

69 Cerebellar Contributions to Cognition and Imagery

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ABSTRACT The cerebellum has traditionally been viewed as an integral part of the motor system. However, recent anatomical, neuropsychological, and neuroimaging work indicates that this subcortical structure may contribute to cognitive processing in a substantive manner. A number of different theoretical frameworks for understanding cerebellar involvement in cognition have been developed. These include functional hypotheses that have emphasized diverse ideas ranging from an essential role for the cerebellum in the control of attention, error detection and learning, internal control of timing, or covert action and imagery. This chapter outlines the principal sources of motivation for this mini-revolution and reviews the evidence in support of these theoretical conjectures.

A decade ago, the inclusion of a chapter on the cerebellum in a section on "Thought and Imagery" would have seemed preposterous. The cerebellum has traditionally been viewed as an integral part of the motor system, with functional descriptions referring to its role in the coordination of skilled movement, motor learning, and the control of balance. Cognitive psychologists have tended to overlook the study of such processes, perhaps because movements are assumed to be built on reflexive units, subserved by dedicated systems that involve few of the kinds of representational capabilities characteristic of cognitive systems. Nonetheless, action systems have recently garnered increased interest in cognitive psychology as researchers recognize that the essence of a complex processing system is to allow an organism to act in a flexible and efficient manner.

As part of these developments, interest in the cerebellum has exploded in the past decade. Much of the work here continues in the motor tradition, especially that in the computational and neurophysiological literatures. However, the view that the domain of cerebellar function can be understood within the relatively narrow framework of motor control and learning is undergoing some serious challenges. Some of the new hypotheses are extensions of functional accounts of the cerebellum's role in motor control, based on the idea that certain

computations originally evolved for controlling action may have been co-opted into other contexts. Other hypotheses are divorced from the motor domain, building on the idea that this massive structure may contribute in a heterogeneous manner to a number of distinct cognitive systems.

Here, we review the evidence motivating this revolution and provide an overview of the different functional hypotheses proposed to account for how the cerebellum might contribute to the executive operations of a sophisticated cognitive system. Given that this paradigm shift is truly in its infancy, our evaluation of the evidence is tempered. We seek to maintain the appropriate level of skepticism demanded by science while avoiding the temptation to suffocate, prematurely, the ideas that may provide the seeds for novel conceptualizations of the relationship between the brain and behavior.

Evidence indicating a role for the cerebellum in higher cognition

The hypothesis that the cerebellum might be involved in higher level cognition did not spring, Athene-like, from the head of Zeus. Over the past century, there have been scattered proposals suggesting that a strictly motoric view might be limited (see review in Schmahmann, 1997). Some of these early hypotheses were inspired by Piagetian ideas emphasizing the link between action and knowledge; others derived from observations regarding the link between the cerebellum and certain autonomic functions. These ideas, however, failed to take hold, in part because the experimental evidence in support of these somewhat radical notions was minimal at best. Moreover, simple clinical observation was sure to exert a powerful bias: Patients or animals with cerebellar lesions exhibit pronounced deficits in motor control. Any coexisting disorders of autonomic function, emotion, or higher mental thought were clearly minimal in contrast to the severe problems in coordination.

New perspectives on cerebellar function are closely linked to the emergence of cognitive neuroscience as an interdisciplinary enterprise. In this section, we briefly

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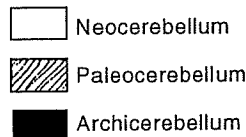
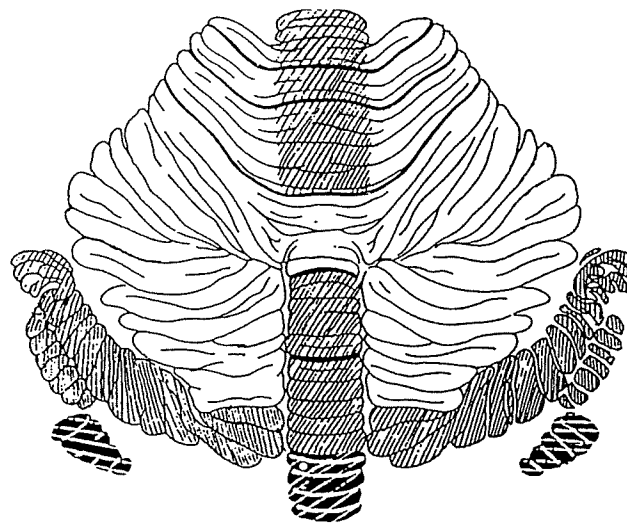


FIGURE 69.1 Schematic drawing of the monkey cerebellum indicating the relative proportion of the three major subdivisions—the archicerebellum, the paleocerebellum, and the neo-

cerebellum. The neocerebellum has undergone tremendous expansion in primates, paralleling similar evolutionary developments in the frontal lobes.

review some of the anatomical, behavioral, and imaging findings that have motivated researchers to propose extensions of the domain of cerebellar function beyond motor control. These results set the stage for the next section, in which we evaluate various functional hypotheses of how the cerebellum may contribute to cognition.

ANATOMICAL CONSIDERATIONS The cerebellum has long fascinated neuroanatomists. While it constitutes about 10% of the total mass of the central nervous system in humans, it contains more than 50% of all the neurons. The cerebellar cortex is traditionally divided into three subregions—the archicerebellum, the paleocerebellum, and the neocerebellum (figure 69.1). The latter region, especially the more lateral zones that constitute the cerebellar hemispheres, would seem to provide the essential anatomical substrate for influencing cognition. This region has undergone tremendous expansion in primates (Leiner, Leiner, and Dow, 1986). The primary input to the cerebellar hemispheres comes from the pontine nuclei. Labeling methods demonstrate that these brainstem nuclei are innervated by both ascending and descending fibers. Of particular interest is the fact that the descending corticopontine fibers not only originate in motor and premotor areas, but are also found in parietal, temporal, and prefrontal cortices (Schmahmann and Pandya, 1997).

