. Therefore, significant frontal lobe “knowledge” is situated in a sensorimotor format. We promote an active rather than passive position for the cerebellum due to the role the cerebellum plays in instructing or teaching the frontal lobes how to predict (anticipate) by “thinking” about movement outcomes [42].

A phylogenetic model portrays new structures and functions emerging in the course of evolution by building onto existing structures [43]. As the cerebellum developed in animals long before frontal cortex expanded, a role for the cerebellum in the function of frontal systems is inherent. Frontal systems have historically been considered those that support the ability to plan and think ahead, and in this way are considered to support abstract thought. We argue that these higher-order abstract thinking skills comprise an extension of the motor control system that is situated in basic anticipatory control mechanisms. We posit that cerebro-cerebellar functions play a critical role in *allowing* frontal systems to plan, to think ahead, and to abstract. In order to lay the foundation for this position, we first summarize a model of adaptation based upon continual sensorimotor interaction with the environment.

Sensorimotor Interaction with the Environment

The vertebrate brain's functional architecture evolved to meet the needs of interactive behavior. This evolutionary trend was strongly conserved throughout the course of phylogeny. As summarized by Cisek and Kalaska and others, our perceptions of the world are not the result of a serial processing or reconstruction processes that use sensory information to build or develop an internal representation of the external world. Instead, neural processing is continuous, while the salient properties of objects, such as what they look like and what they are used for, are represented in the same sensory and motor brain circuits that were activated when the information about that object was initially acquired [44–48]. These neuroanatomic “facts” can be referred to as a “cerebral cortical model,” consisting of body and motor schemas as described by Ito, or praxicons and innervatory programs as described by Heilman and Rothi [49, 50]. Cognitive psychologists might refer to this as “embodied cognition.” Within this information processing model, the ventral “what” pathway and the dorsal “where” pathway have additional functions that go well beyond the realm of object recognition and object location, respectively.

Processing within the parietal cortex dorsal stream and reciprocally connected premotor regions is primarily concerned with pragmatic, practical representations of the opportunities for action that those objects afford or offer [51–53]. This dorsal pathway registers not only where something is, but also “how to do” something. How to grasp, for example, might be determined by an object's shape, size, and movement. This region plays a critical role in procedural memory for action concepts. The posterior parietal cortex (both superior and inferior regions) and its reciprocal connections with premotor areas and the frontal eye fields transform the dorsal pathway into a visual control area for actions. The parietal cortex focuses upon spatial information because this data is critical for specifying the parameters of ongoing and potential actions. It operates within egocentric or “reaching” space [54]. (We will return to these critically important points about the dorsal information processing stream in subsequent sections.)

The ventral information processing stream registers “what” the individual is seeing and information about “what” that object is used for, which is essentially a *semantic* function that can operate in allocentric space. This pathway operates relatively slowly in contrast to the quickly responding dorsal pathway, since the ventral pathway does not primarily serve an “action” purpose [54]. However, because it specifies the reward value of objects (to be described below) it plays an important role in behavioral praxis. The dorsal and ventral pathways have callosal connections and project to the hippocampal formation for memory storage. This overlap allows the systems to operate in a complementary fashion. These two systems are believed to be integrated by the age of 9 months, which has obvious relevance for theories of pediatric neurodevelopment [55].

The ventral pathway provides information for action or behavioral selection by biasing potential actions with information about reward value associated with object identity. This behavioral biasing (which is essentially a form of anticipating or predicting the outcome of a behavior) includes information from basal ganglia reward centers and regions of the prefrontal cortex that predict reward outcomes [56–59]. Several potential actions are available in most situations. Accordingly, these potential activities, choices or decisions are reflected over large portions of the cerebral cortex. *Decision making is thus not strictly localized within the prefrontal cortex.* Instead, it is found within the same sensorimotor circuits that are responsible for processing sensory information, associating information with reward value, and programming and executing the associated actions. This organizational profile allows individuals to engage in a level of adaptive functioning that is characterized by automatic behaviors alternating with episodes of higher-order control. In an

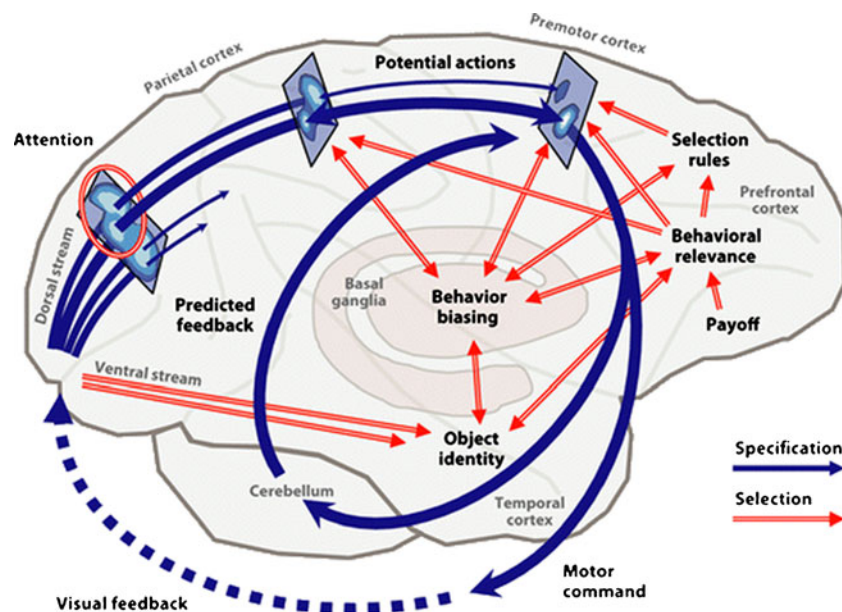
unpredictable environment, the adaptive value of such flexibility cannot be overemphasized.

Within this model, “cognition” is not separate from sensorimotor control [34, 60]. In fact, sensorimotor control is primary and paramount, while conscious cognitive control becomes subordinate. The final “decision,” or the selected action/behavior, is an outgrowth of cortical-basal ganglia interactions. While behaviors result in overt feedback from the environment, action is undertaken in concert with anticipated or predicted feedback through the cerebellum, which appropriately adjusts the behavior through context-response linkage [61]. This model emphasizes sensorimotor interaction and the brain's inherent capacities to predict and anticipate. This allows behavior to occur in “real time” in a manner that is not easily explained through a static “perception-cognition-action” model. As Kinsbourne and Jordan note, anticipation is continuous and

ongoing; the ability to anticipate is an inherent design characteristic of the brain [62]. This sensorimotor paradigm is illustrated in Fig. 1 (For a comprehensive review of this model, see Cisek and Kalaska [34]). The remainder of our discussion focuses upon the specific role of the cerebellum within this model of adaptation.

The Cerebellar Anatomic Underpinning for Sensorimotor Interaction and EF

Cerebellar contributions to motor and non-motor behavior are made possible through the cerebro-cerebellar circuitry system. The importance of this system can be inferred by tracking its evolutionary development. Smaers, Steele, and Zilles examined the cortico-cerebellar system in 19 anthropoid species spanning across 35 million years of divergent



Cisek P, Kalaska JF. 2010.

