

# Adaptation, Expertise, and Giftedness: Towards an Understanding of Cortical, Subcortical, and Cerebellar Network Contributions

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**Abstract** Current cortico-centric models of cognition lack a cohesive neuroanatomic framework that sufficiently considers overlapping levels of function, from “pathological” through “normal” to “gifted” or exceptional ability. While most cognitive theories presume an evolutionary context, few actively consider the *process* of adaptation, including concepts of neurodevelopment. Further, the frequent co-occurrence of “gifted” and “pathological” function is difficult to explain from a cortico-centric point of view. This comprehensive review paper proposes a framework that includes the brain’s vertical organization and considers “giftedness” from an evolutionary and neurodevelopmental vantage point. We begin by discussing the current cortico-centric model of cognition and its relationship to intelligence. We then review an integrated, dual-tiered model of cognition that better explains the process of adaptation by simultaneously allowing for both stimulus-based processing and higher-order cognitive control. We consider the role of the basal ganglia within this model, particularly in relation to reward circuitry and instrumental learning. We review the important role of white matter tracts in relation to speed of adaptation and development of behavioral mastery. We examine the cerebellum’s critical role in behavioral refinement and in cognitive and behavioral automation, particularly in relation to expertise and giftedness. We conclude this integrated

model of brain function by considering the savant syndrome, which we believe is best understood within the context of a dual-tiered model of cognition that allows for automaticity in adaptation as well as higher-order executive control.

**Keywords** Cerebellum · Basal ganglia · Working memory · Expertise · Giftedness · Intelligence

## Introduction

Neuropsychology’s origins rest upon the phylogenetic assumption that human cognition is primarily associated with our significantly expanded cortex, which has evolved over many millennia. This apparently evolutionary belief has been reinforced by studies largely emphasizing adult patients with cortical lesions [1]. The information about brain–behavior relationships gleaned from comparing the behaviors of these pathological groups with the behaviors of unaffected controls seems, unwittingly, to have helped to establish the foundations for the cortico-centric model of higher-level functioning that now dominates neuropsychology. Using cortico-centric models has become the “default” condition for “explaining” areas of human function, ranging from pathology through normal development into giftedness and prodigy. However, cortico-centric approaches are severely limited in their ability to illuminate the active processes underlying human adaptation, including those involved in the “highest” levels demonstrated by gifted individuals.

A central limitation of cortico-centric approaches has specifically involved neurodevelopment. Cortico-centric models unwittingly echo the problems posed by creationist views by failing to place human function fully within a

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developmental context. If ontology recapitulates phylogeny, the cortico-centric view *must* be incorrect and cannot possibly explain adaptation, intelligence, normal and abnormal development, psychopathology, or phenomena such as expertise and giftedness. Models that integrate the functions of the cortex, basal ganglia, and cerebellum, on the other hand, ensure biological continuity while they explain these phenomena. Much of the foundation for this viewpoint is based upon Doya's descriptions of the computations of the cortex, basal ganglia, and cerebellum [2]. Cotterill further developed this view by linking consciousness and intelligence with overt and covert movements, observing that successful adaptation requires the basal ganglia, cerebellum, and neocortex to operate in concert for self-paced probing of the environment [3]. Subsequently, Vandervert described gifted cognition specifically in terms of collaboration between working memory and the cerebellum's cognitive functions, perhaps at the expense of having examined the roles of the neocortex and basal ganglia [4]. In this paper, we present an updated integrated model and focus on specific issues of expertise and giftedness within the context of general adaptation.

Pediatric neuropsychology is concerned with how cognition develops. This aspect of the field focuses upon normal and abnormal cognitive development. Notably, this area of neuropsychology is currently considered a "subspecialty" rather than a foundational area of focus. Initially, as neuropsychology expanded its scope to understand child behavior, the investigation of such disparate childhood pathologies as attention deficit hyperactivity disorder (ADHD), autistic spectrum disorders, learning disabilities, perinatal birth anomalies, extreme prematurity, bilirubin toxicity, and pediatric head trauma was largely guided by the prevailing adult model that presupposed that all relevant brain-behavior relationships were cortically based, with some notable exceptions [5–9]. But looking at the function of cortex in young brains, at ages at which the cortex is immature and minimally "on line" and at which time subcortical processes are so dominant, has left gaps in understanding the development of brain function [3, 10, 11]. We now know that the basal ganglia and cerebellum are often focal areas of involvement in these above-named developmental abnormalities, and we know that they play critical roles in the normal development of functional brain networks [12].

Over the past several decades, information has been accumulating that challenges neuropsychology's prevailing cortico-centric model of cognition and highlights the contributions of underlying, phylogenetically older brain structures and functions operating in concert with the cortex. Jaak Panksepp has pioneered the exploration of the roles subcortical brain structures and primitive affects play in adaptive functioning and in psychopathology [13–15], while research

by Michael Frank, Jeremy Schmahmann, Carol Seger, James Houk, Robert Miller, and Gregory Ashby, among others, has supported a more holistic model of cognition and cognitive development that appreciates the brain's vertical organization [16–23]. Brain-behavior relationships in which cortical and subcortical structures play integrated roles have been "modeled" computationally and have been supported by a range of experimental and brain imaging studies [24–27].

Multiple studies have demonstrated that the cortex, basal ganglia, and cerebellum are critically involved in normal development, while they also play a central role in nearly all disorders [3, 28–38]. The models that have emerged, and which continue to be refined, obviate traditional cortico-centric models of cognition. By including the roles played by subcortical structures, they better explain both normal and abnormal cognitive development and behavior. Using these and other sources of research, Koziol and Budding have defined how the cortex, the basal ganglia, and the cerebellum operate in an interactive way to generate adaptive behaviors, and they have proposed how these functions can be evaluated clinically [39]. Robert Miller has observed that a theory's usefulness resides as much in its ability to predict behavior as in its ability to explain behavior [40]. It follows that, if the aforementioned comprehensive models of brain-behavior relationships are substantive and relevant, they should be able to explain pathological development, normal development, and exceptional development, including expertise, giftedness, and child prodigy. As of yet, however, these models have not been applied to illuminate the brain-behavior dynamics that underlie exceptional levels of function. It is our aim to describe the integrated roles of the cortex, basal ganglia, and cerebellum in expertise, giftedness, and prodigy and, in so doing, to demonstrate the many ways in which these constructs share the same neuroanatomical substrates that underlie basic adaptation.

### Expertise, Giftedness, Prodigy, Intelligence—Definitions

*Expertise* can be defined as the acquisition of exceptional, specialized skill in a particular area of functioning [41]. Expertise can be observed in children and adults. An athletic child can acquire expertise in a sport, a child with an interest in photography can acquire expertise in taking photographs, or a cognitively inclined child can acquire expertise in reading or mathematics. Adults often demonstrate expertise in their occupations or professions. An attorney can possess expertise in a specialized area of law, such as corporate, family, or criminal law. A psychologist can acquire expertise in a specific modality of therapy. A skilled laborer can develop expertise in carpentry, masonry, or painting. An athlete can develop expertise in a specific sport such as golf, basketball, or baseball.

While people with expertise in a particular area may have additional areas of specialization (e.g., a baseball player may develop expertise in golf), in most cases, individuals acquire specialized competence in one area or domain of functioning [42]. Acquiring expertise is typically a result of considerable effort, practice, and work. Expertise is not defined according to the age at which an individual masters a domain, and it is not defined by how much instruction, direction, or support from others an individual requires or receives to develop mastery.

Expertise also is not necessarily dependent upon intelligence. Children who might be considered “ordinary” or “talented” can be motivated to work hard and can therefore achieve expertise, particularly if they have dedicated parents who provide an enriched environment and considerable direction, stimulation, support, and structure. Though expertise in some areas may be served by a strong intellect, Ericsson notes that it is possible for an individual with little overall general ability to possess expertise in certain domain areas [43]. Domain choice is likely influenced by genetic, hereditary, biological, and environmental factors. These influences are beyond the scope of this focused paper. We stress the behavioral geography of the brain within which these biologic influences are manifest or operant.

We propose that the coexistence of expertise in the absence of high—or even average—“intelligence” highlights some of the limitations in the manner in which “intelligence” is defined. Intelligence quotient (IQ) testing measures a purported “g” factor, but there is little agreement as to how to define this operationally and it is difficult to conceptualize or reconcile a “g” factor within the well-established framework of very different abilities and skills that recruit different cortical–subcortical networks [44]. In fact, Lezak and others view “general intelligence” as a confounded concept, particularly in relation to its measurement through psychological tests [45]. The “intelligence quotient” almost always refers to a derived score, summarized from performances on many discrete subtests that are presumed to measure a hypothesized general ability termed “intelligence” [46]. There may, in fact, be no “general” cognitive or intellectual function. Instead, there appear to be a variety of discrete functions that work together in close concert as interactive networks within the intact brain. In this way, cognition is subjectively experienced as an independent, “seamless” function. IQ scores are sometimes good predictors of academic performance, although the actual correlations between IQ and academic performance grade ranges are unimpressive [47]. It is on this basis that our model characterizes adaptation, expertise, and giftedness irrespective of arguments concerning a general ability factor. Instead, this treatise “maps” the brain–behavior geography within which concepts such as

“domain choice” and the possible general intelligence factors such as “g” operate.

*Giftedness* is a term that is most typically applied to children, though it has many different points of reference and operational definitions. A number of national organizations define “giftedness” in different ways, while school systems often employ the standard of IQ testing (or some substitute cognitive measure) to qualify children for placement in advanced classes. While gifted children may earn high, superior, or very superior “IQ” scores on traditional intelligence tests, according to Winner’s classic work, the term *gifted* should be reserved for children who demonstrate three atypical characteristics [48].

First, gifted children begin to master a domain at an earlier-than-average age. A domain is defined as an organized area of knowledge such as language, mathematics, music, chess, tennis, skating, etc. Learning the domain appears to come easily, so these children make rapid progress relative to their more ordinary peers. Second, these children acquire the given domain independently. They require minimal help from adults in the process of acquiring it, and they often teach themselves. Third, gifted children appear to be intrinsically self-motivated in relation to the domain in which they demonstrate precocity. Their interest in it can be obsessive, and their attention to the domain can be characterized as over-focused [49] or what Winner has referred to as a “rage to master.” We employ Winner’s definition of giftedness in this paper because the criteria are straightforward and unambiguous. We will not focus upon the many issues associated with “diagnosing” giftedness or which is the “correct” set of criteria nor will we discuss any possible “pathology” that might be hypothesized to be associated with many of the children that fulfill her criteria.

A *child prodigy* demonstrates all three characteristics of the gifted child but achieves adult level mastery by the end of the first decade of life [50]. Child prodigy should be considered as a subset of giftedness. Therefore, we will not specifically address this rare phenomenon, which appears to be an extension of giftedness heavily governed by biologic factors well beyond the scope of this paper. Vandervert has described the evolutionary pressures that may have generated the development of child prodigy [51].

### Cortex: Current Conceptions of Intelligence and Giftedness

The cerebral cortex is laterally organized, along a left–right hemispheric gradient, and it is organized along an anterior–posterior gradient as well. The central sulcus separates anterior from posterior brain regions. Posterior hemispheric regions are highly specialized “sensory” information pro-

processors [52], with the occipital, parietal, and temporal lobes specialized to process and analyze sensory–perceptual information and experiences [53, 54]. This provides the organism with information about what an object is and where it is. The hippocampal memory system, tucked inside the medial temporal lobe, allows these sensory–perceptual experiences to be retained for subsequent problem-solving [55]. This declarative/episodic memory system allows sensory–perceptual and ideational experience to persist, which represents an obvious adaptive advantage for problem-solving. Magnetic resonance imaging (MRI) data have demonstrated that intelligence is significantly correlated with intracranial cerebral, temporal lobe, hippocampal, and cerebellar volume [56]. As might be anticipated, there are no systematic studies, to our knowledge, that attempt to separate gifted populations from normal control subjects solely on the basis of medial temporal lobe memory system function [57].

Evidence from cerebral blood flow and cortical metabolic activity studies reveals that “thinking” in the cerebral cortex is supported by networks of Hebbian cell assemblies [58, 59], particularly in the temporal, parietal, and frontal lobes. These brain regions are activated differentially, depending upon the given task at hand and the specific type(s) of cognition necessary to address it [60–62]. The prefrontal cortex is activated by all tasks, which likely reflects its primary role in the organization of thought. The authors of these studies interpreted the different patterns of activation and deactivation in cerebral blood flow and cortical metabolic activity as reflections or manifestations of “thinking.” Anterior brain regions, defined as the frontal lobes, function primarily as motor “programmers” that orchestrate thinking and execute behaviors essential for adaptive, successful interaction with a complex environment. The frontal lobes are organized in a hierarchical way. Posterior to the prefrontal cortex, the premotor and supplementary motor frontal cortices program motor activities, while the most posterior frontal regions act on these plans and programs to execute behavior. These regions manage and integrate thinking to allow us to develop “new” programs to meet the demands of novel, unfamiliar circumstances and to plan behaviors in the pursuit of longer-term goals. Aspects of these processes can be said to define cognition.