The output from the cerebellum also suggests that this structure is part of a network that extends beyond the

“motor” system. All cerebellar output originates in the deep cerebellar nuclei. Most prominent in humans, indeed, accounting for more than 90% of all nuclear cells, is the dentate nucleus. Using a transneuronal retrograde tracing technique, Middleton and Strick (1994, 1997) demonstrated that the output from the dentate nuclei is linked with motor, premotor, and prefrontal cortex via segregated thalamic relays. Thus, the cerebellum is not just receiving input from distributed cortical regions; it also has the prerequisite connections for influencing the kinds of functions associated with prefrontal cortex. It should be noted that there have been no systematic quantitative studies comparing the distribution of cerebellar projections to motor, premotor, and prefrontal areas, and little effort has been made to ascertain whether the cerebellum projects to more medial aspects of prefrontal cortex. The emphasis to date has been on establishing the existence of cerebello-prefrontal pathways.

Studies of the neuropathology associated with certain psychiatric disorders also suggest a cerebellar role in cognition and emotion. In vivo structural MR studies have shown that cerebellar pathology, especially in neocerebellar regions, appears to be a consistent feature of autism (Courchesne, Townsend, and Saitoh, 1994; but see Bauman, Filipek, and Kemper, 1997), as post-mortem histological analyses suggest (Ritvo et al., 1986). More recent studies have also shown pathology in non-cerebellar structures, including the brainstem, limbic re-

gions, the corpus callosum, and the parietal lobes (see Courchesne, 1997). Thus, the question as to whether there is a causal link between the cerebellar pathology and autism remains open. Nonetheless, the fact that cerebellar anatomy is consistently abnormal in autism is provocative, given that coordination problems are not generally associated with this disorder. There are also reports of cerebellar abnormalities in the brains of schizophrenics (Katsetos, Hyde, and Herman, 1997).

PERFORMANCE OF CEREBELLAR PATIENTS ON NEUROPSYCHOLOGICAL TESTS A more direct assay on the role of the cerebellum in cognition comes from neuropsychological studies of patients with either focal or diffuse cerebellar damage. The evidence is mixed on the basis of assessments using standardized batteries from clinical neuropsychology (see review by Daum and Ackermann, 1997). In general, patients with lesions restricted to the cerebellum perform within the normal range on IQ tests. It is difficult to compare their performance to normal subjects since the latter are selected in order to match the patients in terms of IQ. Nonetheless, group studies from three different laboratories have found that the patients score in the normal range when given either the complete Wechsler Adult Intelligence Scale or subtests of this instrument (Daum et al., 1993; Dimitrov et al., 1996; Mangels, Ivry, and Shimizu, 1998).

Daum and colleagues (1993) report one of the most comprehensive studies to date. Their study included nineteen patients: In thirteen patients the damage was restricted to the cerebellum, and in six the damage extended to brainstem structures (e.g., olivopontocerebellar atrophy). The patients were given an extensive battery of tests designed to assess frontal lobe function, verbal memory, and visuospatial memory. The performance of the cerebellar-only group was comparable to that of age-, IQ-, and mood-matched control subjects. In contrast, the patients with cerebellar plus brainstem damage performed more poorly than the control and cerebellar-only groups on the various measures. This pattern is evident in related studies (Appollonio et al., 1993). Performance on neuropsychological tests appears to decline as atrophic processes become more advanced, and may well reflect the involvement of noncerebellar structures (Kish et al., 1994).

A number of researchers have borrowed experimental tasks from cognitive psychology to explore specific domains of performance by patients with cerebellar lesions. These studies have shown that these patients may perform poorly even when the tasks minimize motor requirements. For instance, cerebellar patients have difficulty in generating a list of words that begin with a target letter (Appollonio et al., 1993; Mangels, Ivry, and

Shimizu, 1998) or in learning arbitrary associations between different semantic categories (Bracke-Tolkmitt et al., 1989). Results from such testing have been used to provide support for various functional theories of the cerebellum, as we discuss in greater detail below. It should be noted that the interpretation of the findings is often a matter of debate, since many of the tasks involve a number of component operations and similar abnormal performance can be observed in a variety of groups with cortical lesions (Daum and Ackermann, 1997). For instance, impaired performance on tasks associated with the frontal lobes may not be directly related to cerebellar function, but rather may be secondary to changes in cortical processing that arise indirectly from cerebellar pathology.

NEUROIMAGING Neuroimaging data have probably provided the greatest impetus for the cerebellar cognitive revolution. A large body of literature has convincingly demonstrated that changes in metabolic activity in the cerebellum are not simply correlated with the extent of overt motor behavior (for a review of visual studies, see Shulman et al., 1997). Indeed, it is almost harder to find a study using subtractive logic that does not identify a cerebellar locus of activity than one in which the cerebellum appears silent.

Consider the widely cited language studies of Petersen and colleagues (Petersen et al., 1989; Raichle et al., 1994). One contrast sought to identify neural structures associated with the analysis of semantics. On each trial, subjects were presented with a single word, a common noun. In the control condition, they simply had to read the stimulus word aloud. In the experimental condition, they were required to generate a semantic associate of the stimulus word, in particular, a verb associate. For example, for a target word *apple*, an appropriate response might be "peel" or "throw" or "eat." Thus, the perceptual demands were identical in the two conditions—read a single word; and, motorically, the subjects articulated a single word on each trial. Nonetheless, activation in the right cerebellar cortex was significantly greater in the generate condition than in the control condition.

Initially, the cerebellar activation sites were reported with relatively little discussion, reflecting the fact that the existing literature offered scant basis for interpreting these results. But as these serendipitous results turned up across a range of imaging studies, they began to invite attention. Several recent studies have focused specifically on the cerebellum, with a view to identifying task domains that produce signal changes in this subcortical structure. For example, Kim, Ugurbil, and Strick (1994) used a 4-tesla magnet in a functional MRI study to focus on activation in the dentate nucleus. This structure

showed greater activation during a difficult problem-solving task, even though the subjects were actually producing less overt movement in this condition compared to a control condition involving an easy problem-solving task. Other fMRI researchers have hypothesized that cerebellar activation may be related to attention shifting (Allen et al., 1997), memory rehearsal (Desmond et al., 1997), and sensory exploration (Gao et al., 1996).