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Fig. 1 This diagram represents a sensorimotor interaction paradigm for visually guided movement, illustrating interactions between the cortex, basal ganglia, and cerebellum. The dorsal stream, which consists of the parietal cortex and reciprocal connections with premotor regions, is concerned with practical representations or programs for a situation's action opportunities. The dark blue arrows represent action specification, which comprises the parameters for performing the behavior. This processing originates in the occipital lobes and proceeds in a rightward direction through the dorsal pathway. This dorsal pathway registers not only where something is, but also “how to do” something—such as how to grasp—as might be determined by an object's shape, size, and movement. This region plays a critical role in the procedural memory for action concepts. The ventral stream serves object identity (connections between the ventral

and dorsal stream are not directly illustrated; see text). The polygons represent three potential actions (neural populations) along the dorsal route. Competition for action choice or selection is biased by “reward center” input from the basal ganglia to parietal, temporal, and prefrontal neocortical regions. Reciprocal red arrows represent this evaluative biasing process. Therefore, action choices are represented over large regions of cerebral cortex and subcortical regions. The action that is selected depends upon the behavior with the strongest bias. The cerebellum (blue and dotted blue arrows connecting the cerebellum with the cortex in this drawing) adjusts behavior on the basis of internal anticipated or predictive feedback that are inherent in cerebellar control models, which are not illustrated in this diagram and are the subject of the remainder of this paper

evolution. They concluded that neural systems involving profuse cortico-cerebellar connections composed a major factor in the evolution of anthropoid brain organization [63]. In humans, nearly every region of the cerebral cortex (with the exception of the inferotemporal cortex) has reciprocal, segregated connections with the cerebellum (for a review, see Schmahmann and Pandya [64]). While the neocortex has expanded during the course of phylogeny, the cerebellum has also demonstrated a three- to fourfold expansion in sapiens compared to other species [65]. Along with the selective expansion of the cerebellar cortex [66], the dentate nucleus of the cerebellum has dramatically increased in size, and reciprocal connections between the prefrontal cortex and the dentate nucleus have been identified in humans that are not present in other species [67–69]. There is compelling neuroanatomic evidence for a cerebellar role in a variety of processes, including attention, executive functioning, learning and memory, visuo-spatial regulation, language, and affective-behavioral modulation [70–72]. Balsters and Ramnani [73] have also provided supportive evidence for the view that prefrontal projecting areas of the cerebellar cortex process information that is of a purely abstract nature.

While the reciprocal, segregated, closed loop circuitry profile represents the major architectural unit of cerebro-cerebellar interactions, the uniformity of the intrinsic cellular organization of the cerebellum implies uniformity in information processing by the cerebellum, regardless of the area in the cerebral cortex from which the information is received [74]. In other words, the cerebellum performs the same operation on information regardless of its source. This is consistent with Ito's well-recognized proposal that for the cerebellum, movement and thought are equivalent; the control and manipulation of thought content is no different from the control and manipulation of body limbs in problem solving [4]. Once a movement, perception, or thought is “coded” within the neural circuitry of the cerebellum, the input is manipulated in an identical way. The simplistic idea that equates advancement of cognitive skill with neocortical expansion must be revisited in consideration of the neocortex's and cerebellum's coordinated expansion as a *functional ensemble or network* [75].

Cerebellar Control Models

As referenced above in a previous section, direct cortical sensory feedback processes operate too slowly for us to generate effective behaviors in “real time” [33, 76]. Therefore, brain mechanisms have evolved that allow the organism to predict or anticipate sensorimotor feedback in order to generate rapid, automatic, adaptive behaviors. Within the cerebellum, these mechanisms are referred to as

internal models [77]. The cerebellum constructs two forms of internal models, namely, a forward model and an inverse model. Their initial development is made possible through the “mossy fiber” cerebro-cerebellar circuitry system, which essentially allows the cerebellum to copy the contents of cortical, conscious working memory and in so doing, allows the cerebellum to “know” what the cerebral cortex wants to do.

For an adult learning a new task, the first step of learning proceeds consciously and involves neural signals from the premotor and primary motor cortices and the temporo-parietal cortex (Ito, page 184) [49]. Initial learning trials rely on external sensory feedback. As learning proceeds, the parietal cortex acquires a “body schema” and a “motor schema” necessary for the task. In Heilman's terminology, these schema are referred to as praxicons and innervatory programs, respectively [50]. The cerebellum copies these schemata in the formation of forward and inverse models.

Therefore, a cerebellar internal model consists of all of the dynamic sensory and motor processes necessary to perform a movement or behavior. This internal model is formed and adjusted as a movement is repeated. Behavioral refinement occurs because the cerebellar olivary system detects errors or imprecision in performance and allows for correction in predicted feedback and adjustment in movement. As a result, the internal forward model enables the brain to execute the movement with increasing precision, absent the need to refer to feedback from the moving body part. The cerebellum learns through practice to perform operations faster and more accurately, which explains how a person is able to move more skillfully and automatically after repeated practice [42].

In this way, a forward model can be considered a predictor of the consequences or outcomes of motor commands, which allows the behavior to become increasingly precise and automatic and allow it increasingly to be executed by processes outside of conscious awareness. The feedback limb of cerebro-cerebellar circuitry projects the most efficient behavior to motor regions of the cortex, allowing the cortex to store the most efficient representation of the behavior [26, 78, 79]. In other words, the cortex “stores” the actual procedural memory, having been “taught” or instructed by the cerebellar model.

When the behavior is automatic, one way to release it is through a voluntary motor command. But an individual can become so skillful and can acquire such expertise that he or she no longer needs to be conscious of the intention to initiate a movement. In a professional basketball or soccer game, the participants engage in multiple rapid, precise, creative movement sequences, each aspect of which they never could have practiced for each specific context in which they are generated. After the game, when the athlete watches a recording of the competition, he/she recalls little

or nothing about how the artistic movements were executed, and may not even remember the movements themselves. This implies that they were performed automatically, without conscious awareness. These movements occur creatively, “on the fly” and “on-line” as the situation develops and unfolds, absent the need for conscious direction. While aspects of these behavioral sequences have been interpreted as a combination of forward models, cerebellum inverse control models also appear to be necessary in the development of higher levels of skill automatization [80].

Inverse cerebellar models transform intended actions or goals into motor commands unconsciously, in order to reach those goals [31]. In other words, inverse models generate motor commands, helping, or even by-passing the primary motor cortex [49]. At the risk of oversimplification, a forward model can be understood as a *predictor*. An inverse model can be understood as a *controller*. (While a comprehensive review of cerebellar forward and inverse control models is beyond the scope of this paper, the reader is referred to Ito 2005 and 2011; and Kawato et al. 1987 for additional information). In following sections, we will address how cerebellar control models are acquired and localized within the brain, how these models are represented within specific cerebellar modules, and how switching from one control model to another without conscious awareness is necessary to achieve ongoing sensorimotor adaptation. This process represents an anatomic underpinning for concepts such as EF and ‘embodied cognition.’ These concepts, which directly link movement to thought, will provide the foundation for understanding adult behavior as well as pediatric neurodevelopment.