Within this hierarchically ordered system, the prefrontal cortex plans all responses to higher-level, unfamiliar circumstances to which the organism must adapt. In this way, cognitive activity can be understood as an *extension of the motor control system*. That is, we “think” because we must develop plans and strategies to adapt to a changing environment that requires us to “act” differently than we have acted before. New circumstances call for new ways of responding if we are to adapt successfully. We “think”

because habitual, routine, and automatic behaviors do not “work” under novel conditions. The new plans we formulate are expressed or executed through active, “motor” behavior [3]. What this means from the perspective of functional neuroanatomy will be developed further in a later section.

There is no question that cortical structure is related to intelligence and expertise [63, 64], although what is the proverbial “chicken” versus what is the proverbial “egg” remains a relevant question [65, 66]. Holshoff Pol and colleagues examined genetic influences on specific areas of gray and white matter in 54 monozygotic and 58 dizygotic twin pairs, as well as in their siblings. They found that a number of specific focal gray and white matter areas of the brain are highly heritable. Additionally, they found that multiple areas, including the superior occipitofrontal fascicle, corpus callosum, and medial frontal and occipital cortices, share common genes with intelligence. The authors concluded that these areas form a heritable neural network in the human brain that is involved in intelligence [67].

A study by Gray and Thompson concluded that there is strong evidence for the lateral prefrontal cortex supporting intelligent behavior [68]. This region comprises part of a network of brain areas that support activity in various functional units of the brain that are differentially involved, dependent upon the task at hand. An MRI study by Frangou and colleagues found correlations between IQ and gray matter density in the orbitofrontal cortex, in the cingulate gyrus, the cerebellum, and thalamus, in addition to negative correlations in the caudate nucleus [69]. A more recent study by Chiang and colleagues focused on the role of genetics in white matter functions related to intelligence [70]. The authors found that a number of major white matter fiber pathways are highly genetically controlled, and higher diffusion anisotropy was linked with superior intellectual performance in several important systems. Notably, they found no significant correlation between white matter measures and verbal IQ. From this, they postulated that performance IQ, rather than verbal IQ, is more closely associated with physiological parameters, such as nerve conduction velocity, and as such is sensitive to the level of axonal myelination. They proposed conducting subsequent studies to address the issue of processing speed specifically, which would be important information as processing speed has been reported as an index of executive efficiency and control [71, 72].

Shaw, Greenstein, and colleagues found that the level of intelligence is associated with how cortex develops, primarily in frontal brain regions [10]. They found that more intelligent children exhibited an earlier acceleration and a prolonged phase of cortical increase, culminating in vigorous cortical *thinning* by early adolescence. They saw

patterns of dynamic change most prominent in the prefrontal cortex and they observed that the magnitude of frontal activation, demonstrated through fMRI, correlated highly with intelligence as measured by psychometric tests. In addition, the same areas recruited during “intelligence testing” were activated by tasks that required working memory, planning, and the execution of complex, novel behaviors. They concluded that the development of intelligence appears to be associated with a dynamically changing neuroanatomic process. This dynamically changing neuroanatomy involves the interface between regions that govern attention, working memory, and executive control.

In their comprehensive review article related to the normal development of brain circuits, Tau and Peterson observe that, along with the cortical thinning process, which proceeds “back to front,” the perisylvian cortices in inferior parietal and posterior temporal areas and in the left hemisphere appear to thicken between childhood and adulthood [38]. The authors additionally note that *excessive* thinning is associated with psychiatric disorders, particularly schizophrenia, whereas slowed thickening is associated with ADHD [73]. The authors observe that the cellular mechanisms underlying these cortical thickening and thinning processes are as of yet unknown.

Cortically based studies of giftedness often emphasize the role of the parietal cortex. Jung and colleagues’ Parieto-Frontal Integration Theory, or P-FIT, emphasizes the relationship between highly efficient cortical networks that connect frontal and parietal areas and increased cognitive function [74, 75]. Jung and his colleagues have also more recently considered the neuroanatomy of creativity, both specifically and in relation to psychopathology, from this cortically oriented perspective [76, 77]. The well-known, and somewhat controversial, examinations of Albert Einstein’s brain have noted the unusual morphology of his parietal lobes [78–80]. The most recent of these, by Dean Falk, discusses the unusual symmetries and asymmetries found in Einstein’s brain. He highlights the convergence of the postcentral sulcus with the sylvian fissure bilaterally [81], and he notes the marked asymmetry in the width of the lateral postcentral gyrus favoring the left hemisphere, in addition to a pronounced “knob” in the right hemisphere, which is often found among trained musicians. Einstein’s relatively delayed language development and preference for nonverbal problem-solving were correlated to these findings.

It is also possible to consider intelligence as a manifestation of cortical neuron *efficiency* [82, 83]. From this perspective, brighter individuals exhibit lower, and presumably more efficient, brain activation when they perform simple cognitive tasks, while they recruit more cortical resources in very complex task situations. This results in high positive correlations between brain usage and cogni-

tive ability. However, even within this cortico-centric perspective, a variety of other factors need to be considered.

### Hemispheric Lateralization and a Dual-Tiered Model of Behavioral Control

The purpose of an organism is to survive. All organisms exist in the context of an environment, and in order to survive they must interact with that environment. When an organism interacts successfully, we describe that process, and its outcome, as adaptation. Organisms that cannot adapt do not survive.

Vertebrate organisms depend upon foundational sensory and motor capacities to interact with the environment and adapt successfully. Sensory capacities enable them to identify and recognize objects and to figure out where those objects are. Motor abilities enable them to know *what* to do in relation to what they perceive, to know *how* to act (do it), and to know *when* to act (do it). In order to accomplish these functions, the vertebrate brain is organized to allow a division of labor between the left and right cerebral hemispheres and between anterior and posterior cortices.

The specialization of each cerebral hemisphere was established in its basic form about 500 million years ago, when vertebrates first evolved [84]. Current theory proposes that the two hemispheres are organized to contend with input and generate responses along a gradient of novelty versus familiarity. The left hemisphere was first specialized for the control of routine, frequently performed patterns of behavior under familiar, ordinary, predictable circumstances. The left hemisphere’s capacity to use language to classify and express information can be understood as specific type of routinized behavior, and language can be understood as a specialized instance of routinization [85]. The right hemisphere was first specialized to detect and respond to unexpected stimuli within the environment and to problem-solve in relation to novel or unfamiliar circumstances.

Having areas of the brain that are specialized to accommodate and respond to familiar versus novel demands is believed to provide the decisive adaptive advantage in interacting with a changing and complex environment [86–88]. Unfamiliar experiences, and behavioral responses to them, can become familiar and routine with repeated exposure. With enough repetition, some responses become “automatic.” Automatic behaviors are adaptive and efficient. They always “work” under the proper stimulus conditions. They are economical in that they “free up” the cerebral cortex to process and analyze more novelty. Being able to operate more automatically and efficiently in some conditions and more purposefully and deliberately in others is necessary to ensure optimal adaptation in an environment

that presents both familiar and novel circumstances. While we execute most daily tasks automatically, we need to be able to alter a routine if something changes within the environment that renders the routine behavior inappropriate or maladaptive. The capacity to “switch” between releasing routine behavior versus engaging higher-order reasoning is critical for adaptation and depends upon fine-tuned interactions between frontal cortical–basal ganglia networks [89].

Being able to recruit automatic behaviors is necessary for efficiency. Simultaneously, having higher-order control at the ready allows us to be alert to continuing changes in the environment. Having both systems coexisting and working in concert allows us to discover what is familiar within a novel situation and to develop new repertoires to respond to the elements that are unique. Our ability to determine a novel situation’s known stimulus-based characteristics allows us to use what we know from the past to meet the new adaptational challenges the situation represents by developing a behavior that “works” [84, 86]. This dual-tier system allows us to use what we know while we are also able to benefit from experience in interacting with the environment. This, in turn, enriches our knowledge base and provides a foundation for us to integrate more that is novel. This principle of behavioral organization is common to all vertebrates, including humans. It drives all adaptation and it guides the development of expertise for “ordinary” and “gifted” populations alike. We might predict, however, that the gifted would be able to identify the stimulus-based characteristics of problems more quickly, and even intuitively [90, 91].

### Cortical Excitation and Inhibition: the Selection Problem

Characterizing the cortex as a highly specialized sensory and motor processor is a gross understatement. The human cortex makes it possible for us to perceive like no other organism can perceive, to combine perceptions to generate abstract ideas, to move in highly skilled ways, to combine and manipulate ideas and movements, and to make discoveries at a level of complexity that cannot be equaled by any other species. These functions, which are dependent upon the cerebral cortex, are composed of neural networks that require an intricate balance of excitation and inhibition [92]. Accepting the fact that these advanced abilities are unparalleled along the phylogenetic hierarchy, however, contributes to the erroneous, and perhaps even arrogant, conclusion that “the cortex is king” [93, 94]. While the strictly cortico-centric model of cognition that highlights such unparalleled development is seductive to embrace, there are at least two reasons to reject it as inaccurate. The first is the “selection problem,” which we will define in this section. The second concerns speed of information processing and speed of adaptation, which we will discuss later in this paper.

The cerebral cortex is composed of an extremely complex neuronal network. It receives essential inputs from all major sensory systems and it contains a daunting number of connections linking one cortical region to another. These connections are both regional and distant, connecting areas of cortex that are also both proximal and distal [95]. Cortical neurons comprise two major types, specifically, pyramidal and nonpyramidal neurons [96]. Pyramidal neurons have excitatory influences upon each other and are the major source of cortical efferents [97]. Nonpyramidal neurons are the major sites of cortical afferents [96]. However, approximately 25–30% of cortical connections include inhibitory interneurons, which modulate cortical activity [92]. Perceptions and related associative processes dependent upon the neocortex require a delicate interplay between excitation and inhibition in order to achieve balanced and coordinated cortical activity [98]. Interactions between excitation and inhibitory influences appear to be important in the proper “timing” of neural impulses for adaptive perceptual and associative processes [99, 100]. However, the output of this neuronal interaction is primarily excitatory [40]. Nevertheless, when inhibitory influences are affected or diminished, the result is often manifest in psychotic sensory–perceptual phenomenon, such as hallucinations [101].

Many regions of sensory association cortex project directly into the premotor cortex. Ashby and others have proposed that, while these regions also project to the basal ganglia, the reinforcement learning characteristics of the striatum (to be discussed below) allow cortical–cortical associations to be formed through practice. Once these associative linkages have been established, they become independent of basal ganglia influence [102]. According to this model, the acquisition of motor skill automaticity is a process in which control is passed, or shifts, from subcortical procedural learning systems to cortical networks that connect cortical sensory association areas with premotor cortices [103]. Therefore, the cortex would appear to be perfectly capable of selecting an associative response based upon the perception of an appropriate stimulus.

However, the perceptions, associations, actions, and behaviors arising through cortical interaction raise an important question. While the cortex appears to contain abundant inhibitory interneurons that exert local inhibition within and between various cortical regions, do these cortical perceptual, associative, and motor networks have sufficient capability to “select” among numerous and competing simultaneous events? In other words, are neocortical networks sufficient to manage or “solve” the “selection problem” regarding what merits our attention and action in relation to our overall best interests for successful adaptation?

All brain functioning is based upon principles of *interaction*. Every piece of sensory information that an

individual processes, all thinking, all planning, and every behavior that the individual executes rely on excitatory–inhibitory interactions between neurons [97]. However, the bi-directional connections between thalamus and cortex are excitatory, while the connections between different areas of the cortex and the hippocampus are composed of excitatory and inhibitory neurons. This interactional connective network, which Miller refers to as the “CTH network” (cortex–thalamus–hippocampus), is necessary for perception and for the “working memory” (thinking and planning) functions of higher-order behavior [39]. It is easy to understand that an end product based upon excitation, or an “excited cortex,” would represent a primary way of processing and analyzing sensory information and determining behavioral output. However, making executive decisions, whether about the focus of attention or about what behavior is to be executed, requires something beyond the essential interactions of the CTH if behavior is to be directed, focused, flexible, and adaptive. This issue is *critical*. When “executive decisions” are made, these choices are based upon the expectation of rewards and/or positive versus negative reinforcement [104]. This is particularly the case when the cortex identifies multiple possible courses of action.