Functional hypotheses

While the evidence just reviewed is intriguing, the cognitive neuroscience community has yet to reach consensus on how (and even if) the cerebellum contributes to higher cognition. Many of the behavioral tasks used in neuropsychological studies are quite complex and the observed deficits are open to a variety of interpretations. Neuroimaging techniques such as PET and fMRI offer powerful tools for addressing questions of anatomy but, to date, have been of limited value for developing functional accounts of the metabolic changes. In this section, we review some of the functional hypotheses that have been proposed for how the cerebellum contributes to cognition. Our review here is selective. Our criterion was twofold. First, we focus on those that have been articulated with sufficient clarity to allow empirical evaluation. Second, in keeping with the spirit of this section of the volume, we emphasize hypotheses that are most relevant to the study of thought and imagery.

MENTAL COORDINATION AND THE CONTROL OF ATTENTION Theories of the cerebellum and cognition are generally grounded in the belief that, over the course of evolution, the functional capabilities of this subcortical structure have come to extend beyond a more restricted motor domain. In their seminal paper, Leiner, Leiner, and Dow (1986) offered the conjecture that the highly evolved cerebellum of primates plays a central role in mental coordination, analogous to its role in motor coordination. The idea here, although somewhat vague, is that the cerebellum ensures that processing in distributed regions of the central nervous system is coordinated in order to allow efficient and skilled thought, in much the same way the cerebellum apparently contributes to the control of skilled action.

One relatively specific variant of this hypothesis is that the cerebellum is important for orienting attention (for reviews, see Courchesne and Allen, 1997; Akshoomoff, Courchesne, and Townsend, 1997). Attentional functions have been attributed to numerous brain structures (see Posner and Petersen, 1990), and considerable effort has been devoted to identifying the specific contributions of these structures. According to Courchesne

and colleagues, the cerebellar contribution to attentional functions is to rapidly prime task-relevant systems in order to enhance neural responsiveness. This anticipatory effect is assumed to be multimodal. Indeed, the fact that cerebellar neurons are responsive to auditory, visual, somatosensory, and perhaps even affective input, provides one of the main sources of motivation for this theory. The cerebellum is not necessarily the locus of the attentional commands. Rather, the cerebellum ensures that attentional commands are implemented in a rapid and coordinated manner. Thus, cerebellar lesions are not expected to produce dramatic attentional deficits such as neglect, but only to make shifts of attention slower and more effortful.

Evidence in support of the attention hypothesis comes from behavioral, electrophysiological, and neuroimaging studies (Akshoomoff, Courchesne, and Townsend, 1997). A series of studies have compared various patient groups on two monitoring tasks—a control task in which attention remains focused on a single dimension and an experimental task in which attention must be rapidly shifted between two dimensions. In both tasks, subjects are presented with a series of auditory and visual stimuli. On each dimension, one value is designated the target (e.g., red and high pitch) and one value is designated the distractor (e.g., green and low pitch). On the focused-attention task, subjects are instructed to respond to every target on a designated dimension, either color or pitch. On the divided-attention task, subjects alternate between the two dimensions, first responding to the color target, then the pitch target, then the color target, etc. (see figure 69.2).

Compared to control subjects, patients with cerebellar lesions, either associated with autism (Akshoomoff and Courchesne, 1992) or due to acquired cerebellar pathology (Courchesne et al., 1994), show a selective impairment on the divided-attention condition. For both groups, the deficit is evident only when the interval between successive targets is relatively short (e.g., less than 2.5 s). This is consistent with the idea that the cerebellum does not provide the attentional instructions, but rather ensures that such instructions are implemented rapidly (see also Townsend, Harris, and Courchesne, 1996). Importantly, the patients' performance is similar to controls on the focused-attention task regardless of whether the targets occur in rapid succession or are widely spaced in time. This dissociation would suggest that the problem is not motoric since the movement requirements are identical in the two tasks. Evoked potentials to the missed targets are comparable to ignored distractors, confirming that in such situations, the participants have failed to shift attention at the time of target presentation (Akshoomoff and Courchesne, 1994).