Features and Characteristics of Control Models

As is the case for the cortex, the human cerebellum maintains a functional topography, so that different cerebellar regions or zones contribute to different behaviors [81–84]. Functions are represented asymmetrically [85]. The cerebellum is generally organized along anterior–posterior and medial–lateral gradients. Because the prefrontal regions from which cerebellar circuits originate are involved in cognitive functioning and in movement, the outputs of these circuits provide the cerebellum with the anatomical substrate to influence the control of both [70, 86]. Motor information is primarily represented in the anterior lobes, while cognitive information is represented in the posterior and inferior lobes. Limbic information is represented medially, and cognitive information processing is represented laterally. The deep cerebellar nuclei, and specifically the dentate nucleus, also appear to be topographically organized. Dum and Strick (2003) have

proposed a topographic organization within the dentate nucleus of the monkey, and fMRI data demonstrate that the human dentate nucleus is also subdivided into a rostral and more dorsal motor domain and a ventrocaudal non-motor domain [87–89]. These data are particularly significant in relationship to topographically represented and modularly organized cerebellar control models.

Control models have primarily been investigated through studies of tool use. Tool use has a prominent and lengthy history in the anthropologic and phylogenetic study of primates, including sapiens, primarily because levels of cognitive development are reflected by the relative sophistication in development and application of tools [90–93]. Tools can be simple or extremely complex. The skillful manipulation of tools can be considered as extensions of the limbs, therefore reflecting action control. The tools we use might even be considered as newly added parts of the body. The ability to make tools implies ‘EF’ in terms of planning, the ‘off-line’ simulation or imagining the materials necessary to construct tools, the sequential processing necessary for tool assembly, and the motor dexterity required for tool construction and eventual use or application. Tool use requires goal directed action in the service of realizing intentions. We all use tools today, ranging from ‘mechanical’ tools, to writing implements, silverware, bicycles, automobiles, wheelchairs and even crutches, to modern technologies such as computers and “smart phones.” Our adaptation is dependent on our ability to use tools effectively.

Complex tool use requires *semantic/declarative knowledge* about familiar tools and their uses, as well as the *procedural skills* we acquire that are necessary to perform the proper actions with these tools. At the cortical level, these requirements depend upon functionally specialized networks involving temporal, parietal, and frontal areas within the left cerebral hemisphere, (which we described as the dorsal information processing pathway) [94]. At the most basic level, according to functional imaging data, the temporal cortex supports tool identification, while the parietal–frontal mechanisms support tool use skills. While Krienen and Buckner recently identified four separate frontal–cerebellar circuits, of particular interest were the additional findings that two posterior regions of the lateral cerebellum (regions that are characterized by secondary sensorimotor functions of the cerebellum) also projected to lateral parietal and temporal lobe regions [95]. Schmahmann and Pandya have previously identified reciprocal superior and inferior parietal and superior temporal cerebro-cerebellar connections as well [64]. This establishes a functional ensemble or network that can be considered necessary to support rapid and skillful tool use and manipulation.

Realizing intentions and reaching goals accurately, precisely, rapidly and flexibly requires the brain to learn how to control its action on external objects (tools) and to *predict or anticipate the consequences* of this control. These processes require us to mimic the input–output properties of our own bodies as well as the properties of other objects. In other words, they require us to anticipate sensorimotor feedback. These processes define the characteristics of cerebellar control models. The above described circuitry establishes a framework within which these models operate for skilled tool use.

A variety of fMRI studies have focused upon cerebellar activity when human subjects were required to learn to use a novel tool. Many of these studies have been performed and/or summarized by Imamizu and Kawato [31, 32, 96]. These studies have consistently demonstrated significant activity in the lateral cerebellum after learning occurs. It has been concluded that this region of the cerebellum is at least one of the areas where internal control models that represent the sensorimotor properties of controlled objects are acquired. We believe this finding may be of additional significance because it implies that this region is involved in the synthesis of procedural with declarative information. The synthesis of procedural with declarative information, in fact, may be an additional property of cerebellar control models that should be articulated, particularly in view of the manner in which control models are believed to develop (see above). This issue is clearly relevant to further conceptualizing the cerebellum's role in thinking (see Ito [42, 49]; Vandervort et al. [174]; Koziol et al. [3]). When we think during problem solving, we are usually referring to declarative information.

While the modular architecture of the phylogenetically older parts of the cerebellum is known, Imamizu and colleagues investigated whether or not a comparable modularity exists in the lateral cerebellum for cognitive functions [97]. Using fMRI after subjects intensively learned to manipulate two novel tools, they found that lateral and posterior cerebellar activation for the two different tools was spatially segregated, with less than 10% overlap. They also found that subjects could easily switch between using these two novel tools. They interpreted these findings as reflecting modularity within the lateral posterior cerebellum for two different cognitive functions. Higuchi, Imamizu, and Kawato assessed cerebellar activation when subjects used sixteen very common tools (such as scissors, chopsticks, and a hammer) with the assumption that use of these instruments was automatic [98]. They compared this to cerebellar activation when the subjects only mentally imagined using these same tools without actual hand movements. Activation during actual tool use was primarily located in the anterior lobe of the cerebellum. By contrast, activation during imaginary tool

use was localized laterally, in the posterior lobe of the cerebellum. For each tool in the imaginary condition, they also measured the distance of the area of activation from the fourth ventricle and found that imagined tool use was represented in various different posterior lateral areas. They interpreted anterior lobe activation as reflecting the sensorimotor activity of the limb muscles, while they interpreted activation within the various regions of the posterior lobes as reflecting internal models for tool use.

The results imply that internal models for the skillful use of common tools are organized in a modular fashion, with different regions of the lateral cerebellum contributing to the use of different tools, and they imply that purposive, “cognitive” information about objects is modularly represented within the cerebellum. As noted by Ito, it is generally accepted that the operations and “events of the cerebellum are not reflected in consciousness, in which the cerebral cortex has been generally involved” (page 101) [77]. These findings thus also imply that this information is outside of conscious awareness. In our view, this modular organization has implications for understanding the neuroanatomy of embodied cognition, which will be discussed in a following section.

Rapid and efficient sensorimotor interaction with the environment is an inherent requirement for successful adaptation. This implies that humans can switch from one internal model to another based upon contextual information. The cerebellum links a behavioral context to a motor response [61]. This is one of the inherent properties of a cerebellar control model. After practice, when the behavior is automated, the occurrence of the context can trigger the response. When context changes, behavior changes through interactions of forward and inverse models. However, not all behavioral switching is the same. Imamizu and Kawato have identified neural correlates of predictive and post-dictive switching mechanisms for internal models [99]. These identified switching mechanisms have somewhat different neuroanatomies, which has implications for practical behaviors.

Earlier, we described the functional neuroanatomy of the dorsal information processing stream and its significance in sensorimotor interaction. Activation in the dorsolateral prefrontal cortex, the insula, the anterior aspects of the intra-parietal regions, and the lateral cerebellum are related to the switching of internal models [100]. Internal models play an important role in switching mechanisms within the parietal and cerebellar regions. Two types of information appear to be critical for switching internal models. One type, contextual information, can be perceived before movement execution. The other type, information about the difference between actual and predicted sensorimotor feedback, is computed either during or after movement execution. Contextual data, which is essentially information

known beforehand, allows for predictive switching; this recruits activation within the superior parietal lobule. However, when switching is dependent upon prediction error for postdictive switching, activation is observed within the inferior parietal lobe and prefrontal cortex. In these ways, there are regional differences in the neural substrates between predictive and postdictive internal model switching mechanisms at the level of frontal–parietal interactions in combination with cortico-pontine cerebro-cerebellar circuitry [31].