Similarly, the “CTH” might generate a few actions that are all relevant and should be executed, but a “gating” or selection system is needed to coordinate these so that they are executed in sequence. This is particularly important when one action achieves a subgoal on which future actions depend if the overall goal is to be reached. Within the domain of higher-order control, multiple working memory items might be relevant for solving a novel problem. The cortex should continue to represent all of these items; however, only one of them should influence behavior in any given moment. Since within the CTH the bi-directional connections between the thalamus and cortex are excitatory, an *inhibitory* system would function to select the cognitive representations to guide motor action selection. To put these functions in practical, analogous terms, just as a car must have an accelerator and brakes to get where it is going safely and efficiently, a cortical system based upon excitation *must have inhibitory controls* if it is to function adaptively, in the best “executive” interest of the individual as a whole.

If progressively refined executive decisions are to be made, if expertise is to be acquired, and if the “gifted” child is to exhibit an excessive preoccupation in a “rage to master” a specific domain, then essential inhibitory interactions must co-exist with the interactions of cortical associative processes to *focus* attention and to *select* behavior. Cortico-centric models are unable to explain this type of inhibitory function effectively [105, 106]. For example, GABA, the major inhibitory neurotransmitter in the cortex and brain, may have global control over the CTH network by governing levels of

arousal or consciousness [107]. However, this global influence does not provide specific areas of the cortex with direct, explicit signals that convey information about motivational relevance for making executive, adaptive attentional choices and behavioral selections. Influence over specific areas of the cortex (and/or CTH) requires an inhibitory gating or selection system that is also capable of learning reward/reinforcement probabilities of behaviors and selecting those with the highest probabilities, particularly when the cortex identifies multiple possible actions [108, 109]. In this regard, adaptive behavior depends upon the ability to flexibly alter choices and behaviors in response to changes in reward and punishment contingencies. The basal ganglia and specifically the striatum have consistently been implicated in these processes [110].

As reviewed by Redgrave and others, attentional and behavioral resources are limited [111]. It is impossible for the CTH system, even with abundant inhibitory interneurons, to function effectively without setting priorities and considering the goal of the organism as a whole. Nobody—from the ordinary person to the talented to the expert and gifted—can “pay attention” to everything simultaneously nor can anyone engage in every activity or motor program. Successful adaptation requires a manner of prioritizing attention and action in order to meet situational requirements. A “selection problem” emerges when two or more competing sensory and/or motor systems seek simultaneous access to a restricted resource [111]. Solving this “problem” successfully requires inhibitory control over the associative CTH network in addition to an ability to convey the motivational significance (reward value) of possible targets for attentional focus and behavioral selection. While the cortex perceives, associates perceptions with one another, and generates “candidate” actions, the ideal gating system would get to “see” or “view” which actions the cortex has generated based upon the input and would then “boost” or release the most appropriate/rewarding one.

The first and largest regions of the brain that appear to be capable of exerting such an inhibitory/gating influence are the basal ganglia [40]. Examining the functions of the basal ganglia in directing attention and selecting behavior provides clues to understanding the role of this subcortical region in adaptation and in the development of expertise and giftedness [112]. While the cingulate cortex has repeatedly been implicated in focusing attention, in the shifting of attention, and in inhibitory control [113–115], the anterior cingulate exerts its influence through the circuitry of the cortico-striatal–pallidal–thalamic–cortical loop [116–118]. This is another critical point, perhaps first suggested by Cotterill in his highly cogent discussion of the relationship between directing attention and activating movement and the important implications of this for cognition, consciousness, intelligence, and creativity [3].

## Solving the Selection Problem: the Cortico-Striatal–Pallidal–Thalamic–Cortical Circuit

The cortico-striatal–pallidal–thalamic–cortical circuit includes a white matter tract that is the primary and most important mechanism regulating the activity in different cortical regions [119–121]. The circuit’s name reflects the anatomical connections between these different brain areas and emphasizes the circular nature of these connections. Accordingly, the cortex projects to the striatum (composed of the caudate and the putamen), which projects to the globus pallidus, which projects to the thalamus, which then projects back to the cortex to the same region from which the circuit originated, thus forming a closed “loop” [122–124]. It is generally accepted that looped, architectural, neuroanatomical connections of this nature typically perform modulatory functions [1, 125, 126].

Seven differentiated, prototypical circuits have been identified that connect the frontal lobes to the basal ganglia and thalamus. Each circuit follows the same general projection pattern and remains segregated from the other circuits. They are named according to their points of origin. The first five circuits identified include the dorsolateral prefrontal circuit, the orbitofrontal circuit, the medial/anterior cingulate circuit, the skeletal–motor circuit, and the oculomotor circuit [122]. Subsequently, posterior sensory circuits, including the temporal and parietal circuits, have been revealed that follow the same connective pattern [127]. Figure 1 illustrates the connective pattern of the five/seven prototypical circuits.

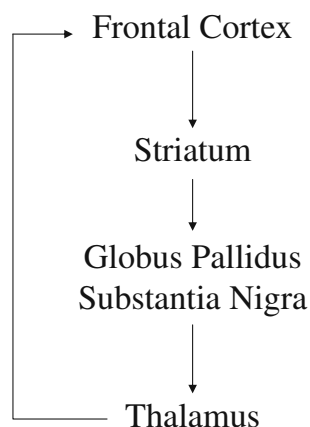
Each of these segregated and discrete circuits has separate functions and projects to discrete targets in the striatum, pallidal complex, and thalamus. The skeletal–motor circuit mediates movement, the oculomotor circuit originates in the frontal eye fields and controls visual search eye movements, the dorsolateral prefrontal circuit mediates the activation of cognitive activity, the orbitofrontal circuit is an inhibitory circuit that plays an important role in

mediating adaptive social behavior, and the medial/anterior cingulate circuit governs motivation [117]. The temporal and parietal circuits are involved in categorization and information integration learning [128, 129]. Each circuit features two essential connective profiles: the direct and indirect pathways. When the cerebral cortex—which always has an excitatory, activating influence—activates a direct pathway, the striatum releases the tonic inhibitory control that the globus pallidus interna exerts on a specific “target” nucleus of the thalamus. Thus disinhibited, the specific thalamic nucleus can activate a specific region of the cortex. The result: Perceptions are activated if the circuit is a sensory circuit. Behavior is released if the circuit is a motor circuit. When the cortex activates the indirect pathway, this increases the inhibitory influence that the globus pallidus exerts on the thalamus (through the intermediate connections between the globus pallidus externa, to the subthalamic nucleus, to globus pallidus interna, and back to thalamus). This inhibits the thalamus so it can no longer exert an excitatory influence on the cortex. The result: Perceptions are inhibited if the circuit is a sensory circuit. Behavioral release is inhibited if the circuit is a motor circuit. Therefore, the circuitry of the basal ganglia inherently serves as a gating mechanism. Rather than directly activating behavior, the basal ganglia enable particular cortical perceptions or actions to be “boosted” or released by way of pallidal influence over the thalamus [130].

In essence, this circuitry allows the basal ganglia to tell “which” regions of the highly compartmentalized cortex “when” they should and should not become active. This process allows attention and action to be focused in a particular direction, while it precludes attention and action from being focused in other directions, thus “solving” the selection problem. (This represents an oversimplified characterization of functional and dynamic cortical–basal ganglia relationships for the sake of brevity, sufficient for the purpose of understanding issues relevant to the topics of this paper. We assume that the reader has a working knowledge of this circuitry. Detailed and comprehensive descriptions can be found in Utter and Basso [119], Lichten and Cummings [117], and Miller [40] as well as others.)

Parkinson’s disease and Huntington’s disease primarily affect the basal ganglia. Multiple studies of patients with both disorders demonstrate the ways in which the basal ganglia and the circuits that include them govern the brain’s intention programs [131–134]. The brain’s intention programs include the ability to form intentions and to bring them to fruition. They can be divided into four categories: knowing when to start a behavior, knowing when not to start a behavior, knowing when to persist with a behavior, and knowing when to stop a behavior (personal communication, Heilman and Valenstein, 1999).

**Fig. 1.** Simplified version of frontal–subcortical circuit



Parkinson's disease is, in part, characterized by difficulties in initiating movements and difficulties in stopping them and by perseveration that makes switching from one movement to another difficult. Huntington's disease is characterized by the release of fragments of unwanted, purposeful movements. Individuals with both of these diagnoses are aware of their motor abnormalities, and they are aware of their inability to overcome them and control their movements with conscious intention. These two diseases primarily involve motor circuitry. Because all cortical–striatal circuits run in parallel and are governed by the same organizational principles and functional mechanisms, the inability to translate intention to action that manifests in motor problems in these patients would be predicted to manifest in a variety of other pathologies when other circuits are involved [30].

Koziol and Budding, Bradshaw, and Lichter and Cummings have described a variety of cognitive, motivational, and affective/emotional outcomes that result from disturbances in intention programs associated with pathology in the five originally identified prototypical circuits. The obsessive ideation and compulsive behavior accompanying obsessive–compulsive disorder (OCD) and the executive control dysfunction seen in ADHD provide what may be the most obvious examples of what happens when circuitry involving cognition is impacted. OCD involves disturbances within the basal ganglia [135–137]. For example, OCD patients with hand washing compulsions can articulate that they *know* that their hands are clean, yet they continue to be bothered by the idea that their hands are dirty and are compelled to wash them repeatedly. This provides an elegant illustration of the perseverative ideation and the clear loss of control over intention that result when knowing when to stop a behavior is not working.

The behaviors of children with AD(H)D can reflect pathology within all four of the brain's intention programs. These children often initiate behaviors impulsively, at inappropriate times. They interrupt others and blurt out answers to questions. These reflect problems knowing when not to start a behavior. Problems not knowing when to stop can be reflected in the persistence of such maladaptive behavior, irrespective of the negative feedback it generates. Difficulty knowing when to start can be seen in episodes of procrastination and apathy toward activities that are not inherently rewarding, while not knowing when not to stop may be evident in lack of persistence on such tasks once initiated as well as their propensity to stray “off task.”

Given this way of conceptualizing ADHD, it is no surprise that the basal ganglia are implicated in the disorder [138, 139]. When the basal ganglia tell the cortex “when” to become active, this can always be conceptualized within the context of these intention programs. However, understanding how perception and action are “gated” also

depends upon an understanding of how the basal ganglia “select” on the basis of the motivational significance or reward value of the possible selections, as indicated earlier in this section. This requires a review of the dopaminergic reward system.

### Reward and Motivation: Mediating Perception and Action Selection

The basal ganglia have been implicated in a variety of motor and cognitive functions, and this makes it difficult to discover a single unifying function of basal ganglia structures [31, 112, 140–143]. The previous section reviewed the basal ganglia's inherent gating functions. This section reviews their instrumental and reinforcement learning functions, as well as their modulation by dopamine.

For the purpose of succinct and cogent discussion, we assume that the reader is thoroughly familiar with the dopaminergic projection system. In brief review: The medially located substantia nigra/pars compacta, along with the adjacent ventral tegmental area, are the sources of dopaminergic pathways that project to the structures of the basal ganglia, the limbic system, and the prefrontal cortex [96]. This projection system is composed of the nigrostriatal, mesolimbic, and mesocortical pathways. Instrumental and reinforcement learning, as well as the anticipation of positive and negative reward, are governed by the activity within these dopaminergic pathways.

This extensive dopaminergic projection system is a critical reward circuitry. It has been hypothesized that the prefrontal cortex (lateral and ventromedial regions) codes for the anticipation of reward and drives reward-seeking behavior on the basis of expected outcomes [104, 144, 145]. These specific circuitries include the anterior cingulate/ventral striatal regions. The orbitofrontal and medial frontal cortex projection systems are parts of the brain's circuitries related to certain types of *consummatory* reward or reinforcement. These regions become active with the actual enjoyment the individual receives [146]. The ventral striatum becomes highly active with the *anticipation* of reward, especially under conditions of high certainty, and remains active during periods of consumption [147]. This “extended” basal forebrain region is extremely rich in dopamine [148–150]. This system is believed to regulate a diverse set of behaviors, ranging from the control of movement to the modulation of desire, motivation, and cognition [151]. This system governs attention, different aspects of reward, mood, and certain appetitive drives. Disturbances within this system are associated with a wide variety of psychiatric and behavioral problems, from addiction to schizophrenia and almost all disorders “in between.”