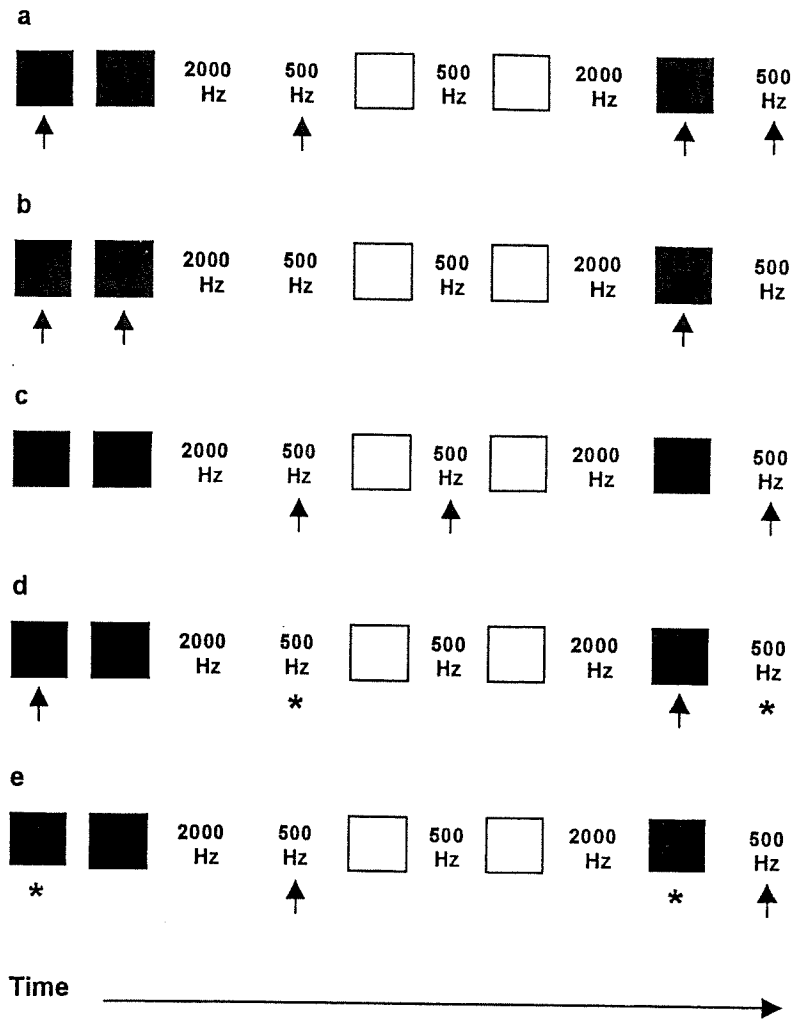


FIGURE 69.2 Attention tasks developed by Courchesne and colleagues to examine the cerebellar role in shifting attention. A stream of tones and colored patches is presented. In the divided-attention condition (a), subjects alternately responded to targets on the two dimensions and the inter-target interval was varied. In the focused-attention conditions, subjects responded only to the visual targets (b) or to the au-

ditary targets (c). In the Go/No-go version of the tasks, subjects alternated between the two dimensions, but responded only to targets on the visual (d) or the auditory (e) dimension. Patients with cerebellar lesions show a significant improvement in the Go/No-go version, despite the fact that the attention-switching demands are similar to those of the divided-attention condition.

While the attention hypothesis is intriguing, three other laboratories have failed to find a deficit in the performance of cerebellar patients on a visual selective-attention task that requires rapid orienting between spatial positions (Dimitrov et al., 1996; Helmuth, Ivry, and Shimizu, 1997; Yamaguchi, Tsuchiya, and Kobayashi, 1998). One possible account of this discrepancy is based on the idea that the deficits observed on the divided-attention task in the studies of Courchesne's lab reflect a more generic resource problem, one that is indirectly related to the motor problems of the cerebellar patients. The divided-attention task is considerably more difficult than the focused-attention task. In fact, many of the participants, both patients and controls, are near ceiling in the latter condition. Perhaps the patients have to devote

more processing resources to monitoring their key presses, a problem that causes them to miss rapidly appearing targets in the divided-attention condition. Motor control is certainly effortful for patients with cerebellar lesions, both in initiating and in terminating a movement.

Ravizza and Ivry (1998) have recently tested this hypothesis with a simple variant of the divided-attention task. In this version, subjects were again instructed to switch back and forth between the two dimensions following the detection of a target. However, they were to make overt responses to the targets on just one of the two dimensions. Targets on the other dimension simply required a covert shift of attention. With this design, the number of attentional shifts was equated in the two-response and one-response versions

of the divided-attention task. However, the rapid shifts in the latter condition never came on the heels of an overt response, ensuring that resources would not be diverted due to the production and termination of a preceding response. Ravizza and Ivry replicated the cerebellar deficit on the divided-attention condition when responses were required to targets on both dimensions. However, when overt responses were required on just one dimension, the patients with cerebellar lesions showed a large improvement, reaching performance levels comparable to those of control subjects. Thus, these results cast doubt on the hypothesis that cerebellar lesions disrupt attentional orienting, and suggest that the patients' deficits may be indirectly related to problems in motor control.

A sensory variant of the coordination and attention theoretical framework comes from the work of Bower and associates (see Bower, 1997), who have recently promoted the hypothesis that the emphasis on the cerebellum as a motor structure is somewhat misguided. Rather, they argue that the fundamental characterization of the cerebellum should focus on its role in sensory exploration. The intimate links of the cerebellum with motor systems reflect the fact that animals, especially humans, use somatosensory information as a way to gain knowledge about the environment and manipulate objects.

This theory does not posit a necessary role for the cerebellum in primary sensory or cognitive functions. Rather, the cerebellum is viewed as a support system, facilitating the efficiency with which sensory systems (especially the somatosensory system) acquire information. Gao and colleagues (1996) tested this hypothesis in a recent fMRI study. Activity in the dentate nucleus was monitored while subjects performed a series of tasks involving both active and passive manual exploration. In one experiment, subjects were asked to successively manipulate a series of unseen objects. In one condition, they simply picked up the objects, then placed them down. In the other condition, they had to pick up the objects, then judge if they matched a target object. Dentate activation was considerably greater in the discrimination condition. Similarly, the dentate was more active when various textured surfaces were passively moved across the subjects' stationary fingers if the subjects were required to evaluate the textures.

The sensory exploration idea is intriguing. While it has currently been applied to the somatosensory domain, Bower (1997) suggests the hypothesis may be more general. In one sense, this hypothesis is similar to the attention-shifting hypothesis outlined above. However, the cerebellum need not be viewed as essential for directing the focus of attention, nor for implementing

these shifts in a coordinated fashion. Rather, the focus of attention may be guided by noncerebellar structures, while the cerebellum contributes by ensuring that the selected information is processed with maximal efficiency to satisfy current task demands (see also Courchesne and Allen, 1997). A current weakness with this hypothesis is that, at present, there are minimal supportive data from patient studies. Somatosensory and proprioceptive functions are not generally assumed to be disturbed in patients with cerebellar lesions, although the examination of these functions has been rather crude.

ERROR DETECTION AND LEARNING A different focus of the role of the cerebellum in cognition is based on the idea that this structure operates as an important source of feedback, monitoring movement and thought in order to modify ongoing behavior, then using this information to alter future performance. This theoretical perspective draws upon the motor learning literature to explain cerebellar involvement in learning certain types of cognitive tasks, particularly those that improve with practice. These tasks include the verb-generation task described above, puzzle tasks in which the goal is to solve a puzzle in as few moves as possible while observing constraints on how the pieces can be positioned (e.g., the Tower of Hanoi), and motor sequence and trajectory learning tasks. Across these and related tasks, neuroimaging studies have demonstrated that cerebellar activity is high during initial performance of the task, that activity decreases as performance becomes more skilled and accurate, and that shifts in cortical activity co-occur with changes in cerebellar activity (e.g., Raichle et al., 1994).