Dias-Ferreria, Sousa, and Costa reviewed studies that identify ways in which the frontal cortices are connected to the olivary system and serve as additional, alternative pathways to the well known cortico-pontine projection system [64, 67, 101]. It has been proposed that these fronto-cerebellar (olivary system) connections are involved in switching from voluntary to completely automatized behaviors during skill learning. These connections additionally provide automatic sensorimotor surveillance during the performance of actions or behavioral sequences in an increasingly precise and accurate manner. These regions have all been implicated in higher-order functions requiring stimulus-outcome encoding and automation of recurrent behaviors, while they also provide additional circuitries through which control models can use stimulus-response contextual coupling to initiate automatized behavior.

These switching mechanisms have practical implications to the degree that they influence behavioral adjustment speed and the ability to make transitions in a constantly changing environment. In this way, these mechanisms would appear to be related to the “executive control” of behavior. These switching mechanisms are also essential to our initial description of a behavioral model based upon ongoing sensorimotor interaction with the environment. Similarly, these switching mechanisms have implications for pathological behaviors. For example, parents of children with neurodevelopmental disorders often describe their offspring (children and young adult) as having difficulties in making transitions. These children rely on routine, often to the extent of becoming “oppositional.” This presenting problem also correlates with aspects of the recently identified cerebro-cerebellar circuitry involved in different presentations of Attention Deficit Hyperactivity Disorder [102, 103]. This “switching” circuitry may be dysfunctional in children with this described behavioral rigidity.

Embodied Cognition and the Cerebellum

A school of thought in cognitive psychology focuses upon the concept of “embodied cognition,” which seeks to place cognition within a sensorimotor context. However, while this concept of embodiment has become increasingly

popular, there is limited agreement on what the term “embodied cognition” exactly means and to what extent “embodiment” includes sensorimotor versus higher level cognitive function. Svensson and Ziemke [104] argue that the key to understanding the embodiment of cognition is the sharing of neural mechanisms between sensorimotor processes and higher-level cognitive processes. However, just what exactly is a “higher-level” cognitive process? As Saling and Phillips [30] have pointed out, and we agree, automatic behaviors are efficient and not mindless. They are essential to “executive functioning” in that they serve the best interest of the organism as a whole for the purpose of survival, and yet they are not typically considered “higher-level” processes.

Similarly, sensorimotor and procedural learning systems and “higher level cognitive” learning and memory systems have traditionally been understood as supported by distinct, separate neuroanatomies involving the neostriatal system and the medial temporal lobe (hippocampal) system, respectively. While the brain's memory systems operate in parallel to support behavior, how these procedural and declarative memory systems interact is not fully known and contradictory findings have been reported [105, 106]. However, when considering the role of interactions of learning and memory systems in embodied cognition, the computational model originally proposed by Doya is of critical significance [107]. With respect to a “global architecture” of ongoing adaptive behavior, the “supervised” learning modules (internal models) of the cerebellum are reciprocally connected with body and movement schemas stored in parietal and frontal cortices (cerebro-cortical models). The basal ganglia's instrumental learning system, essentially a reinforcement-based learning module, functions to evaluate the given state/situation while selecting an action, stored in the cortex, based upon the outcome valence of that evaluation.

Doya's computational work originally conceptualized the declarative/episodic “unsupervised” learning modules of the cerebral cortex as the medium for representing the conditions of the external world as well as the internal context of the individual. The neocortex was characterized as providing the common representational basis for the cerebellum and the basal ganglia “between which there are no direct anatomical connections” (page 966). Nearly the entire neocortex projects to the neostriatum (with the exception of the posterior regions of the occipital lobes), while the cortex similarly projects to the cerebellum (with the exception of the inferior temporal cortex). While it is certainly true that this organizational profile ensures that the cerebral cortex, basal ganglia, and cerebellum are all working with the same data or information, it is now known that *the basal ganglia and the cerebellum are reciprocally connected*.

The cerebellar dentate nucleus projects directly to the striatum, which is the primary input region of the basal ganglia [108]. The subthalamic nucleus also projects to the cerebellar cortex [109]. Therefore, the basal ganglia and the cerebellum communicate with each other. In addition, it has recently been demonstrated that the cerebellar dentate nucleus modulates dopamine release in the medial prefrontal cortex, which plays a role in behavioral outcome prediction and can influence the instrumental reinforcement learning within the basal ganglia [110]. It remains to be hypothesized and demonstrated how these pathways might function in the brain's learning system interactions. Our discussion is presented solely to better establish a theoretical groundwork or hardware for procedural and declarative memory interactions that are fundamental to definitions of “embodied cognition.”

Emulation/Simulation and Learning

It is well known that mental rehearsal or imagining the execution of a motor activity (which is essentially the off-line simulation of action that can be described through declarative recall) improves motor performance [111]. It is also documented that similar brain regions are recruited and activated during the performance of an activity and when imagining doing it [112]. Wadsworth and Kana [113] found that viewing tools seems to generate prehensions and anticipations about using them, and that the imagined action of using a tool mirrored brain responses underlying the functional use of the tool. The authors found that perception and contextual coupling along with imagination of tool use appeared to generate precursors to overt action control over tools. Similarly, it has been found that *planning the use of a tool activates a distributed network in the left hemisphere*. This network consists of the posterior superior temporal sulcus, and proximal regions of the middle and superior temporal gyri; inferior frontal and ventral premotor cortices; parietal areas including the anterior and posterior supramarginal gyrus; and the dorso-lateral prefrontal cortex. It should be noted that these regions include what has been described as the “mirror neuron” system [49, 114, 115]. With the exception of the left DLPFC, *adjacent and partially overlapping regions* of left parietal, frontal, and temporal cortex are *engaged during action execution*. This entire lateralized network comprises a functional ensemble for the interaction of semantic and motoric representations upon which meaningful skills depend [116]. (This complex network was previously illustrated in Fig. 1.) Declarative knowledge can thus facilitate procedural learning.

So, imagine that you wanted to learn how to use a new tool, and that until now the only experience you had using

the tool was through observation and your own practice via mental imagery. You would already “know” how to use the tool. Your observations and imagery actually represent semantic, declarative knowledge; this is information about gripping and moving/turning the tool that you could “declare” through putting in words. This information is retained in posterior cortices in interaction with the medial temporal lobe memory system. In order to improve your performance, you practice repetitively. You control “action” by incorporating “declarative knowledge” (which is what you know about the tool) to guide your behavior through “executive control.” With continued practice, your use of the tool improves. Your tool use eventually becomes rapid, flexible, and automatic. You have “learned” more about the input–output properties of the tool (its sensorimotor properties) and how it works (its dynamic properties) by actually using it. Your use of the tool has become automatic and you no longer think about the “executive control” guidance involved in first using the tool.

So what has occurred here? You have constructed and modified cerebellar and cortical internal control models, and the behavioral product includes both procedural and declarative information. Your procedural and declarative knowledge have been grounded in sensorimotor anticipation [20]. In this way, you have used declarative knowledge to develop and modify a “new” behavior. The improvement in your performance reveals that your unconscious “on-line” sensorimotor predictions were correct, while your semantic declarative knowledge about the tool and how to use it remain available for “off-line” simulation (or thought) that you could communicate or “declare” to another person. In this way, your overall knowledge of the tool has become an “embodied cognition” through the operations of control models. The cerebellar control model allows for the automatic, nonconscious application of tool use knowledge, while declarative, semantic, cortically represented information about the tool's use remains available for “off-line” simulation and planning. This interaction between procedural and declarative/semantic memory systems is at the heart of “embodied cognition.” To the extent that cerebellar control models assist in the development of procedural learning, the cerebellum would be involved in “embodied cognition,” as is suggested by the tool use studies by Imamizu, et al. referenced above.