There are several models that describe how the cortex—and specifically the frontal lobes—interact with the dopaminergic reward system [152, 153]. There are also differences in regional and brain network activation in response to the anticipation of reward and in response to unexpected reward and punishment. For example, Robinson et al. recently found that the posterior dorsal striatum responded only to unexpected reward, while the anterior ventral striatum responded to both unexpected punishment as well as unexpected reward [110]. Further, Stocco and colleagues have recently developed a model that considers ways in which the basal ganglia implement a conditional information-routing system, which is posited to direct the transmission of cortical signals between pairs of regions by separately manipulating the selection of sources and destinations of information transfer. The model includes a putative system for controlling the release of dopamine [154]. While these data further point to the complexity of the reward system, it is well beyond the scope of this paper to provide such an all-encompassing review. For simplicity, we focus on the basic gating mechanism of the basal ganglia, summarized above, which also illustrates how the basal ganglia “learn,” in response to positive and negative reinforcement, while we restrict this discussion to aspects of the dopaminergic reward system.

The direct and indirect pathways project from the frontal and sensory cortices to the matrix compartment of the striatum. Orbitofrontal and paralimbic cortices project to regions of the striatum called “patches” or striosomes [126]. These projections include input from motivational centers, such as the amygdala and hypothalamus. This pathway does not follow the routes and mechanisms of the direct and indirect pathways. Instead, these striosomal connections project directly to the substantia nigra complex, the region where dopamine is “manufactured” or synthesized [40]. This constitutes a limbic–basal ganglia circuit.

This pathway allows information about rewards and behavioral states to be integrated within the basal ganglia, providing the basal ganglia with information of motivational importance, while limbic regions evaluate the motivational significance of sensory input. Information about the outcome of this evaluation is projected to the substantia nigra to control the dopamine system in reward-driven association learning [40]. The basal ganglia function as a reinforcement learning system [2]. This affective, evaluative information provides a framework for understanding the dopaminergic reward system's contribution to motivation through interactions with cortex in order to establish priorities and ultimately in making decisions and choices, which in turn addresses aspects of what we have referred to above as the “selection problem” [152].

Learning, avoidance, and the extinction of responses all appear to be significantly dependent upon dopaminergic activity [155]. Motivated behavior is controlled, in part, by

learning. Within the striatum, learning is mediated by dopamine. Dopamine acting on medium spiny neurons enhances or facilitates transmission along the direct pathway. The reader will recall that dopamine receptors within this pathway are called D1 receptors. Dopaminergic activity within this pathway reduces the inhibitory output of the Gpi. This releases thalamocortical output, makes cortex active, and generates behavior. In instrumental learning terms, this means that a behavior is more likely to occur, which can be called a positive feedback effect within the striatum. Dopamine inhibits neurotransmission within the indirect pathway. The reader will recall that dopamine receptors within this pathway are called D2 receptors. The indirect pathway acts as a “brake.” Within this pathway, dopamine aids in releasing the brake, allowing the direct pathway to exert more influence over Gpi output. Therefore, dopaminergic activity has the overall effect of releasing behavior. Increases, or “bursts,” in dopaminergic activity should facilitate positive reinforcement learning [156].

Dopamine depletion has opposite effects. Decreased levels of dopamine increase neurotransmission within the indirect pathway, therefore increasing inhibitory output of the Gpi, with the result of reducing or suppressing thalamocortical output [157]. In the absence of sufficient dopaminergic release within the direct pathway, the behavioral system is in a state of inactivity due to the indirect pathway's greater influence. This results in excessive cortical inhibition, which suppresses behavior. In instrumental learning terms, activity within the indirect pathway makes a behavior less likely to occur, which can be termed a negative feedback effect within the striatum [158]. Therefore, “dips” in dopaminergic activity should result in negative reinforcement learning. The negatively reinforced behavior should be avoided in the future. Learning, avoidance, and extinction of responses all appear to be dependent upon dopaminergic activity [155]. While aspects of this instrumental learning model are the focus of continued debate, controversy, and theoretical refinement, the general model presented has received support from studies of patients with basal ganglia disorders such as Parkinson's disease and DSM-defined conditions such as attention deficit hyperactivity disorder, in addition to studies of normal control subjects [134, 156, 158–165].

The dopaminergic learning and “motivational system” can therefore be understood in relation to phasic changes in dopaminergic activity within the direct and indirect pathways. This gating system can be applied to numerous decisions in life, which ultimately come down to making discriminations among a variety of available behaviors. For example, you could decide to complete reading this paragraph or to update the content of cortical working memory by consulting a reference work, you could continue to focus on this manuscript all the way through to its completion while

screening out background information, or you could switch activities in order to watch a more interesting and rewarding television program. These decisions are made on the basis of motivation, what we find rewarding, and/or to possibly avoid a negative outcome. The basal ganglia gating system that we have outlined here allows the brain to choose or select between these options [152].

This solution to the “selection problem” explains how we select where to focus attention and how we select which action (s) to take in relation to what we focus on. Yet making appropriate attentional and behavioral selections does not, in and of itself, lead to adaptation, much less does it lead to expertise and giftedness. Knowing where and upon what to place attention, knowing what to do, and knowing when to act tells us nothing about “how” to engage, execute, and ultimately achieve mastery. We are often impressed by the expert’s quickness in problem-solving, the speed with which a gifted mathematician performs calculations, and the seemingly “intuitive” nature of many discoveries. The mental speed with which the expert can function seems to be contradicted by the accepted notion that the cortically based controlled processing upon which this higher level function purportedly depends works slowly [72, 86, 166]. Eysenck and numerous others have suggested that the information processing of the highly intelligent person is faster than for the ordinary individual [167–169]. But what can drive this speed of processing? Can the cortex work so fast? This brings us to our second problem of “speed” of adaptation. We believe that understanding what drives the speed of processing requires an understanding of the roles of cerebral white matter and of the cerebellum in vertebrate, primate, and human behavior.

### **Cerebral White Matter: Pathways to Automatic and Higher-Order Control**

Cerebral white matter comprises bundles of fiber pathways. These pathways send neuronal axons that link cerebral cortical areas with each other and with subcortical structures and regions. This linkage system allows for the distributed neural networks that subserve sensorimotor behavior, affect and emotion, and cognition [170–173]. The specific ways in which white matter tracts function in relation to gray matter regions have remained open to debate. However, Mandl and colleagues have developed a methodology which might begin to allow for the examination of task-dependent changes in white matter function [170]. It is generally accepted that myelinated (white matter) fiber tracts “speed up” information processing.

As recently described and modified by Schmahmann et al., there are several types of white matter tracts [95]. The cortico-cortical association fibers connect other ipsilateral cortical regions with each other. These tracts, especially

those that connect the prefrontal cortex with parietal and certain temporal lobe regions, are essential for working memory, which we have already described as essential for higher-order control and are related to intelligence. The commissural fibers pass to the contralateral cerebral hemisphere and allow the hemispheres to share information. Cortico-striatal fiber tracts connect the cortex to the basal ganglia, which we have seen are critical to the brain’s intention programs. In addition to frontal–striatal connections, fibers course from the temporal lobes to the body of the caudate and from the parietal lobes to the tail of the caudate, which are regions that govern various types of category learning. Pontine fiber tracts descend from nearly all regions of the cerebral cortex to the pons (which in turn projects to the cerebellum) and other brainstem structures. The functions of this particular fiber tract will be discussed in the next section. Thalamic fibers project back to cortex. Therefore, every area of the cerebral cortex is linked with other cortical and subcortical areas through these white matter pathways [95, 174]. These white matter pathways are phylogenetically similar across vertebrates and are considered to be under genetic influence [175].

While this widespread connectional system forms the anatomic underpinnings of cognitive and behavioral networks, it is particularly important for “gifted” function because prefrontal white matter volume has been related to levels of intellectual development and cortical processing speed. For example, one recent study demonstrated that the stability of motor tapping (synchronizing tapping to metronome clicks and then comparing to tapping rate after stopping the metronome) was highly correlated with intelligence and related to regional volume in the right hemisphere prefrontal white matter regions [176]. These authors concluded that temporal accuracy on simple, automatic timing tasks that placed minimal demands on working memory and executive functions was correlated with intellectual performance while sharing the same neuronal correlates, specifically, increased white matter volume. The authors additionally concluded, on the basis of the fMRI results in this study, that larger prefrontal white matter volume likely reflects a larger number of cortico-cortical connections, which would be important for coordinating a broad range of cognitive activities dependent upon working memory functions. However, the prefrontal cortex is also one of the most prominent regions of origin of the pontine fiber system, a white matter tract that projects to the cerebellum [177–179].

### **Cerebellar Contributions to Speed of Information Processing: Developing Automaticity**

The cerebellum is traditionally understood as a coordinator of movement. However, it would be more accurate to state

that the cerebellum regulates the rate, rhythm, and force of behavior in order to coordinate and refine its *quality*. The poor regulation of the rate, rhythm and force of movement, seen in people with cerebellar problems of ataxia and dysmetria, demonstrates the critical role that the cerebellum plays in controlling the quality of what we do. As the cerebral cortex has expanded during the course of evolution, the cerebellum has also demonstrated a three- to fourfold expansion in sapiens compared to other species. The dentate nucleus of the cerebellum—which lies deep within the cerebellum—has dramatically increased in size, and reciprocal connections between prefrontal cortex and the dentate nucleus have been identified in humans that are not present in other species [180]. However, the argument cannot be made that the cerebellum increased in size simply because the brain as a whole increased in size. Rather, prefrontal inputs to the human cerebro-cerebellar system have evolved selectively to serve numerous aspects of human adaptation [177, 179, 181, 182]. The simplistic idea that equates the advancement of cognitive skill with neocortical expansion needs to be revisited in order to consider the coordinated expansion of the neocortex and the cerebellum as a functional ensemble or network [183].

There are two primary sources of input into the cerebellum. One is through the mossy fiber system and the other is from the climbing fiber inputs of the inferior olive [184]. The mossy fiber system receives its afferents from the pons, which receives its input from the cerebral cortex. This is often referred to as the cerebro-cerebellar system because the cerebral cortex is its primary source of input. The olive appears to have three sources of input. One projection system links the cerebral cortex with the red nucleus to the inferior olivary nuclei and then through the climbing fibers to the cerebellar cortex [184]. A second system originates in the zona incerta of the thalamus (which receives projections from the frontal cortex) and projects to the inferior olive and back to cerebellum through climbing fiber inputs [185]. A third system is the olivocerebellar projection pathway, which projects from the deep cerebellar nuclei to the olivary nuclei and, from there, through the climbing fiber system to the cerebellar cortex [186, 187].

While the basal ganglia can be understood as an inhibitory control region, the cerebellum can be considered as the brain's behavioral refinement mechanism. When a motor program is selected through frontal–striatal interactions, the neural signals that comprise this program are relayed to the cerebellum (through the mossy fiber input system). The cerebellum is essentially sent a “copy” of this motor program. This establishes a cerebellar “model” of what the brain has decided to do. Because higher-order control associated with cortical sensory processing works slowly, the brain cannot rely upon cortical sensory feedback to guide behavior (as an example, imagine the speed of

sensory feedback required to reach for a cup of coffee. This is an automatic behavior established through practice and anticipation). The cerebellum forms an internal model that is adjusted as the behavior is repeated. As this model is refined through a learning process, the brain can perform the movement precisely without referring to sensory feedback from the moving limb. This explains how we are able to move more skillfully with repeated practice [90].

The cerebellum refines the signals necessary to execute the motor program based upon prediction or anticipation. These inhibitory refinement signals adjust the amplitude of the behavior and become the cerebellum's forward model of the behavior. Output signals that travel from Purkinje cells to the deep cerebellar nuclei are exclusively inhibitory [187]. This inhibitory influence emphasizes the cerebellum's role in behavioral refinement. While learning new behaviors requires practice if they are to be executed successfully, the repetition entails a process of behavioral adjustment, or correction, from trial to trial. The olivary system serves as an “error detection” mechanism within this process. When the behavior does not “fit” the cerebellar model, the olivary system codes the error and sends a correction signal to the cerebellum through the climbing fiber system, which modifies the forward model.

Continued successful repetition of this forward model allows for the most efficient representation of that behavior to be stored. The behavior is now automatic and can be performed flawlessly. This stage of the process is called the inverse model, which now controls the behavior. This represents a simplistic, succinct explanation of cerebellar functioning. The cerebellum essentially “speeds up” information processing by constructing models based upon anticipation instead of direct sensory feedback while honing, timing, and fine-tuning the efficiency of that behavior as it is successfully repeated.