Many of the cognitive tasks associated with cerebellar activation and practice-dependent changes are quite complicated, and thus the cerebellar activation can be interpreted in many ways. The cerebellar changes could reflect a correlation with learning, rather than a causal involvement. Some support for a causal relationship comes from converging neuropsychological studies. For each of the general tasks described above, impaired acquisition of skilled performance has been demonstrated in subjects with cerebellar damage or atrophy, though not all of the findings have been replicated.

The idea that the cerebellum is involved in the detection and correction of errors offers a potential causal link between on-line performance and learning. At the center of this idea in the motor domain is evidence that the cerebellum modifies output in the face of unexpected perturbations or sensory input. For instance, it has been hypothesized that during locomotion, corticocerebellar signals provide an efference copy of corticospinal motor commands that can be compared with afferent informa-

tion provided by spinocerebellar circuits (Kawato and Gomi, 1992). When a mismatch is detected, descending output from the cerebellar nuclei allows for rapid, on-line adjustments in the motor patterns without requiring extensive cortical intervention. Moreover, the error signals generated when the movement is perturbed are then used to modify the production of similar movements in the future (Gilbert and Thach, 1977). Similar ideas form the basis of computational models of the cerebellum's role in simple associative learning tasks such as eyeblink conditioning (reviewed in Thompson, 1988). Unexpected aversive stimuli such as an airpuff are assumed to provide an error signal in the cerebellum, modifying the animal's behavior so that it will make an anticipatory blink in the future when presented with the same context.

The cognitive generalization of this hypothesis implicitly assumes that the cerebellum has evolved so that it can now provide a more generic error-correction role, modifying internal thought in addition to external movement. Canavan and his colleagues (Bracke-Tolkmitt et al., 1989; Canavan et al., 1994) reported severe deficits on a conditional learning task in which the subjects had to learn the correct mapping between colored shapes and arbitrary verbal labels. The subjects were given no explicit instructions; rather, learning was solely through trial and error, with the experimenter indicating whether a response was correct or not after each trial. Fiez and colleagues (1992) report a case study of a patient who suffered a large infarct in the posterior and inferior region of the right cerebellar hemisphere. On standardized neuropsychological assessment, this patient's performance clearly indicated superior overall cognitive function. Yet the patient's performance on relatively simple verbal discrimination tasks, again involving trial-and-error learning, was extremely poor. Moreover, on a variety of tasks, he failed to use explicit verbal feedback from the experimenter to modify his responses. The same patient also failed to learn and perform the verb-generation task normally. Specifically, he produced a large number of inappropriate, but semantically related responses (e.g., producing "old" as a synonym for "garbage").

The dissociation between this patient's overall intelligence and his performance on these seemingly simple tasks is quite striking. It is not clear, however, whether these results provide strong support for the error-correction hypothesis. Issues remain, at least in part, because no explicit models have been developed to explain how error-correction would be implemented in a cognitive task; thus it is hard to evaluate whether some of the patient's difficulties fit within an error-detection framework. For example, the patient performed poorly in judging

whether two words were synonyms and in identifying whether common words were nouns or verbs. Since we can assume that he was, or had been, familiar with these words in the past, these deficits may indicate a disruption of semantic knowledge rather than an inability to make use of current error signals (and, indeed, he was given no feedback on such tests). A second issue is that of reproducibility. Helmuth and associates (1997) failed to replicate these findings in a group study of patients with focal cerebellar lesions. On the trial-and-error verbal discrimination task, these patients showed comparable learning functions across blocks of trials as age-matched control subjects. Similarly, on a speeded semantic generation task, the patients, while slower than controls, showed similar improvements over successive blocks.

Related to the ideas of both error detection and attention is the notion that the cerebellum may best be characterized as a predictive device, a neural structure that is specialized to make anticipatory adjustments (e.g., Courchesne and Allen, 1997; Paulin, 1997). For instance, through experience, a particular sensory context or internal state could become associated with a particular motor response or adjustment of the internal state. Eventually, the occurrence of a specific context could trigger the occurrence of a specific external or internal response; this procedure could be applied iteratively in order to produce a temporal sequence of internal events or overt responses. Models such as these emphasize the dynamic properties of cerebellar function (Raymond, Lisberger, and Mauk, 1996). A consistent feature of cerebellar theories is the focus on this system as performing predictive functions—the ability to anticipate forthcoming information and ensure that actions correctly anticipate changes in the environment.

GENERALIZED TIMING FUNCTION A specific variant of the prediction idea is that the cerebellum operates as an internal timing system, providing the precise representation of temporal information across a range of tasks (Ivry and Keele, 1989; reviewed in Ivry, 1997). The timing hypothesis originates in an analysis of the motor control deficits observed in animals and patients with cerebellar lesions. Cerebellar symptoms such as intentional tremor and hypermetria can be interpreted as resulting from the disorganization of the temporal pattern between agonist and antagonist muscles during rapid movements (Hore, Wild, and Diener, 1991). When asked to produce periodic movements, patients with cerebellar lesions exhibit a large increase in variability, and this increase is associated with central control processes regulating the timing of central motor commands (Ivry and Keele, 1989; Ivry, Keele, and Diener, 1988; Franz, Ivry, and Helmuth, 1996).

The timing deficits for these patients extend beyond the motor domain, being manifest in a variety of perceptual tasks that require the precise representation of temporal information. This temporal processing deficit has been found on perceptual tasks across different sensory modalities including audition (Ivry and Keele, 1989; Mangels, Ivry, and Shimizu, 1998), vision (Ivry and Diener, 1991; Nawrot and Rizzo, 1995), and somatosensation (Grill et al., 1994). A recent speech perception study provides an especially compelling demonstration of the importance of the cerebellum in temporal processing (Ackermann et al., 1997). Patients with cerebellar dysarthria, a difficulty in speech articulation, were unable to discriminate speech sounds that differed solely in the duration of an intersyllabic silent period (figure 69.3), yet performed comparably to control subjects for sounds that had different spectral cues.