Our example illustrates how *unconscious cognition* can guide “automatic” EF behavior to the extent that use of the tool is adaptive to the situation and serves the individual's best interests at the time. We believe this viewpoint challenges traditional “perception-cognition-action” behavioral control paradigms while it allows for the concept that unconscious cognition guides adaptive executive function. However, the theoretical underpinning of our example has not yet been demonstrated in an evidentiary way and

warrants investigation at an experimental level. Further, while our example might “work” to explain adult-level “embodied cognition,” at first glance, the proposal may be problematic for the pediatric population, which is the topic for discussion below.

Pediatric Neurodevelopment

Humans are not born with well-developed sensory and motor systems, nor are they born with well-developed medial temporal lobe memory systems upon which declarative (semantic and episodic) memories depend. This is illustrated by the phenomenon of “infantile amnesia,” which refers to the fact that we are unable consciously to recollect events or experiences from the first 2 to 3 years of our lives [117]. The phenomenon of “childhood amnesia” refers to the period from 3 to 5 years in which more event (episodic) memories are accessible to adults, but these memories are lacking in specific detail and center around global feelings of familiarity and a few facts [118]. Infantile and childhood amnesia are not simply manifestations of hippocampal and/or temporal lobe immaturity. Rather, functional immaturity of the association and prefrontal areas of the neocortex represent the main limiting factor [119]. Semantic memory (memory for facts) and episodic memory (memory for events/experiences of one's life) are developmentally dissociable. Raj and Bell [120] note that children can acquire semantic information as early as the first year of life, demonstrated by increasing vocabulary and language skills, while their episodic memory system, which binds facts, events, and experiences and is more dependent upon prefrontal cortex, develops later. Hayne and Imuta conclude that by the age of 3 years, children exhibit rudimentary episodic memory skills. The semantic memory system develops first, which appears to provide structure and meaning to the episodic memory system. Similarly, procedural memory systems are functionally “on-line” before declarative memory systems, while the two systems (declarative and procedural) are developmentally dissociable and follow different developmental trajectories [119]. We consider the how these features of child functioning relate to information acquisition below.

The Development of Motor Skills and EF

Over the past decade or so, considerable interest has emerged concerning the relationship between motor skill development and the subsequent development of cognition, and particularly executive function. In infancy, sucking skills predict neurodevelopmental outcomes; babies who exhibit poor suck coordination are likely to experience

complex motor and cognitive delays later [121]. Suck, feeding, and the production of speech and language are encoded and modified by overlapping neural networks of cortical, subcortical, and brainstem regions that support “executive control” later. Piek and Dawson et al. [122] have demonstrated a strong relationship between early gross motor problems and the later development of particular EF deficits in processing speed and working memory (as assessed by the WISC-IV) in school-aged children. In another study, Westendorp et al. [123] compared 7- to 12-year-old children with learning disabilities to age-matched normal controls on measures of locomotor skills and object-control skills as well as reading and mathematics tasks. Children with learning disabilities performed more poorly on all motor tasks. Additionally, a relationship was observed between reading and locomotor skills and between mathematics and object control skills. A larger lag in specific learning skills was accompanied by poorer specific motor skill scores. Many investigators have been puzzled by this apparent link between early motor and later cognitive, EF development. Why does motor development predict the development of executive cognitive ability and academic skills?

We are well aware that there can be considerable variability in neuromotor development from kindergarten through adolescence [124]. Nevertheless, we believe that understanding the relationship between motor development and EF is deceptively simple. The brain did not evolve for the specific or explicit purpose of developing cognition. While the clinical scientific focus has been upon higher-order cognitive phenomena, the fact that perceptual and motor capacities developed *first*, and dramatically, as we have ascended the phylogenetic scale has been ignored.

We were not born to think. We were born to move. Human creative ideas are nothing in the absence of the manual dexterity that allows tools to be made, complex architecture to be constructed, art to be created, and instruments to be played. Communication of complex information and ideas is accomplished through abilities that require complex motor skills such as gesture, speech, writing, or typing [125]. Humans can make precise, highly differentiated movements, can combine individual movements into high-order sequences that can be simulated or thought about, and can execute movements and their unique combinations rapidly and automatically, even without conscious thought. It is no biologic accident that the body parts with the greatest sensory sensitivity, motor activity, and dexterity have the largest regions of representation within the brain [126].

The fundamental purpose of an organism and a person is to survive through environmental interaction. This requires ongoing sensorimotor learning within a changing environment. Movements are not random. They are organized and

purposeful, even during infancy and childhood [127, 128]. Lockman [129] has characterized tool use as a continuous developmental achievement that is rooted in the perception-action routines that infants employ to gain information about their environments. Infant pointing is meaningful movement. Tomasello, Carpenter, and Liszkowski have demonstrated that when 12-month-old infants point for an adult, they are in some sense trying to influence the adult's mental state [130]. By 3 years of age, toddlers do not indiscriminately imitate actions with a tool. Rather, they selectively reproduce actions that have a desired causal effect [131]. Therefore, it is essential to consider why a movement is made, in addition to how movements are planned, and how a movement anticipates what is going to happen next. These features of movement require EF, if only on a rudimentary level.

The development of goal-directed action management *required* development of anticipatory control mechanisms in order to predict the sensorimotor outcomes of action in “real time” as situations develop. This resulted in the development of mechanisms for “on-line” sensorimotor anticipation in order to adjust to the environment “on the fly” and “off-line” simulations of possible potential actions in order to generate purposive, intentional, goal-directed behaviors in the future [52]. These “off-line” simulations include “executive function,” which is essentially an extension of the motor control system. Therefore, movements in the normally developing child should never be considered random; they are always purposive and accomplish goals.

In this way, motor development and EF are inexorably and inextricably linked because deviations/abnormalities in motor development represent an early failure in “action control” which is essentially an early form of “EF.” Instability in the development of the motor system impacts upon the ability to develop “cognitive control” over motor systems. The motor system *allows* cognition to evolve in order to develop simulative, “off-line,” cognitive control capacities. We believe that deficits within the motor system, as might be manifest by abnormalities or inconsistencies in motor development, generate (or at the very least, predict) developmental disorders. This is a viewpoint that is shared by many other researchers [127, 128, 132–134].

Within human development, we believe these control mechanisms proceed in a predictable way, and they allow for overlap as the behavioral repertoire expands. First, there is movement (even if only manifest by the seemingly simple yet goal-directed suck reflex). Next, movement and cognition are coincident. As we move, we detect and observe movements of objects, and in this way, we discover objects and learn about their properties. Subsequently, movement and cognition coexist. We might move to obtain something we perceive or move in response to something

we perceive, or we might move to acquire a new skill, such as learning to dress by using buttons and zippers, learning to tie shoes, or learning to use silverware. Finally, cognition becomes subordinate to movement, as behavioral automaticity is achieved, and the “off-line” executive simulation of activity becomes necessary only for novel problem solving. In this way, we can directly link movement to thought, and can understand “EF” as an extension of the motor control system [3, 135, 136].