### Functional Organization of the Cerebellum

The circuits that connect the neocortex to the cerebellum, like those that connect the cortex and the basal ganglia, are highly segregated. Each circuit forms a re-entrant loop, meaning it follows a path that originates in the cerebral cortex and terminates in the same area of cortex from which its input originated. Each cerebro-cerebellar circuit originates in a highly specific cortical region. Specific points of origin include the prefrontal and all other frontal cortical areas, the parietal lobes, the superior temporal lobes, and paralimbic cortices. These regions initially project to the pontine nuclei where they maintain their segregation. From the pons, circuits project to specific zones of the cerebellar cortex through the mossy fiber inputs and, from there, to specific, deep cerebellar nuclei, particularly the dentate nucleus, which has expanded signifi-

cantly during the course of evolution in order to accommodate these projection fibers. The original cortical projections maintain their individual, initial segregation throughout these pathways, from the cortex inward. They maintain this segregation within the deep cerebellar nuclei, and also as they project back out to the thalamus and to the specific cortical regions from which they originated [121, 185]. The prototypical cerebro-cerebellar circuitry is depicted in Fig. 2.

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 [178, 188–190] and functions are represented asymmetrically [191]. 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 [192], the outputs of these circuits provide the cerebellum with the anatomical substrate to influence the control of both [177]. 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 more laterally [178, 193]. The inferior temporal lobes, essential for the category learning as described by Ashby, Seger, and others, do not appear to project to the cerebellum, which suggests that the cerebellum does not play a role in the categorization functions that facilitate aspects of procedural learning. At the same time, considerable evidence indicates that the cerebellum is essential for the automation of serial-order processing, which is another component of procedural learning [194, 195].

Over the past 15 years, just as evidence has accumulated that demonstrates that the cerebellum is connected to sensory and motor regions of the cerebral cortex, connections have

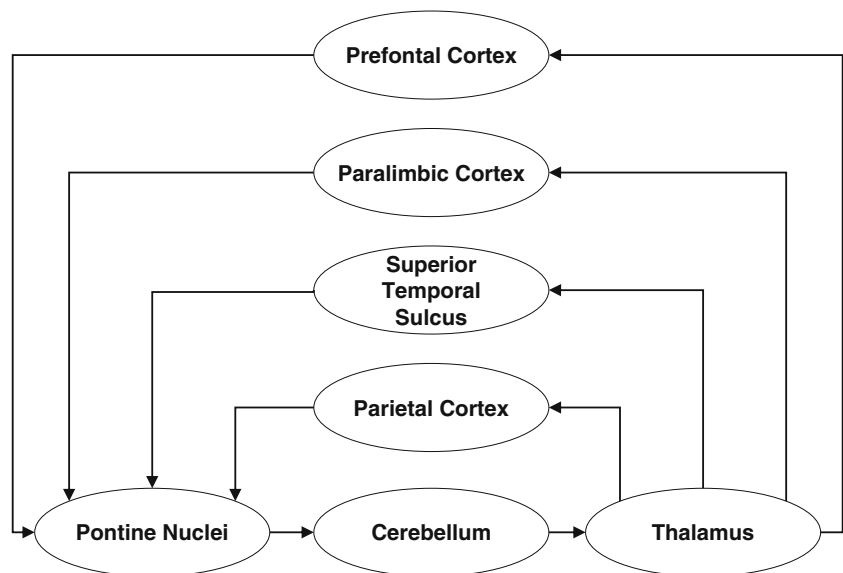
also been demonstrated between the cerebellum and nearly all regions of the parietal, temporal (though not inferior temporal), frontal, and prefrontal lobes [177, 182, 196–198]. Not surprisingly, as this broad spectrum of connections has been discovered, so has the understanding of the range of functions in which the cerebellum participates been expanded. In addition to its traditionally assigned roles in motor coordination, balance, and motor aspects of speech, activation has consistently been found related to cognitive and affective regulation, language, and spatial cognition [195, 199–201], and on tasks assessing attention and executive control functions, particularly working memory [202–207]. In fact, it can be difficult to find a task that does not recruit cerebellar activation. But why does this occur?

### Functions of the Cerebellum

In the main, the cerebellum's function is to refine the information it receives from the cortex and to send a refined, modified, or “corrected” neural signal (from the deep cerebellar nuclei, whether this output signal is primarily excitatory or, less frequently, inhibitory) back to the circuit's point of origin [208]. The widespread connectational pattern of the cerebro-cerebellar circuits implies that the cerebellum has both motor and non-motor roles, including regulating aspects of complex cognitive processing [207, 209]. This has obvious relevance for all cognitive processes including thinking and executive functioning, as well as for the complex cognitive processes observed in giftedness [210–214].

While the basal ganglia, through recursive interactions with the cortex, decide “when” to act by allowing the thalamus to release behavior, the cerebellum “teaches” the brain “how” to act within its specific circumstances. It

**Fig. 2.** Connections between the cerebellum and the neocortex



performs this role through refining the rate, rhythm, and force of behavior and adjusting the behavioral amplitude of responses so behavior is of appropriate *quality* for the given situation. For example, the volume of speech needs to be different in a library than at a rock concert. How quickly one speaks needs to be adjusted in relation to the capacities of the listener and the urgency of the situation. Words need to be integrated into meaningful prosodic strings, with emphasis placed appropriately, if the speaker's meaning is to be inferred. "You're going?", for example, connotes a completely different meaning than "You're *going*?" The cerebellum plays a role in the dynamics of these aspects of automated social skills communications.

### From Movement to Thought: the Construction of Cerebellar Models

Ito has proposed that for the brain, movement and thought are equivalent [215]. The control and manipulation of thought content is no different from the control and manipulation of body parts in problem-solving; so, once a movement or thought is "coded" within the neural circuitry of the brain, the brain will manipulate the input in an identical way. The basal ganglia perform their characteristic operations on motor behaviors and on thoughts. They inhibit the impulse to jump from one's seat as they inhibit the impulse to respond to a distraction with a shift of attention. The cerebellum performs its characteristic operations on movement and cognition as well [180, 215, 216]. While the white matter circuits between cortex and cerebellum provide the pathways for the cerebellum to change the quality of information projected to the cortex, the uniformity of the cerebellum's intrinsic cellular organization implies uniformity in the processing of information, regardless of its source of origin within the cerebral cortex.

In order for the cerebellum to exert an influence on behavior, it needs to "know" what the cortex has in mind and what it has decided to do. Cortical cognitive control can be referred to as "working memory" and is modulated by interactions between the prefrontal cortex, posterior cortices, and the basal ganglia [217]. However, widespread distinct and segregated cerebro-cerebellar circuits from the cortex to the cerebellum inform the cerebellum about the brain's plans and about the sensory characteristics of the environment. This circuitry allows the cerebellum to "copy" the content of the brain's cortical "working memory," or plans, and intentions. In the following general example, the content of cortical working memory is a motor program. It has long been understood that expertise in a given motor skill can be acquired by generating that motor behavior repetitively. Motor movements become quicker and more precise with repetition and practice. It is therefore no

surprise that, in sports, diligent practice is the key to the development of expertise. However, the same principles hold true for cognition, as will be described in the following paragraphs.

It is believed that the role the cerebellum plays in such processes is to facilitate the development of progressive, short-cut, anticipatory control models [218, 219]. These "models" comprise the most efficient neuronal pathways through which the repeated bodily movements can be executed most quickly [2, 220, 221]. In essence, a cerebellar internal "model" of what the brain thinks it will do is based on its storage of the multiple episodes during which it has already done so. As the movements are repeatedly executed and as anticipatory, predicted "feedback" is received from each instance, the cerebellum has more information and becomes increasingly accurate in its predictive capacities. It uses these increasingly accurate predictions to inform successive executions of the behavior. This allows behavioral execution to become smoother and faster and allows the brain to store the most efficient representation of that behavior [112].

Sensory feedback is cortically based, and it functions slowly [72, 86, 90]. This means that, if movements are to be rapid, coordinated, and smoothly and competitively controlled, they cannot depend on sensory feedback alone [222–224]. Cerebellar models allow behavior to become independent of cortical control and "working memory" input and to rely less and less on sensory feedback from the moving limbs for accuracy. With successful repetition, behaviors governed consciously by cerebellar feedforward models become more automated. As automaticity develops, it reflects the development of cerebellar "inverse" models. Inverse models permit rapid, coordinated, highly skilled movement to occur at an unconscious level, without the involvement of cortical motor programming regions.

The cerebellum's role in motor sequence learning has been demonstrated experimentally. Molinari and colleagues found that cerebellar lesions induced specific impairment in this capacity, which implicates a role for cerebellar circuitry in detecting and recognizing sequences of events [225, 226]. Park and colleagues investigated cerebellar volume in basketball players who had learned complex motor skills and had practiced them intensively for a long period of time [227]. They found morphological enlargement in cerebellar vermal modules VI and VII. Doyon and colleagues used fMRI imaging to demonstrate that procedurally acquired sequences of movements activated motor-related cortical (frontal) regions and that this activity was modulated within the cerebellum [228]. Higuchi, Imamizu, and Kawat used fMRI to visualize brain regions activated in human subjects who were imagining using a variety of common tools and in others who were actually using them. They found brain activity in the posterior region of the parietal cortex, in the

supplementary motor area, and in the cerebellum in both groups. They found that imagining activated premotor and right hemisphere pars opercularis and lateral cerebellar regions, while actual tool use activated the primary motor area, the thalamus, the left hemisphere pars opercularis, and more medial cerebellar regions. This suggests that the neural mechanisms involved in skillful tool use are organized modularly within the cerebellum and that thinking about acting (cognition) and acting (skilled motor behavior) are represented in separate cerebellar zones. We consider this modular segregation as extremely significant because it supports the idea that functions within the human cerebellum are segregated and specialized.

Vandervert asserts, and we agree, that working memory and the internal models established in the cerebellum collaborate through “deliberate practice” to produce mastery. Four critical research findings support this assertion [229]. These findings include that the cerebellum acquires internal models to manipulate a “new” tool through learning and that the cerebellum represents a cognitive component of the models for using tools more laterally [230], that various cognitive internal models are modularly organized within the cerebellum along a lateral-posterior gradient [230], and that the outputs of internal cerebellar models are projected to the premotor areas of the cerebral cortex (including Brodmann’s areas 44 and 45 for verbal material) after learning [231].

Once a representation is acquired, the model is referenced and refined to permit what is learned to be executed automatically [232]. The same cerebellar models that support the automatic execution of motor behavior also support the automated processing of information in cognitive and affective domains. Novel cognitive operations that initially rely on interactions between the networks of prefrontal and other brain regions that constitute “working memory” are increasingly mediated through cerebellar models as stimuli lose their novelty with repeated exposure and practice. The cerebellum functions as a “learning machine” as it uses exposure and practice to hone the speed and efficiency of working memory processing, thus “freeing up” slower working cerebral cortices so that their resources can be directed to resolving novel problems. The less mental “fuel” we need to use in a given situation, the more we have available to direct to other problems that require it. This represents a decisive adaptive advantage.

Balsters and Ramnani demonstrated that the prefrontal projection areas of the cerebellar cortex process cognitive information that is of a purely abstract nature [233]. The cerebellar region in question is HVIIA (Crus I and Crus II). This lobule receives projections from the prefrontal cortex via the pontine nuclei, and this area returns projections to the same areas of the prefrontal cortex via the ventral dentate nucleus and mediodorsal thalamus [127]. The

cerebellum’s role in thinking, cognitive expertise, and giftedness is to “speed up” cortical information processing held in “working memory” and make thinking more efficient. The cerebellum plays a comparable role in adaptively regulating emotional tone through circuits that connect it with paralimbic areas [234, 235]. Additionally, the cerebellum may play a role in facilitating motivation through its connections with the basal ganglia. For example, Hoshi, Tremblay, Feger, Carras, and Strick demonstrated that the dentate nucleus (which is primarily excitatory in its output) includes a projection into the striatum [236]. This pathway could conceivably enable cerebellar output to influence basal ganglia function, including the dopaminergic reward system, and thus influence motivated behavior. Bostan, Dum, and Strick recently discovered that the subthalamic nucleus of the basal ganglia (which often plays a critical role in stopping behavior and preventing impulsive responding) has a substantial projection to the cerebellar cortex [237, 238]. In addition, the subthalamic nucleus has three subdivisions, namely, the sensorimotor, associative, and limbic aspects. This connectional pattern provides an anatomical substrate for substantial two-way communication between the basal ganglia and the cerebellum to regulate several discrete functions. The functional specificity of this system might underlie aspects of a motivational network, including at the level of intensity that characterizes the “rage to master.” In this regard, the rage to master might be understood as a product of the cerebellum’s ability to enhance motivation in relation to a domain that the basal ganglia’s selection ability keeps in sharp focus. In other words, the “rage to master” is fundamentally a manifestation of the dynamic interplay between cortical and subcortical networks.