Again, one might suppose a generalization of function over the course of evolution: A form of representation that evolved as part of a limited task domain might become accessible for the performance of other tasks that can exploit this specialization (Rozin, 1976). Within the framework of the timing hypothesis, the cerebellum must be critical for tasks that require precise timing, whether or not they are motoric. This hypothesis also provides a parsimonious account of the task domain of the cerebellum in learning, namely, when the response requires the representation of the temporal relationships between different stimuli or stimuli and responses. In eyeblink conditioning, for example, the learned response is adaptive only when it occurs at the right point in time, that is, when the animal has extracted the precise timing between the conditioning and unconditioned stimuli (Ivry and Keele, 1989). Without the cerebellar cortex, the association may be formed, but it loses its adaptive value, as evidenced by the fact that the animal no longer blinks when the aversive stimulus is presented (Perrett, Ruiz, and Mauk, 1993; Anderson and Keifer, 1997).

The research in this area has focused on tasks that impose real-time processing demands, and the corresponding computational models here have focused on how metrical temporal information might be represented in the cerebellar cortex (e.g., Buonomano and Mauk, 1994; Fiala, Grossberg, and Bullock, 1996). The representation of the temporal information is a central component of much of our perceptual experience and a prerequisite for skilled behavior. Consider the frog by the river gathering up an evening meal of flies, or the basketball player looking to pass the ball to a teammate who is moving toward the basket. Anticipating the future position of a moving stimulus and coordinating the multi-limb gestures required to interact with that stimulus re-

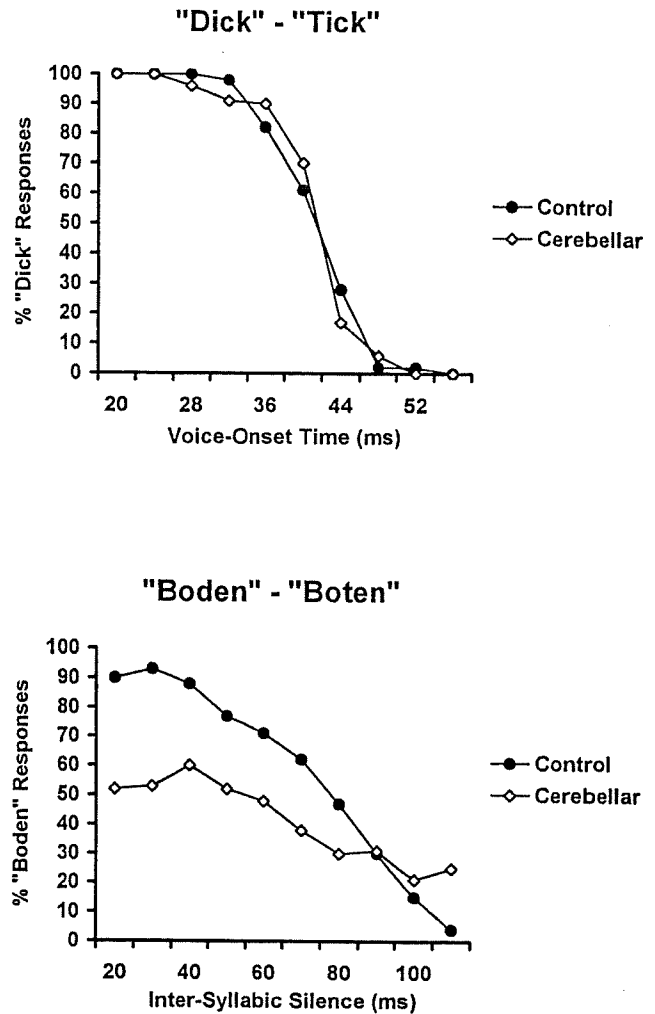


FIGURE 69.3 Identification functions for two speech continua in control subjects and patients with bilateral cerebellar lesions. For the tick-dick continuum, the voice-onset time was varied in steps of 10 ms. This change in the timing between voicing and the release of the stop consonant produces both temporal and spectral changes. For the boten-boden continuum, a silent interval was inserted between the syllables, thus providing only a temporal cue. The patients showed poor discrimination performance in this condition. (Adapted from Ackermann et al., 1997.)

quires extremely precise timing. The cerebellum appears to be an exquisite device for this form of dynamic processing, and its manifestation in both perception and action reflects the intimate links between these domains that are required for skilled behavior.

As currently articulated, the conceptualization of a cerebellar timing system is limited to the relatively narrow temporal range that might be relevant for the control of coordinated movement. Here again, the motivation is based on an evolutionary perspective. An internal timing system likely emerged from a system that had access to information that contained temporal regu-

larities. A candidate here would be the pattern generated by a locomoting organism (be it terrestrial, arial, or aquatic). While locomotion signals might be generated by relatively simple spinal mechanisms, a hierarchical control system might be essential for endowing flexibility as well as for producing corrections in response to unexpected perturbations (Arshavsky, Gelfand, and Orlovsky, 1983). Perhaps the cerebellar timing system took root in this manner and the temporal extent of the cerebellum is constrained by its links to locomotion cycles.

The timing hypothesis is a narrower, more specific statement of how the cerebellum might be viewed as a predictive device. It is possible that a cerebellar timing function is simply one manifestation of a more general predictive capability (Ivry and Keele, 1989; Courchesne and Allen, 1997; Bower, 1997). On the other hand, in many situations, animals need to anticipate future events that do not require precise detail of the temporal structure of the series of intervening events. For example, the temporal requirements for knowing when to move on to a new foraging patch or when a signal light will change to green are quite different from that needed to anticipate when to swing a tennis racquet in order to serve a tossed tennis ball. And in other situations such as anticipating the next move in a chess game, skilled performance requires a predictive capability, but one that has essentially no temporal requirements. It remains to be seen whether the cerebellum contributes to tasks that entail prediction in this more generic sense. The timing hypothesis predicts that the cerebellum will not play a role in such tasks since its domain is assumed to be limited to tasks requiring a particular form of computation, the representation of the temporal relations between events.