Movement Control in Childhood: Neuroanatomic Candidates

The brain regions and mechanisms controlling complex movement and “EF” in adults are in process of becoming well understood [26, 30–32, 39, 40, 137–141]. Development of movement programs is under the influence of frontal lobes (including the frontal eye fields) and posterior parietal interactions. Program execution is presumably the result of frontal–basal ganglia interactions. The superior temporal sulcus (STS) is recruited in detection and in certain types of movement guidance. The “EF” of “working memory” that guides new behavior appears to operate on the basis of a parallel cortico-basal ganglia interaction model, while the learning of procedures and their adaptation across contexts appears to be under the influence of the cerebellum.

Considerably less is known about the development of neuroanatomic control mechanisms and processes in children. A child slowly develops within an environment that demands ongoing sensorimotor interaction. Before infants master the ability to reach and grasp objects, they repeatedly try to move their hands to the objects, and they persist despite numerous failures. Children often try to walk very early, when they can locomote more efficiently by crawling [133]. While we fully appreciate that motivation is important in generating behavior, in these examples, there is no obvious “reward,” and in this regard, we currently have limited knowledge about how the reward system develops aside from the rewards that are linked to attachment mechanisms (the discussion of which is outside the scope of this paper) [142].

Despite the fact that *activity* is so central to child development, the cerebellum is rarely considered within the context of motor development. We know that the vestibulocerebellum is believed to be mature at the time of full-term birth, while studies of newborn babies and infants reveal that reciprocal cerebellar–vestibular interconnections are already fully myelinated [143, 144]. Cerebro-cerebellar circuitry very closely resembles adult circuitry during the course of development [145], while by the age of 4 years, ponto-cerebellar tracts attain a staining of adult type/

resemblance [146]. In addition, at birth, the cerebellar cortex exhibits its well-established architecture. All the Purkinje cells are present, as are the climbing fibers that synapse with the cell bodies [147]. Cerebellar adult volume can be achieved between the ages of 7 to 11 years, with peak size typically reached at the age of 11.3 years in females and 15.6 years in boys [145, 148]. Superior motor development in typically developing right-handed children is dependent upon the establishment of neocortical left-hemisphere dominance in intrinsic motor network connectivity. This includes frontal motor cortices, basal ganglia, and thalamic connections. Supplementary motor–anterior cerebellar connectivity is included in this circuitry profile [149].

The cerebellum is also important because cerebellar development is affected by premature birth. Premature birth is a common enough occurrence, and even relatively mild prematurity, defined within the range of 37 to 38 weeks can be associated with structural abnormalities within focal cerebellar brain regions [150]. There is an abundant clinical literature which demonstrates that preterm birth is associated with a high incidence of cognitive disorders [151, 152]. The cerebellum's growth and development are rapid during late gestation, but this growth is impeded by premature birth [153]. Very preterm birth, defined as less than 32 weeks gestation, is associated with three possible patterns of abnormality in cerebellar development. First, there can be volume reduction of the cerebellar hemispheres and a smaller vermis. Second, there can be volumetric cerebellar hemispheric reduction with an enlarged fourth ventricle and a deformed vermis. Third, there can be normal cerebellar shape but with extensive reduction in its dimensions [154]. These types of abnormalities have been associated with a variety of EF, cognitive, and motor difficulties [155–158]. These EF, action control deficits are often chronic [159, 160]. Therefore, it is clear that perturbations in cerebellum development can often result in “cognitive” deficits. These deficits, and their persistence, may result from the fact that preterm delivery disrupts the developmental program of the cerebellum [161].

Control Models in Children

Within this general context, it is possible to hypothesize how the cerebellum might develop internal control models, particularly with respect to tool use. Tools—such as silverware, which children must learn to use and master—can be considered “extensions of the limbs” that “enhance the efficiency with which skilled actions are performed” [162]. The use of silverware in children has obvious implications for the development of anticipatory control models, particularly since a child cannot “see” her mouth

while learning to use the tool (this process mimics the finger-to-nose test that requires a cerebellar control model; Ito [49], pg. 169). Tool use in children is heavily dependent upon dorsal information processing pathway development and integrity. The “visual control area for actions” consists of reciprocal premotor frontal-posterior parietal lobe connections, connections between the parietal lobe and the frontal eye fields, connections between the frontal eye fields and the cerebellum, and the connectional profiles of separate frontal-cerebellar circuits, including the motor circuit and the two circuits that associate segregated regions of the lateral cerebellum with lateral parietal and STS temporal lobe regions [54, 95, 163–165]. In our discussion, we again focus on the possible role of the cerebellum.

By the time children are 3 years old, most use an adult, radial clenched grip for silverware, with the thumb pointing towards the head of the tool, although before that time (and afterwards in some children), children experiment with a variety of grip patterns before they develop a grip preference [132]. Based upon imaging studies of tool use in adults, we would expect that the anterior region of the cerebellum would be one of the areas activated for silverware grip. The movements used for bringing food to the mouth using a spoon and using a fork are somewhat different, while the grip and movement of the knife, which is a tool use that is developed later, is different from movements required for the spoon and fork. Yet with repeated practice, as months and perhaps years go by, the normally developing child develops mastery, automaticity, and flexibility with all of these grips and related egocentric movements.

Based upon brain imaging investigations, we would predict that the characteristic movements required for each piece of silverware would be represented in proximally close, yet distinct regions of the modularly organized lateral posterior cerebellum [98]. If we extrapolate from the adult evidence, we would have little reason to suspect that the localization of silverware use would reorganize within the cerebellum once the use of these “tools” was acquired through the development of models (body schema, motor schema, and cerebellar internal control models).

We have used this example to illustrate several points. First, a complex and widespread network of brain regions would initially be necessary to acquire the behaviors. Second, because the frontal cortices and cerebellar regions to which they project develop relatively slowly (though they just about keep pace with each other) [166], we would expect these behaviors to develop relatively slowly, even though the dorsal and ventral streams are integrated by the age of 9 months [54]. Lastly, and most importantly, the example illustrates that *procedural learning* can lead to and facilitate the development of *declarative, semantic knowledge*.

Semantic memory, dependent upon the temporal and parietal lobes, frontal brain regions, and the basal ganglia, concerns knowledge that allows for the formation of categories, word meaning, and concepts [167, 168]. Language can be considered a semantic system. It is the “great categorizer” that allows us to bring meaning to our perceptions. Semantic categorization is an advantage because it allows information to be grouped conceptually, while similarities and differences can simultaneously be specified to allow these concepts to be manipulated and applied. For example, while we know that apples, bananas, strawberries, and oranges are conceptually similar because they are all fruits and can be substituted as nutrients, we also know the properties of these fruits are different. Generalization and specificity both guide eating behavior in relation to fruit, but it is also influenced by fruit preference (reward valence) and availability. This process is subserved by sensory neocortical regions, the prefrontal cortex, the medial temporal lobe memory system, and the basal ganglia and its dopaminergic reward system [167, 169, 170].