### The Role of the Cerebellum: a Practical Example

Examining your experience of reading of this paper may provide a means of understanding the ideas it presents. We will assume that if you are reading this paper, you are an “expert” reader, who knows the “rules” of reading, including how to read words, how to discriminate correct grammar, syntax, semantics, and sentence structure, and how to derive meanings of words. For you, most reading is automatic. In the earlier sections of the paper, in which ideas were somewhat familiar, you likely read quickly and comprehended everything with little or no effort. You were reading and comprehending in “real time.” However, as you reached the sections about the basal ganglia and cerebellum, you likely began to read more slowly. You might have paused to think about terminology, to contemplate functional neuroanatomy, and to consider the ideas and theories put forth. You might have re-read a sentence or

two, especially if the material was unfamiliar to you or if it contradicted something you previously had been taught. At that point, you were no longer reading in “real time.” What occurred? Why did this happen?

Your initial fluent reading was automatic. So long as the information was relatively simple, logical, and familiar, it was projected to cortical working memory and then through circuits in the cerebellum. Because the material was similar enough to information you have encountered before, the predictions your cerebellar forward internal models made were met well enough. Cortical information processing could “speed up” to permit you to read and comprehend quickly. An inverse internal model within your cerebellum allowed you to read all the words correctly, while the content-dependent “sensory–perceptual” cortex allowed you to glean meaning from what you read.

When you encountered novel terminology or content, however, or if you encountered information you experienced as contradictory or controversial, you could no longer rely on a cerebellar model that had met the material before. You could no longer generate forward predictions effortlessly. You had to slow down as you relied more on your measured and deliberate cortical “working memory” processing. Reading the material a second and third time allowed you to establish a new forward model. In essence, you took something novel and made it more routine or familiar. This made the material easier to understand and you were able to re-read and comprehend this “new”—but not longer “new”—information in real time. With more repetition, your understanding and assimilation may have even become a little more “automatic.” This example illustrates the relationships between your cortical processing, working memory, and the cerebellar contribution to your ability to adapt. These processes occur in other domains of expertise besides reading. They are clearly applicable in the case of giftedness and prodigy.

### **Cognition as an Extension of the Motor Control System**

Understanding that the cerebro-cerebellar circuit mediates the acquisition of expertise for motor skills as well as for affective and cognitive behaviors is a critical component to understanding Winner’s concept of giftedness. Consider the following example.

Suppose you decide to update your office by replacing your existing cabinets. You purchase several multi-piece units from a large Swedish furniture store that ships everything in flat boxes and provides complex directions for assembly. You open the boxes and, using cortical, working memory prefrontal-parietal lobe connections, establish a plan to assemble the first one. You decide to build the frame first and then to put together the drawers.

Doing this efficiently requires you to derive a “working memory” plan, comprised of a series of ordered thoughts about what to do. You derive this plan then translate it into a motor program, which you execute when you pick up the allen wrench and start screwing components together.

You rely on your cortical working memory when you are thinking about assembling your cabinet *and* when you are actually doing it. The plan you make is the conceptual analog of the motor movements you ultimately generate to carry your plan through. In this way, cognition (in this case, working memory) can be seen as an extension of your motor control system.

The first cabinet takes you an hour to put together. You modify your plan as you approach the second cabinet, having discovered that all drawers need to be assembled before you integrate them into the frame, having discerned which holes are meant for bolts and which are meant for little wooden pegs, and having experienced that tightening bolts on one side of a cabinet before all connections on the other side have been joined is a mistake. Your approach to the second cabinet is more efficient, as you can assemble pieces with less effortful cognitive input than you required on the first. You move faster and make fewer mistakes as your assembly skills become increasingly automatic and require less higher-order control. By the time you get to the last cabinet, you are a whiz! The first cabinet took an hour to assemble, but the last one takes only 10 min. You have transformed from an unskilled laborer into an “expert” assembler.

This example illustrates the degree to which adaptation depends on our ability to interact with the environment effectively. Cognitive activity allows our motor responses to be flexible, so the motor system can generate new behaviors in relation to things that change in the environment. As such, it is reasonable to conclude that cognitive activity evolved as a *result* of the motor system and that the evolution of cognition has in turn become an integral factor in streamlining motor activity *and* thought to make each of them more efficient.

But the higher-order cognitive control that operates in novel circumstances works very slowly, while the critical adaptive advantage lies in our ability to “automate” the skills necessary to function within different life domains. The function of cerebro-cerebellar circuitry allows our behavior to become more automatic and procedural with repetition. Cerebro-cerebellar circuitry, acting upon the content of working memory, does not differentiate between manipulating a serial-order sequence of body parts (movements) or a sequential order of thoughts. Indeed, motor and cognitive development are intimately intertwined, as eloquently described by Diamond [239]. Consider another example.

You decide to take up golf. This process makes considerable cognitive and motor demands. On the cognitive side, you need to learn about the range of golf clubs that can be used and how to match the choice of club to the

circumstances. Each wood and each iron, for example, are used for different distances under different course conditions, and the putter is in a class by itself. You must learn about the different hand grips and the different swings or strokes associated with each club, and you must learn how to estimate distances the ball must travel. When you play, you must incorporate all this conceptual information with knowledge of the weather and the conditions of the grounds. All these aspects of learning to play golf are cognitive activities.

To play, you transfer this cognitive information into your motor system. You get to the course, your executive makes a plan regarding which club to select, and you recall and retain in working memory the knowledge about how to swing it. From this conceptual base, you step up to the tee and take your first swing. And your second. And your third. Early swings, guided entirely by effortful thought, are likely to be disintegrated and clumsy. With repetition, (if you can tolerate the humiliation and stick with it), you develop cerebellar models that render your swing increasingly automatic and fluid. These models will allow you to process all the essential information necessary to generate an effective swing much faster than you could ever hope to accomplish were you to depend upon your cortex and the slow processes inherent in cortical sensory–perceptual feedback. With enough repetition, your swing will become so automatic that conscious, cognitive control can disrupt it. It is reasonable to assume that a tournament or two has been lost because a distraction was introduced that made the golfer “think” about what he or she was doing at the last hole.

The cerebellar processes involved in becoming an expert golfer or basketball player are the same as those involved in developing expertise with a computer keyboard, learning how to read and spell words efficiently, developing the skills necessary to perform a full range of arithmetic computational operations, or learning the layout of the piano keyboard in the process of becoming an expert pianist [34, 240]. Each skill requires automaticity in functioning that depends on forward and inverse cerebellar models, which become increasingly refined as behaviors are practiced and repeated. Speed, focus, rate, rhythm, and overall refinement of movement, thought, and emotional/affective tone become increasingly “adapted” as the expert become more experienced [241, 242]. As Vandervert observes, we can think of “giftedness” as a manifestation of these same basic adaptive processes.

### **An Integrated Functional Neuroanatomy of Giftedness**

Our theory of giftedness and prodigy needs to take Winner’s three main factors into account. These characteristics include the gifted child’s precocity, which results in

rapid progress in the domain and mastery at an early age; the child’s achievement of mastery with minimal adult assistance and his or her ability to be motivated by the excitement associated with making “discoveries”; and the centrally important “rage to master,” which fosters high achievement through a combination of high interest in a domain coupled with an ability to learn it easily. These essential features of “gifted” populations are supported by white matter circuits that connect the cortex to other parts of the cortex to support working memory, by white matter circuits that connect the cortex and basal ganglia to guide selection, and by forward and inverse models that are mediated through white matter circuits that connect the cerebellum and cortex to facilitate cortical information processing. These processes operate simultaneously and analogously and provide a solid illustration of network and computational models of brain–behavior relationships.

### **Precocious Interest**

There is limited objective data available that explains the phenomenon of precocious interest in a particular domain [243–245], and none of it clarifies which comes first. Does a gifted child have a precocious interest in a certain domain because of an innate ability, or does ability depend upon environmental exposure or experience? We know that biology and training are both important and that they interact [246, 247], while the heritability of IQ in young children is modified to some degree by socioeconomic status [65]. From a neuropsychological perspective, it appears that the infant’s environment and his or her unique temperament contribute to the development of precocious interest in a domain. Temperament is associated with emotion and its regulation, which are foundational for attentional focus and inhibitory control [248–250]. Focus and inhibitory control, in turn, are governed by the activity in circuits between the cortex and basal ganglia and the cortex and cerebellum. So, how can we understand the neuroanatomic geography through which domain choice must navigate?

Visual processing, attention, memory, and cognitive control rely on the development of distinct yet interconnected sets of anatomically distributed cortical and subcortical regions [38]. The developmental process through which these circuits become organized is remarkably complex. It is influenced by genetic predispositions and environmental events, and it is influenced by neuroplastic responses to experiential demands. Each demand and each response the brain makes to it influences how neurons are connected to one another and influences how they communicate. This occurs within individual brain regions and circuits and across neural pathways (p. 147).

Brain structure and function change dramatically during the early postnatal period and onward. Brain volume increases during the first year of life, which is greatest in the cerebellum, followed by other subcortical brain regions including the basal ganglia and then by regions within the cerebral cortex. The neural circuits that subserve attentional functions mature before the circuits and networks that support socio-emotional processes do [116, 251, 252], and the fundamental capacity for working memory is solidly in place by middle childhood [253, 254]. In other words, the mechanisms that support attentional and action selection, motivational interest, working memory, and cerebellar rehearsal of the content of working memory content are in place early in development. This creates the neuroanatomic stage upon which giftedness plays out.

The development of circuitries between cortical and subcortical regions has been correlated with the development of cognitive and behavioral functions [38]. Various anatomical and functional neuroimaging studies have demonstrated that abnormalities within the orbitofrontal cortex, anterior cingulate circuitry, and the striatum (caudate and putamen) disrupt the functioning of frontostriatal circuits [255, 256]. Differences in the development and maturity of these circuits also help to explain the behavioral “oddities” and comorbidities that are often attributed to children who are described as gifted [257]. Because this manuscript focuses upon adaptation, expertise and giftedness, we have made a concerted and conscious effort to avoid cognitive psychopathologies that might be associated with the diagnosis or “misdiagnosis” of deficits within these operationally defined parameters. Our future work will directly address these controversial issues.

### **Precocious Interest, Independent Mastery, and High Achievement**

According to Kinsbourne, there are two ways to generate a behavior [258, 259]. A behavior can be generated because it is inherently reinforcing. These are the activities that a child—or adult—enjoys performing. Different people find different activities inherently reinforcing, which is likely a function of innate biologic capacities or predispositions coupled with their experiences in the world. Participating in successful experiences is rewarding, provided that our reinforcement circuitry is functionally intact. Hence, the more we do, the more we want to do, and the more reward comes our way. Participation brings interest, which focuses attention and guides behavior. Were someone born with a biological predisposition to experiencing reward, such as with a hyperactive medial/cingulate–striatal–thalamic–cortical circuit, an early interest in performing an activity could be readily enhanced by the feeling of reward obtained from participating in it [260].

Understanding how the relationship between the cerebral cortex and the basal ganglia governs intention programs helps to explain several essential features of giftedness. The intrinsic motivation to mastery, the sharp focus of attention, and the intense, obsessive interest in the domains gifted individuals pursue imply an over-focused, *perseverative* attention that is resistant to distraction. Within the interactive mechanisms of the prefrontal cortex–basal ganglia, we hypothesize that these characteristics particularly involve medial/anterior cingulate circuitry that projects from the medial frontal lobe/cingulate cortex to the ventral striatum/nucleus accumbens region, to its specific target in the rostromedial nucleus of the thalamus and then back to the anterior cingulate area. The place and role of the nucleus accumbens within this circuitry drives this prediction. The nucleus accumbens is a critical reward/reinforcement center located within the basal forebrain [31]. Hypoactivity within this circuit is manifest in disorders characterized by a lack of motivation and even apathy.

In contrast, hyperactivity within this circuitry would generate the intrinsic motivation to propel perseverative attention and intense, obsessional interest [120, 261, 262]. We believe that this is one of the central neuroanatomic processes driving the “rage to master,” seen in gifted children [42]. In this regard, the striatal direct pathways are functionally matured in childhood, while the indirect pathways are immature in young children, attaining adult levels in approximately the middle of the second decade [263]. While the development of the cortico–basal ganglia system appears to be under genetic influence, precocious development within this circuitry would easily account for enhanced motivation. Therefore, the multiple white matter connections between cortex and basal ganglia, which are greater in gifted children, as cited above, would support this level of activity and the resulting extreme behavior, while functions transacted in circuits that connect the cerebellum with this “limbic striatum” contribute as well by exaggerating the “force” of the motivation.