IMAGERY, COVERT ACTION, AND WORKING MEMORY As reviewed above, the neuropsychological record is mixed regarding some of the more cognitive interpretations of cerebellar function. Nonetheless, there remains the challenge of interpreting the consistent finding of cerebellar activation in imaging studies, even when motor demands are equated in the experimental and control tasks. One hypothesis is based on the observation that there is a correlation between task difficulty and the degree of cerebellar activation (Ivry, 1997). Across a wide range of studies, metabolic activity in the cerebellum is most pronounced for the more difficult condition when pairs of tasks are compared.

It is, of course, necessary to operationalize "difficulty." One metric is based simply on the number of possible responses afforded by a situation: Tasks associated with a large number of possible responses are more difficult than those associated with a small number of possible responses. For example, in the language study of Pe-

tersen and colleagues (1989), there are more possible responses in the generate condition in which subjects must generate a semantic associate to the stimulus word compared to the control condition in which the subjects simply have to repeat the stimulus word. Similarly, in the difficult problem-solving condition of another study (Gao et al., 1996), there were four possible moves on each trial compared to just one in the easy condition. Perhaps the cerebellum is involved in the preparation and planning of candidate responses. The increased cerebellar activation in "difficult" conditions might reflect the parallel preparation of all the possible responses. By engaging in response preparation prior to completion of response selection, the system is able to respond in a more rapid manner. This hypothesis is in accord with the documented deficits in reaction time associated with cerebellar lesions (Meyer-Lohmann, Hore, and Brooks, 1977; Spidalieri, Busby, and Lamarre, 1983).

While this response preparation hypothesis can account for many of the imaging results, there are some notable exceptions. In a stem completion task (e.g., say "cougar" after seeing the stem "cou_____"), cerebellar activation was found to be greater when there were few possible completions for the target stem than when there were many (Desmond, Gabrieli, and Glover, 1998). This result is the opposite of what one would predict based on the response preparation hypothesis. Another intriguing exception comes from a study comparing phonological and visual judgments of letters (Sergent et al., 1992). On each trial, a single letter was presented in the center of the screen, oriented either normally or mirror-reversed. In one condition, subjects judged the orientation, pressing one button if the stimulus was in its normal orientation and another if the stimulus was mirror-reversed. In a second condition, the same stimuli were presented, but now the judgment was based on whether or not the stimulus contained a target phoneme, the sound "ee" (as in B, D, or T). The tasks appeared to be of equal difficulty, both by the response alternative metric described above (two per trial) and by the fact that reaction times were comparable, with the phonological task taking slightly more time. Nonetheless, cerebellar activation was more pronounced in the orientation task.

An alternative view of the response preparation hypothesis is that response preparation and related action-related processes are essential to the critical cognitive operations required for these tasks. For instance, it is likely that imagery, in the form of mental rotation, is required for performing letter orientation judgments. A number of other neuroimaging studies have implicated the cerebellum in imagery tasks, especially when the task requires imagining motoric gestures. Compared to baseline

conditions involving rest, cerebellar activation is found when people imagine hitting a tennis ball (Decety et al., 1990) and when people perform either active or imagined hand gestures (Peter Fox, personal communication). Parsons and Fox (1998) report that cerebellar activation can occur even when subjects are not instructed to imagine movements. In their task, subjects were required to discriminate between line drawings of left and right hands shown from different perspectives. Based upon data from behavioral studies, it appears that subjects make these judgments by imagining they are moving their own hands to match the orientation of the stimulus hand.

Many verbal tasks may engage an articulatory form of imagery. For example, a key component of Baddeley's (1992) influential model of working memory entails a process by which linguistic information is actively maintained over short delays via covert (silent) articulatory rehearsal. The imaging literature suggests that the cerebellum may be an essential component of this rehearsal system. For example, increased blood flow is observed in the cerebellum when subjects are required to maintain five words over a 40-s delay interval (Fiez et al., 1996), or when they must decide whether each letter in a sequence is the same as the letter presented two trials previously, the so-called "two-back" task (Awh et al., 1996). It is important to note that task-related activation here, and in all of the imagery studies cited above, is not limited to the cerebellum. Meta-analyses indicate that the cerebellum, supplementary motor area (SMA), and Broca's area are active during verbal, but not spatial, working memory tasks, whereas regions such as dorsolateral prefrontal cortex are active during both verbal and spatial working memory tasks (figure 69.4; see also Fiez et al., 1996). This selective activation has led to the hypothesis that SMA, Broca's area, and the cerebellum comprise the neural basis of an articulatory rehearsal system (Awh et al., 1996; Fiez et al., 1996; Paulesu, Frith, and Frackowiak, 1993).

In evaluating the cerebellar contributions to imagery, one issue is whether its contributions to imagined movement are identical to its contributions to real movement. In terms of articulatory rehearsal, for instance, it may contribute to motoric aspects of internal speech representation in much the same way that it contributes to overt speech production. This hypothesis is consistent with behavioral evidence showing links between overt and covert articulation; for example, the number of items that subjects can maintain in working memory is correlated with the amount of time it takes to say them aloud (Baddeley, Thomson, and Buchanan, 1975). However, the observation of load-effects on cerebellar activation argues against overly simplistic interpretations of