In our procedural learning example, the child learns how to use tools efficiently within the semantic category of silverware, while also acquiring the ideas that a spoon does not serve the functions of a fork; that a fork, because of its prongs, can never serve the function of a spoon; and that while a knife is used for spreading and/or cutting food, it can also be implemented for other functions outside of the category of silverware use. Silverware and dishware use are directly tied to the semantic, declarative category of food texture; a spoon is used for liquid, such as cereal or soup, which is served from a bowl; a fork is used for food with solid texture, which can be placed on a plate or in a bowl, while the size and texture of meat or fish often necessitates it be cut with a knife. A cup requires a different grip than does silverware, and even though the cup holds liquid, its content satisfies thirst, and not hunger; the category of liquid, which encompasses both soup and juice, belongs to the general semantic category of food, although these nutrients serve different internal needs. By the time a child is 2 to 3 years old, when association cortices start to mature for the purpose of storing semantic associations and when language begins to emerge, interaction with the environment leads to exposure to different objects and “tools” that are directly linked to separate and overlapping categories of semantic, declarative knowledge.

This grasp of categorical similarities and functional differences, which has been *acquired through sensorimotor anticipation inherent in the processes of eating and drinking*, is at the heart of declarative semantic knowledge. In other words, declarative, semantic knowledge, which is by definition available for “off-line” use (thinking and planning), has actually been obtained through, and is

grounded in, direct sensorimotor interaction with the environment. In this way, the “EF” of eating and drinking and the semantic conceptualizations acquired from participating in the activity all become “embodied cognitions.” They require the interaction of multiple brain networks within which the knowledge and behaviors are stored and later manipulated. These processes begin with the first movements of childhood and are continuous throughout development and adulthood.

While traditional theories of learning and memory typically recognize procedural and declarative memory systems as distinct, independent functions and processes, this sensorimotor learning model demonstrates that there is considerable overlap between them. Procedural and semantic knowledge are blended and become “embodied” as information is acquired through the brain's ability to gather knowledge on the basis of its anticipatory and predictive capacities. It is this procedural-declarative developmental learning interaction that makes semantic information available for “off-line” use in other cognitive processes, such as planning. The overlapping, widespread cortical network, which includes temporal and parietal and parietal–frontal regions, provides the underpinning to store this semantic, declarative information so it can be used for “off-line” conscious cognitive purposes. At the same time, the cerebellar control model allows for the application of the procedures for silverware used in our example, with “cognition” falling outside of conscious cognitive awareness. While traditional theories of learning and memory emphasize *differences* between procedural learning and semantic memory systems, a sensorimotor learning model not only respects these differences, but it also reveals *interactions* between these systems [52, 104]. The fact that recruitment *in essentially the same networks* is demonstrated in neuroimaging studies that assess perceptual/semantic tasks involving planning and executing activities related to tool use helps to illustrate the neuroanatomic underpinnings of “embodied cognition” [116].

Discussion

We have presented a model of behavior that supports a dual-tiered model of adaptation. This model is characterized by automatic behaviors that alternate with episodes of higher-order decision making and control. While most daily behaviors fall into the realm of automatic functioning with rapid “on-line” adjustments made through a process of sensorimotor anticipation, information remains available for “off-line” use and manipulation for the purpose of developing intentions, plans, and goals. This paradigm is derived from a behavioral model that requires ongoing interaction with the environment. From a neuroanatomic

perspective, this model is based upon interactive brain networks that involve differentiated regions of cortex along with subcortical structures.

We have limited our discussion by emphasizing the role of the cerebellum in only certain motor and non-motor processes. While cerebellar function can be interpreted within different schools of thought that emphasize its varying roles [171], we have focused upon a rapidly emerging literature that stresses the cerebellum's ability to construct internal models for the unconscious control of adaptive behaviors occurring in “real time.” These forward and inverse models control behavior and cognition on the basis of anticipation or prediction, as has been eloquently described by Ito [42]. We do not believe that the brain evolved for cognition *per se*; rather, the brain evolved for the control of action or movement. This phylogeny required mechanisms that could automate and adjust behavior on the basis of anticipated sensory feedback. At the same time, they could allow for the “off-line” manipulation of action control for the purpose of intentional, goal-directed behavior and novel problem solving for an individual interacting with an ever-changing environment that called for flexibility and innovative behaviors.

In describing the control of action, we have described the concept of “embodied cognition” which directly links movement to thought, and we have specified that “thought” may not necessarily be conscious in nature. For example, just as we typically “move” to accomplish goals without being consciously aware of the sensation of movement, we also “think” without being consciously aware of “thinking.” This is made possible through cerebellar internal control models. We have observed that this can be demonstrated in other species besides humans. Whether we see human thought as “abstract” in any particular circumstance depends upon our definition of abstract. From the brain's perspective, thinking about doing something, such as manipulating the necessary nuts, bolts, and other pieces in proper order to assemble a cabinet or bookcase, is not much different than performing the actual processes. This might be inferred from the imaging data we reported. As we have indicated, both the processes of mental manipulation and actual object assembly recruit many of the same brain regions.

As Ito has indicated, once a to-be-controlled object is coded within the cerebellum, movement, and thought become equivalent; the cerebellum will manipulate the input in an identical way [4]. This type of manipulation, in the absence of movement, is a form of abstract “thought.” We also recognize that prefrontal projecting areas of the cerebellar cortex process information that is of a purely “abstract” nature [73]. In our view, this reflects the modular organization of the cerebellum and the dentate nucleus to which its Purkinje cells project [89]. Throughout the course

of phylogeny, a critical role for the cerebellum has been to allow the brain to anticipate the outcome of sensorimotor behavior. As the neocortex, including the frontal and prefrontal lobes expanded in parallel with the cerebellum, the basic functions, processes, and interactions remained the same. The abstract thought of prefrontal cortices serve an extension of this system. The “data” stored and manipulated within the motor regions of the frontal lobes primarily consist of sensorimotor knowledge; the knowledge of the prefrontal cortex is based upon the manipulation of ideas. Just as the cerebellum informs motor regions about the most efficient way of executing behaviors, it instructs the prefrontal cortex how to manipulate ideas for problem solving. These brain regions do not function in isolation; they operate as a functional network or ensemble.

Just as certain cerebellar modules are organized to think about the sensory and movement properties of certain objects and to anticipate how movement will be associated with a predicted outcome, Crus I and Crus II (HVIIA) appear to be modularly specialized for abstract thinking. All thinking, or thought manipulation, includes the eventual participation in action control. This includes the abstract thinking required to compose this paper, which accomplished the action-based potential for communication. A key proposition is that the prefrontal cortex has no *inherent* ability to “think ahead” but instead, learns to do so through experience (personal communication from E. Goldberg, April, 2011). What the cerebellum does for movement, it does for thought—including abstract thought. During the course of development, the inherent properties, characteristics, and functions of the cerebellum instruct or teach the prefrontal cortex how to “think ahead,” which is at the heart of abstract thought. This process mimics how cerebellar control models instruct motor cortices to anticipate sensorimotor, behavioral outcomes.

While ontogeny recapitulates phylogeny, this entire developmental process occurs through a process of sensorimotor learning. Thought is characterized by anticipation and prediction. The cerebellum plays a role in driving the modulation of thought manipulation and speed and accuracy outcomes, and it plays a more general role in instructing the prefrontal cortex to expect, predict, or anticipate outcomes throughout the course of neurodevelopment. While the motor cortices “think” about movements, the prefrontal cortex “thinks” about “thoughts.” The forward-focused prefrontal cortices of this paper's authors, for example, worked hard as the authors manipulated the ideas necessary to develop these themes. The development and manipulation of these themes was grounded in the authors' *anticipation or prediction* of how the thought content would be interpreted by the reader.