If we recall that cerebellum regulates the rate, force, and rhythm of the input it receives—whether it be associated with motor behavior, affect, motivation, or cognition [264], it is believed that the cerebellum would accelerate the “force” with which that reward was experienced [235]. In this way, a sensitive reward system is the recipient of just that much more good feeling from the same activity that generates a more ordinary amount of good feeling and satisfaction in a more ordinary reward system. For example, it has recently been demonstrated that the cerebellum becomes extremely active during sexual activity. While sexual activity is an arousing motor behavior that is associated with autonomic responsiveness (and presumably those regions of the cerebellum that contribute to the processing of arousal through reciprocal reticular and hypothalamic connections), it

would be expected that regions of the cerebellum participating in motor and autonomic regulation would be activated, which was demonstrated in this particular investigation. However, significant recruitment and activation were also observed within the medial cerebellum, with the highest levels of cerebellar activity observed within the vermal region, which Schmahmann has termed the “limbic cerebellum.” [264]. Sexual activity is inherently powerfully rewarding and presumably dependent upon the activation of “pleasure centers” [265, 266]. The “limbic cerebellum’s” role in sexual activity makes neuroanatomic sense given that the same cortical regions projecting to the striatum also project to segregated regions of the cerebellum, while the feedback projections arrive at the same points of origin [112, 267]. It is likely that the “loops of interaction” from the ventral or “limbic striatum” to the cerebellum regulate the “force” of interest and reward. This process regulates emotional tone and can easily be construed as driving precocity, early and persistent motivation, and the “over focused” attention and selective inhibitory control characteristics of the gifted child. In this regard, we are merely translating the reward characteristics of a survival behavior to a cognitive domain, while relying on the principle that functional brain systems are organized in parallel [268].

The neuroanatomic foundations for these hypotheses are supported in at least four ways. First, as reviewed above, prefrontal regions, which participate in “coding” for the evaluation of reward, project to the striatum through the striosomal pathway, along with projections from other cortico-limbic/paralimbic regions. As indicated, this pathway provides the basal ganglia with information concerning the reward value of various thoughts and behaviors. These limbic areas assess the significance of “sensory input.” Information concerning the expected or anticipated outcome of this evaluation is projected to regions of the basal ganglia that control the dopaminergic system in reward-driven association learning [40]. This allows the basal ganglia to “see,” learn, and/or release the most rewarding activity. Participation in the activity then generates further interest and reward, which propels motivation.

Second, these same paralimbic cortices send projections to the cerebellum through cerebro-cerebellar circuitry [269]. The cerebellum’s contribution to affective function has been established and reviewed by Schmahmann [270]. Cerebellar connections have been established for arousal (the reticular system), autonomic function and emotional expression (hypothalamus), emotional experience and expression (limbic system), and cognitive dimensions and appraisal of affect (paralimbic and neocortical association areas). Therefore, cerebro-cerebellar circuitry has been established for a potential role in motivation [271–273].

Third, while defining the cerebellum as a “refining mechanism” is overly simplified, it remains useful to think

of the cerebellum as functioning to modulate the “rate, rhythm, and force” of behavior [274, 275]. In this regard, we postulate that excitatory connections from deep cerebellar nuclei back to these regions of origin (reticular system, hypothalamus, limbic and paralimbic cortices) can play a critical role in influencing the reward system in relation to generating the “rage to master.” Anderson, Mass, and Frederick et al. have established roles for the cerebellar vermis as a locus of sensorimotor integration and motor planning as well as in incentive-related behaviors [276].

Fourth, it has recently been discovered that the basal ganglia (which run on the basis of reward-driven association learning) and the cerebellum are directly connected with each other [238]. As noted above, the dentate nucleus projects to the striatum (caudate and putamen), which is the source of most input into the basal ganglia—including information about motivational valence—while the subthalamic nucleus (STN) (essential for “stopping” activities and which is topographically organized into sensorimotor, limbic, and association subdivisions) projects to the cerebellar cortex. Therefore, the neuroanatomic groundwork appears to exist for the cerebellum to influence dopaminergic reward-driven behavior (motivation). At the same time, abnormal signaling from the STN to the cerebellum might serve to enhance incentive-related, motivated behaviors, which would further contribute to the “rage to master” [277]. These connective patterns suggest that neuroscience may need to rethink its original conceptualization of the “dopaminergic” reward system as confined to cortical–basal ganglia relationships, while it considers motivation and incentive-related behavior from a more integrated perspective that encompasses cortical, basal ganglia, and cerebellar interactive circuitries and includes consideration of the role played by neurotransmitters other than dopamine [278, 279], a discussion which unfortunately is beyond the scope of this manuscript.

While some behaviors are generated in the context of immediate reward, others are generated with a promise of a reward later, after they are completed. These are typically understood as behaviors that depend on higher-order control and/or “executive functions.” These executive systems are not as well developed in children as they are in adults [280, 281], whose reciprocal connections between prefrontal and sub-cortical regions are more mature. Houk and Wise conceptualize output from the cerebellum as guiding the frontal cortex, training prefrontal regions to perform in a highly efficient and “automatic” manner [267]. The enhanced reward, reinforcement, interest, and motivation that accrue by participating in tasks associated with a given domain allow basal ganglia and cerebellar inputs to force these functions on the prefrontal cortex. This would contribute to the over-focused attention of the gifted child and his/her “rage to master”. The drive in the “rage to master” seems to

have a life of its own and an all-encompassing ability to direct attention, even if the child is uncomfortable in the short term while thus engaged. In this way, the rage to master might be considered a type of compulsion. We believe that these circuitries, operating within an interactive framework of other cortical and subcortical interactions, generate the high levels of motivation and achievement described by Winner.

At the same time, we believe that hyperactivity within dorsolateral prefrontal circuitry contributes as well. Reduced cognitive flexibility associated with hyperactivity within this circuitry makes shifting set difficult and further drives perseverative behavior. In gifted children, this would manifest in an obsessive, rigid preoccupation within a domain of interest to the exclusion of interest in—or ability to direct attention to—other domains of life. What propels mastery and achievement in one area may limit the development of competence in other “domains.” From a clinical point of view, these children could easily be described as exhibiting abnormal attention. In fact, they do. Benefits are associated with their ability to master a domain or domains at levels of complexity that go far beyond what “ordinary” children can accomplish. But there are social consequences because limited exposure to, and ability to profit from, non-domain related experiences may lead these children to behave in ways that seem odd, strange, socially peculiar, or deviant. Groups of gifted children have been described as misunderstood or even “misdiagnosed” on this basis [257]. However, we believe that these features of the presentation of gifted children make good sense from a neuroanatomic point of view and even put this population “at risk” for developing psychological and psychiatric disorders.

Ericsson, Krampe, and Tesch-Romer have demonstrated that the levels of achievement reached in athletics, ballet, bridge, chess, piano, violin, and the like correspond very highly with the amount of “practice” in which the individuals in question have engaged or participated [43, 282]. Even if achieving mastery is very difficult, those who spend the most time working toward it, repeating and practicing skills over and over again, are the people who reach the highest levels of achievement and performance. Ericsson and his colleagues refer to this type of repetition as “deliberate practice.” Hyperactive dorsolateral prefrontal-basal ganglia circuitry would easily propel the lack of flexibility inherent in this level of deliberate practice.

Ericsson and colleagues also found that the higher the level of achievement attained the earlier the level of exposure to the domain. This association was attributed to the earlier age at which deliberate practice was initiated, which allowed more hours of it to be accumulated [283]. A recent study of achievement of chess mastery reached identical conclusions [284]. Those who achieved the highest levels at the grand-master level started to play chess at a younger age and devoted more time to playing. People who came to the game

when they were older could become very good players, but they never achieved the same levels of mastery that were observed in the younger players and the “chess prodigies” regardless of how much they practiced. These findings suggest that indeed “practice makes perfect,” but not under every condition. And it suggests that the younger, more “plastic” brain can develop the neuronal connections for the skill in question earlier in life and more quickly than the older adolescent or adult. As the brain matures, it becomes less able to organize and reorganize neuronal connections [285]. This has been reported by Diamond in her discussion of the cerebellum, motor development, and executive control and has also been demonstrated in very young children with the surgical removal of posterior fossa tumors [239, 286].

Though Ericsson conceptualizes the dynamics of “deliberate practice” as occurring within the framework of an entirely cortico-centric model, the neuroanatomic impact of “deliberate practice” is explained by the collaboration of cortically based working memory functions and the cognitive functions of the cerebellum [4, 51, 90, 215, 220, 224]. All deliberate practice, or repetitive working memory functions that are presumably localized in prefrontal-cortical networks, are “copied” within the cerebellum. While Ericsson concretely refers to deliberate practice as under conscious control, his conceptualization fails to take into account Imamizu’s and Ito’s findings that the quality of adaptive functioning, expertise, and even giftedness improves with repetitious experience mediated by the cerebellum *outside* of conscious control [220, 230].

It is important to highlight and reiterate that the cerebellum develops *both* forward and inverse models. In other words, the cerebellum constructs “pairs” of models. The forward model is a representation of mental activity that originates within cortical working memory. The inverse model is the unconscious representation of that model, which fosters automatic behavior independent of conscious cognitive control. The cerebellum is constantly constructing multi-pairs of models that constitute a complex modular architecture for the control of mental processes [229, 287, 288]. These authors, and Ito, propose that new, higher levels of performance are facilitated when these modular architectures of mental activity are projected to new working memory processes within the cerebral cortex [90]. These concepts represent significant steps forward in our understanding of the neurodevelopmental geography of expertise and giftedness. These concepts take Ericsson’s ideas and expand them into a neuroanatomical framework that refines our understanding of how they operate.

Imamizu and others have referred to this process as Hierarchical Modular Selection and Identification for Control (HMOSAIC) [230]. Forward models are constructed on the basis of anticipation. Since cortico–cortico sensory feedback works slowly, fluid movements (or sequences of thoughts and

ideas) cannot occur in “real time” if they are modulated or controlled by the cerebral cortex. By anticipating sensory input and storing a memory of behavioral outcomes, the brain learns, through practice, from the repetition of successful forward models. The brain learns from its experience of interacting with the environment. The successful forward model eventually becomes an inverse model, which controls movements (or thoughts and ideas) automatically, independent of conscious control. Moving from one skill level to the next with practice allows previously acquired routines to be connected to higher levels of performance, as forward and inverse models are combined [230].

The modular specificity of segregated cerebro-cerebellar circuitry, the regional specialization of the cerebral cortex, and the compartmentalized organization of the basal ganglia and cerebellum explain why an individual can master one domain and not another, why an athlete can master a sport but not a cognitive activity and vice versa, and even why an individual with low general ability—or low “g”—can acquire expertise in a particular domain. The modular, hierarchical organization of this system serves as an important key to understanding that motivational, cognitive/attentional, emotional, and motor modules are all involved and interact to contribute to the precocity, self-motivation, the “rage to master,” and the rapid progress in the domain of choice that are all characteristic of what is observed in giftedness. In simple terms, deliberate practice results in gradually increasing hierarchical control by the cerebellum. These levels of cerebellar control might be considered as analogous to the levels of expertise. The greater the cerebellar control the greater the development of new, higher levels of performance. The processes by which levels of expertise are established occur within the hierarchically organized framework of cognitive–subcortical control.

### Intuition and Discoveries

Not only do gifted children make rapid progress within their domain of choice, but they also seem to make discoveries. These discoveries have been described as “intuitive,” and the nature of this intuition has been vigorously debated on [289–291]. From the point of view of functional neuroanatomy, not all intuition is alike. Certain intuitive skills are under the mediation of the basal ganglia. Other types of intuitive thinking appear to be under the control of the cerebellum. We explore these types of intuition in the following two sections.

### The Basal Ganglia, Intuition, and Expertise

Gregory Ashby and his colleagues refer to aspects of the development of expertise as related to “information

integration learning,” a specific type of category learning that is considered to be under the mediation of the basal ganglia and, specifically, with involvement of the temporal and parietal circuits [128, 292]. In this model, accurate, expert decision-making occurs at a “pre-decisional” stage, when information from two or more stimulus dimensions is integrated. This occurs as part of an automatic process, dependent upon reward-based instrumental learning/categorization, that is not under conscious control. Experts relying on information integration to generate optimal strategies for decision-making often find it difficult or impossible to describe the strategies they are employing in verbal terms. The learning and decision-making are experienced as “intuitive.”