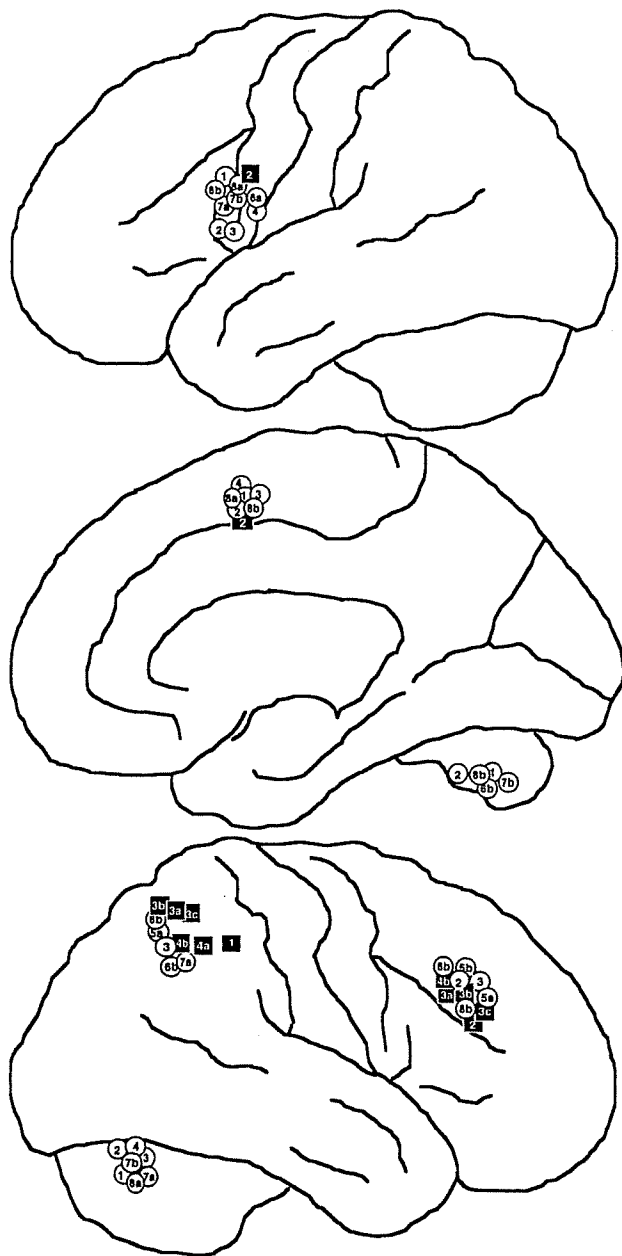


FIGURE 69.4 The loci of peak activation associated with verbal working memory tasks (open circles) and spatial working memory tasks (filled squares) are plotted from a number of different PET studies. Broca's area in the left hemisphere, supplementary motor cortex in the superior medial cortex, and the medial and right lateral cerebellum are typically activated in verbal working memory but not spatial working memory tasks. Other areas, such as the right dorsolateral prefrontal cortex and the right inferior parietal cortex are activated by both verbal working memory and spatial working memory tasks. Verbal working memory coordinates drawn from (1) Awh et al., 1996; (2) Fiez et al., 1996; (3) Jonides et al., 1998; (4) Paulesu et al., 1993; (5) Petrides et al., 1993; (6) Salmon et al., 1996; (7) Schumacher et al., 1996; (8) Smith, Jonides, and Koeppe, 1996. Spatial working memory coordinates drawn from (1) Courtney et al., 1996; (2) Goldberg et al., 1996; (3) Owen et al., 1996; (4) Smith, Jonides, and Koeppe, 1996.

the relationship between real and imagined movement. As a control condition in studies of verbal working memory, subjects have been asked to internally rehearse relatively simple material that does not impose a memory load (e.g., count from 1 to 5 repeatedly or silently repeat a single letter). Cerebellar activation is greater in the experimental working memory condition than in these rehearsal conditions (Fiez et al., 1996; Desmond et al., 1997; Awh et al., 1996). Furthermore, cerebellar activation has been found to be higher in direct comparisons of high- versus low-load conditions (Desmond et al., 1997). While some of the changes in cerebellar activation reflect increases in areas active during both simple rehearsal and working memory tasks, others reflect the recruitment of areas that are not significantly active during simple rehearsal.

Viewing cerebellar contributions to verbal working memory from a more motoric perspective need not reduce its cognitive importance. A breakdown in the articulatory rehearsal system could have widespread consequences. Consider, for example, that verbal working memory is central to our ability to perform tasks that range from solving mathematical equations to comprehending sentence clauses. Furthermore, articulatory rehearsal and recoding have been associated with many other language tasks outside the domain of verbal working memory, such as speech recognition and the generation of word phonology. This may explain cerebellar activation in verbal fluency, stem completion, and verb generation tasks. Successful production of correct responses for these tasks may involve the ability to retrieve and maintain potential responses using a covert articulatory process (Desmond, Gabrieli, and Glover, 1998). There is also limited but provocative evidence implicating cerebellar dysfunction in developmental dyslexia (Fawcett, Nicolson, and Dean, 1996). Perhaps an inability to engage in fluent covert articulation interferes with the development of salient phonological representations. Without such codes, children are likely to have severe problems in acquiring reading skills (Lieberman and Shankweiler, 1991).

Conclusions

As reviewed in this chapter, the cerebellum has stepped out from the shadows of its traditional role as part of the motor system, essential for the control of fine movement and balance. Patient, imaging, and modeling studies have brought the study of cerebellar function into the mainstream of cognitive neuroscience, with researchers hypothesizing links to attention, learning, memory, language, and thought. We have reviewed a diverse set of literatures here, seeking to identify the principal sources

of motivation for this mini-revolution and outlining some of the recent theoretical conjectures.

In general, we have adopted a somewhat skeptical perspective, seeking convergence from anatomical, neuropsychological, and neuroimaging studies for the proper evaluation of the various functional hypotheses that have been developed over the past decade. We do not intend this skepticism to be taken as an attempt to dismiss these hypotheses. It is essential to maintain an open mind as researchers develop experiments that will allow strong inference and seek theoretical accounts that may integrate various hypotheses. At the same time, the conservative nature of evolutionary processes leads us to expect that there will be some continuity between the contributions of the cerebellum to motor control and the contribution of this structure to language and thought.

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