The cerebellum is also a critical player in “EF,” whether this EF is an appropriate movement in “real time” or an appropriate, higher-order plan of action to be executed later. Moreover, understanding cerebellar contributions to abstract thought also help us understand how prefrontal–cerebellar interactions assist in solving novel problems, which forms the base of creativity and innovation. As Ito recently stated,

“It has been proposed that when a stimulus is presented in the realm of thoughts and ideas, it is maintained in the working memory, where it is compared with mental models stored in the temporoparietal cortex. Comparison is also made to cerebellar internal models, which have been copied from mental models and stored in the cerebellum. If a received stimulus matches a mental model or an internal model, the stimulus is considered at the level of conscious awareness to be familiar and the thought process is completed. If the stimulus is truly novel, however, existing models will not recognize the stimulus. Error signals are then generated that (1) suppress at the level of conscious awareness acceptance of the idea that the mental model is familiar, (2) activate the attentional system, which in turn activates the working memory system, which will then strengthen the search for stored mental and internal models, and (3) modify internal models in the cerebellum if errors continue to occur. Eventually, the stimulus will find a matching counterpart in the pools of mental models and internal models. ...The final process is an “aha” at the level of conscious awareness; that is, expression of the fact that a successful conversion has taken place. In other words, the original stimulus is no longer novel. These preceding processes and mechanisms may well be the basis for creativity and innovation (Ito 2011, pp197–198).” (This description also directly links movement to thought, emphasizing that what cerebellar models do for movement, they also do for thought).

We realize this paper has implications that go well beyond the scope of this manuscript. For example, although we have mentioned how observation might enhance learning, we have not examined how the “mirror neuron” system (which plays an important role in observational learning) might contribute to the acquisition of procedures and declarative, semantic concepts in other areas of functioning. We have not fully explored implications for language in particular, which would be a useful next step, particularly since Broca’s area 44 presumably evolved from—or is at least proximal to—what has been identified as a component of the frontal mirror neuron system. The evolution of tool use and language have much in common

from an anatomic point of view [90, 91, 172–174]. Ullman has presented a model of language functioning that includes dissociable procedural and declarative memory systems that are dependent upon the same or at least similar brain networks that subserve other functions, including those functions described in this paper [175, 176]. While the cerebellum’s role, with its forward and inverse models, has not been specifically investigated within Ullman’s “declarative/procedural” model of language, we suspect it is involved in anticipatory processes associated with automaticity.

Similarly, we have not specifically explored the clear implications for social cognition and “theory of mind.” Glenberg and Gallese [177] have hypothesized that the same premotor circuitry that controls action (adjacent to the mirror motor neuron system) instantiates the “off-line” simulation of the observed actions of other people. Gallese and colleagues have hypothesized that the ability to understand other people’s intentions relies primarily on the motor cognition that underlies one’s own personal capacity to act [178]. Motor acts form the essential framework or building blocks around which all activity is produced, perceived, and understood. Investigations of Autistic children reveal abnormal patterns of sensorimotor learning as well as impairment in the execution of “skilled” motor gestures, which very strongly correlates with impairment in social and communicative functions. According to Mostofsky and Ewen [179], this suggests that anomalous action model formation, or abnormal cerebellar control models, may contribute to impaired development of social, communicative, and motor capacities in autism. This clearly implicates the cerebellum in the formulation of a “theory of mind.”

While the cerebellum can easily be envisioned in participating in so many functions, the question emerges as to whether or not it is capable of “running the whole show.” We believe the cerebellum plays a critical role in pediatric neurodevelopment because it participates in a network or ensemble of connected brain regions that drive very broadly defined sensorimotor procedural learning and “action control.” This, in turn, indirectly contributes to development of semantic/declarative systems that allow for the “off-line” manipulation of information and simulative processes such as planning. Over the course of development, this allows the prefrontal cortex to learn to “think ahead” in higher-order control processes. As such, the ability to anticipate is an inherent design characteristic of a brain that develops “bottom up.” However, sensory perceptions are retained in the regions in which they are processed, while innervatory action/motor programs are stored within motor cortices. Cerebellar control models, which refine and adjust behaviors outside of conscious awareness, are stored within the cerebellum. As we have

referenced above, the cerebellum, through its anticipatory and correction functions, allows the cortex to retain the most efficient representation of a behavior. Without a cortex, the cerebellum might be “useless” because it would have no information upon which to base anticipatory control. By contrast, without a cerebellum, the cerebrum remains capable of storing experience and motor programs.

Therefore, an adult with a history of normal adaptive functioning who experiences an acute onset condition, such as stroke or tumor, is likely to demonstrate at least some recovery (dependent upon extent and location of lesion). Developmental history establishes an experiential background. While these patients generally do not achieve optimal pre-morbid levels of functioning, they do attain some improvement [180]. Functioning is less efficient without cerebellar input, but past experience retained in cerebral cortex assists in adaptation. On the other hand, a child who never had much of a functional cerebellum to begin with (cerebellar agenesis and posterior fossa tumor are just two beginning examples) experiences chronic adjustment deficits, depending upon the type of pathology and the age of onset of the condition, which determines the level of cortical experience. Finally, certain psychiatric disorders are characterized by cerebellar pathology. Affected individuals (as in autism and schizophrenia, to name just two examples) are chronically fed “bad data” from an abnormally functioning cerebellum, which often results in chronic impairment in EF. Therefore, within this interactive model in which brain networks operate as a functional ensemble, there is no single brain region that can function independently in “running the whole show.” This makes both intuitive and phylogenetic sense.

While much of our argument is based upon a well-established neuroscientific knowledge base, we realize that aspects of this model, such as the developmental characteristics of memory systems and how different memory systems might interact, is based upon minimal experimental evidence. However, we have attempted to provide an “interim solution” to these issues while we have generated a framework for future consideration. We hope that the hypotheses we presented will contribute to future studies in this field.

Summary

In this paper, we examined the close relationship between movement and thought. In doing so, we rejected a traditional serial-order processing model of adaptation as well as the phylogenetic notion that the brain evolved for the explicit and specific purpose of “thinking.” Instead, we presented a model of behavior based upon continuous interaction with the environment in which behaviors occur

in “real time.” Within this model and the dual-tiered paradigm of adaptation it supports [135], we proposed that the brain evolved for the purpose of controlling action. This development required the evolution of both on-line (motor skill acquisition) and off-line (simulative thought rehearsal) sensorimotor prediction mechanisms. We focused on a fundamental and comprehensive interactive role for cerebellar control models within these mechanisms. Why movements are made, how movements are planned and executed, and how movements might anticipate outcomes are questions at the heart of understanding executive function and action control, while the acquisition of movements play an important role in defining aspects of embodied cognition. We discussed how this might be the case in both adults and children. By directly connecting movement to thought, we have also examined important ways in what this model might apply to language processes, communication processes and social cognition, and we have suggested how the model might apply to concepts such as theory of mind.

Conflict of Interest Statement The authors have no conflicts of interest associated with this manuscript.

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