All “expertise” does not appear to be alike. In professions and activities in which visually dependent categorization is critical, the basal ganglia play a vital role in learning and in the acquisition of expertise [141, 142, 293–295]. Ashby provides the example of decision-making by the expert radiologist versus the competent novice. How is it that the novice is uncertain as to whether or not an ambiguous radiologic image is a tumor, while the seasoned, experienced radiologist immediately dismisses it as benign “noise” in the system? Ashby and others believe that years of practice and experience allow expertise to be acquired at a level that permits correct categorization to become intuitive. Information acquired consciously is integrated with the process of ongoing categorization and decision-making that goes on in the background. This results in the acquisition of expertise, presumably founded upon instrumental reward and procedural learning processes. Immediate feedback plays a critical role in facilitating this type of procedural learning [128]. This “feedback” is associated with the “reward” which generates the development of this type of intuition. A consciously perceived visual “fact” is associated with an abstract, non-verbal experience while coupled with instrumental reward. Then, in the future, under similar conditions, the same instrumental choice or decision is made. Because part of the association was abstract and could not be verbalized, the decision is experienced as “intuitive.”

Aspects of expertise in the game of chess are also believed to be dependent upon skills in rapid visual–perceptual categorization [296]. One study examined whether expert chess players and novice chess players differentiated and recognized “checking” chess piece configurations and “non-checking” piece configurations differently. Chess experts were superior to novices in the speed and accuracy with which they judged both types of piece configurations. The authors concluded that facility with perceptual chunking or categorization enabled experts to engage in complex visual processing outside of conscious awareness [283]. These data are consistent with the categorization functions mediated by

the basal ganglia. The cerebellum does not appear to take part in this type of category learning.

Understanding the role of the basal ganglia illuminates the dynamics contributing to the development of expertise in individuals who develop a high level of competence through experience, but it does not explain the gifted individual's ability to make intuitive discoveries in areas of adaptation not based upon categorization learning [48, 50]. To understand this, we need to turn our attention to the cognitive functions of the cerebellum.

### The Cerebellum, Intuition, and Cognitive Discoveries

In his Internal Model Hypothesis, Ito describes “intuition” in problem-solving arising from the relationship between the cerebellum's rapid, unconsciously mediated manipulation of motor and cognitive activities and explicit thought processes that are consciously experienced, or occur, within the cerebral cortex [90]. The prefrontal cortex, along with the appropriate parietal and/or temporal cortices, is activated as the individual establishes a conscious “model” of the problem within the higher-order control system of cortical working memory. Cerebro-cerebellar circuitry copies the content of this working memory within the cerebellum. As problem-solving thoughts are consciously repeated, an internal model is formed within the cerebellum that mimics the cortically based working memory model. The unconsciously driven forward model established by this process replaces the original, consciously driven model that was maintained in working memory. At the same time as we might consciously remain aware of our original plans and strategies, the forward model is manipulating thoughts and ideas within the cerebellum, which is operating outside our conscious awareness.

We remain aware that we are thinking because the prefrontal cortex (and associated cortical regions) that initially conceptualized the problem remains activated. These areas receive feedback as the cerebellar manipulation of the forward model begins to represent a correct solution. This “solution” is projected back to the prefrontal cortex through the feedback arms of the cerebro-cerebellar circuits, which completes the loop. We now have conscious awareness of the solution, which we feel we have grasped intuitively, as if it “popped up” out of nowhere [90, 229]. This explanation illustrates further how output from the cerebellum guides or directs frontal systems and trains and instructs prefrontal-cortical networks to permit us to manage and control “problem-solving” with increasing efficiency [224, 267]. In very simple terms, the forward model appears to instruct or “teach” the prefrontal cortex about the discovery or solution. It then becomes “old hat” and becomes the inverse model, a new automatic behavior. This process occurs outside conscious awareness.

This model allows us to understand how problem-solving capacities necessary for adaptation, expertise, and the intuitive solutions that characterize “giftedness” exist along a spectrum or continuum. They are explained by the hierarchical organization of the HMOSAIC. In fact, the development of skill in all endeavors—from academics, to art, to chess, to dance, to music, to sports, and to the discoveries of modern technology and thought in general—can be explained within this “network architecture.” This is the functional neuroanatomic geography within which all these processes occur. We make no claim to understanding a “g” factor or the issue of domain of interest. We are simply proposing that multiply determined factors such as general ability, talent, and interest are modifying factors that operate within this geography of brain–behavior relationships.

### The Savant Syndrome

While neuropathological conditions are in general outside the focus of this paper, it seems appropriate to briefly discuss the “savant syndrome,” since this condition has been reported to occur in patients with severe mental handicaps that significantly impair functional adaptation. Although “savant” might be defined in a variety of ways, we adhere to a very strict definition, in accord with what was initially described by Treffert in his summary of the observation of Dr. Down [297]. The savant syndrome is an exceedingly rare condition. This term refers to individuals with significant mental or cognitive handicaps—from autism to mental retardation to schizophrenia—who simultaneously demonstrate seemingly superior ability in a particular domain of functioning [298]. The primary areas in which these spectacular abilities are observed usually concern music, art, mathematics, or declarative memory functioning [42]. Savants typically do not demonstrate superior functioning in multiple areas of cognition. However, whatever ability they possess stands in marked contrast to the severity of their disorder. In fact, these individuals are usually so impaired that they are unable to live independently; they require the support of family or some form of custodial care. We believe this is a key point in understanding the condition.

In attempting to explain the savant syndrome, investigators have heretofore relied upon a cortico-centric model of cognition. These investigations have generally been restricted to what the savant *can do*, and the “splinter skill” has been attributed to cortical functioning. We believe that it is misleading to attempt to understand the given skill in isolation. Instead, we believe that it is essential to consider the skill of the savant within the context of his/her disability or impairment. This is a synergistic approach that is consistent with a dual-tiered model of brain functioning that integrates the roles of the cortex, the basal ganglia, and the cerebellum in adaptation.

For the sake of brevity, our discussion of savants will be restricted to those with diagnoses of autism (in contrast to considering the more expansive concept of autism spectrum disorder), since it has been observed that this syndrome occurs in approximately 10% of the patient population diagnosed with classic autism [297, 299]. We are unaware of frequency estimates of savant in other diagnostic conditions. Savants have been described as exhibiting abnormalities in multiple cortical brain regions [298]. It may very well be that the syndrome is not a monolithic, unitary entity, or “one thing,” and that it might occur for more than one reason. Because of the condition’s rarity, there are no systematic studies with patient groups that share the same pathology and comparable savant behaviors. Explanations of the savant syndrome are thus highly theoretical. They are based upon minimal behavioral and neuropathological evidence and therefore remain controversial. The savant syndrome’s rarity might itself be accounted for by the putative relationships between multiple brain regions. Most behaviorally defined pathologies involve abnormalities in multiple cortical and subcortical brain areas (as reviewed by Koziol and Budding [39]). The more the involvement of abnormal brain tissue/functioning at multiple levels (e.g., cortex, basal ganglia, cerebellum) the less likely it is that the person thus afflicted will develop functional skills.

Behavior resulting from damage to a particular brain region does not reveal the function of that brain region. Instead, the resultant behavior reveals how intact brain areas perform behaviors without the affected brain region’s input or contribution. Most cases of autism feature multiple regions of impaired brain function, including many cortical areas [303], but autism has been consistently associated with varying degrees of cerebellar abnormality [300–302]. The autistic child has *never* experienced the cognitive benefit of a fully functional cerebellum; the cerebellum essentially “feeds” the cortex “bad” information. We thus propose that the degree of neuropathology is inversely proportional to the likelihood of savant syndrome development. In other words, the more widespread the pathology in the brain the less likely the development of savant behavior. Savant syndrome might be exceedingly rare because there are so few cases of autism that do not have such widespread pathology.

This is an extremely significant point. It explains why the autistic savant is unable to function independently, without some form of custodial care. The autistic child, and/or savant, does not develop a dual-tiered system of cognition and development. Deprived of functional cerebellar input, there is no opportunity to develop the forward and inverse models that are critical for instructing, directing, or guiding frontal systems. Without cerebellar models to instruct and train prefrontal-cortical networks to develop hierarchically organized automatic behaviors, the individual lacks the capacity to

control and manage efficient, flexible problem-solving in novel situations. Without cerebellar models, executive functioning and the associated dual-tiered system necessary for autonomy and adaptation do not develop successfully. It is thus within this context that the seemingly “superior” ability of the savant should be considered.

We believe that the savant’s exceptional abilities, which manifest particularly in music, art, math, or specific memory functioning, are in large part manifestations of interactions between specific regions of the cortex and the basal ganglia. Cortical–basal ganglia interactions mediate rule-guided behavior [304]. A functional cortex interacting with regions of functional basal ganglia can generate adaptive behaviors, but these behaviors are rigid and inflexible. For example, imaging and rare autopsy investigations reveal a sparing of temporal regions in certain cases of autism, primarily within auditory cortex and the planum temporale, which are the brain regions known to support musical ability [30]. Numerous studies have demonstrated that musical performance features significant cortical–striatal interactions [305–307]. The compositional and improvisational competence that has been demonstrated in autism is restricted to an adherence to highly structured, familiar musical “rules,” and therefore differs from the spontaneous and original improvisations of the normal control professional musician [308]. In this regard, the seemingly superb musical ability of the savant is *not* so similar to what is observed within the professional musician and does not meet the definitional requirements of “giftedness” as described by Winner. The absence of forward and inverse models limits creativity or improvisational “discovery.” (Treffert has indicated a growing belief that, over time, certain musical savants have developed some improvisational skill. However, this slow development of improvisational ability does not at all meet the criteria of “giftedness” proposed by Winner nor does Treffert’s observation provide an operational definition of improvisation. This renders his conclusion impossible to evaluate from an objective viewpoint.) Studies have also investigated auditory–motor interactions in music perception and production [309]. These studies have implicated the supplementary motor cortex, the basal ganglia, and the cerebellum in the performance of music as a natural human activity. Unfortunately, these studies focus on the normal control subject and shed little light on the processes and brain regions that are involved in savant musical ability.

Cortico-striatal interactions are centrally important in other domains of behavior in which savants excel. As Winner also points out, the artistry in the drawings of the savant lack creativity, and while the actual artistic product is extremely accurate and often esthetically pleasing, the reproductions are drawn from the subject’s observation and/or memory. Ferretti, Roulet, and Sargolini have demon-

strated that the ventral striatum plays a critical role in interacting with the medial temporal lobe during spatial information processing and spatial memory. This demonstrates that cortical–basal ganglia interactions govern “rule-guided” behaviors, including those associated with making and storing visual graphic representations [310]. While mathematical calculation models differ considerably in their assumptions concerning the representation of arithmetic facts, one model proposes that these mathematical facts are stored as *sequences*, which would again be the product of cortical–striatal interactions [311]. Superiority in aspects of memory (train schedules, timetables, athletic records, horse-race winners, calendrical recall) involves a ritualistic, obsessional preoccupation with some limited aspect of the environment. Some of these “skills” are dependent upon rules, regularities, and redundancies that are implicit [30]. Superiority in this type of memory can be understood, in part, as the product of the behavioral sequencing processes of cortical–striatal interactions, while certain aspects of superior declarative recall can be understood as the product of an intact CTH network. In fact, it could be argued that, in the absence of appropriate cortical-cerebellar interactions, certain cortical regions might be more “available” for the storage and retention of information processed within the CTH network. This could conceivably generate superior storage capability.

Finally, it is of interest to note that there is no savant on record who has ever made a “new discovery” that has contributed to the advancement or knowledge domain of any area of expertise, whether it be music, art, or mathematics [42]. The superior abilities of the savant, therefore, are really not the same as the flexible ability of the expert nor are they comparable to the capacity for discovery and true brilliance of the gifted. Without cerebellar models, adaptation, expertise, and giftedness cannot be achieved. We believe that the proposed dual-tiered model of adaptation that requires the participation and interaction of cortex, basal ganglia, and cerebellum represents nature's solution for flexible, effective adaptation and provides the opportunity for the development of expertise and giftedness.

## Summary

We have presented a comprehensive model of human adaptation that considers cognition as an extension of the motor control system. This model is dependent upon critical reciprocal relationships between the neocortex, the basal ganglia, and the cerebellum. We have included an extensive functional review of cortico-striatal and cerebro-cerebellar circuitry, including a putative direct functional relationship between the basal ganglia and cerebellum. These networks

allow for a dual-tiered model of behavior characterized by the flexible co-existence of elegant and automatic stimulus-based responding alternating with higher-order executive control. While this model can and has been applied to various pathologies, this system additionally enables a neuroscientific understanding of expertise and giftedness, including diverse presentations such as savant syndrome. This model therefore also allows giftedness to be considered in relation to the various pathologies with which it is often seen to occur. This in turn allows a more fully integrated understanding of human cognition across multiple levels of function and development.

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