The Cerebellum, Timing, and Language: Implications for the Study of Dyslexia

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The functional domain of the cerebellum has been greatly extended over the past decade. Prior to this period, discussion of the cerebellum was restricted to the neuroscience and neurology literatures and focused on the role of this subcortical structure in the performance of skilled movements. Most psychologists would have been hard pressed to localize the cerebellum, let alone entertain the idea that it might contribute to cognition. Yet with the advent of modern neuroimaging techniques and emergence of cognitive neuroscience as a new interdisciplinary field, a paradigm shift has been launched. PET and functional MRI studies consistently report cerebellar activation associated with mental operations such as memory retrieval, verbal fluency, and the control of attention (Fiez & Raichle, 1997; Courchesne & Allen, 1997). Neuropsychological studies have shown that patients with focal or diffuse cerebellar pathology are impaired on a wide range of cognitive tasks, especially those associated with higher executive control (e.g., Appollonio et al., 1993; but see Daum & Ackermann, 1997).

A less explored but equally provocative role of the cerebellum is its potential link to a number of developmental psychiatric disorders. Most prominent among these is autism. Structural MRI studies have consistently reported abnormalities in cerebellar volume in children with autism, (e.g., Courchesne et al., 1994), and post-mortem studies have confirmed a severe loss of Purkinje cells in autistic individuals (Bauman et al., 1997). More recently, MRI studies have identified cerebellar hypoplasia in other psychiatric populations including schizophrenic adults (Nopoulos et al., 1999) and children diagnosed with attention deficit and hyperactivity disorder (Mostofsky et al., 1998). This linkage is puzzling and raises a number of important questions. One might ask whether the cerebellum supports an essential cognitive function that, when impaired, can lead to very different disorders if combined with other neural insults and/or environmental contexts. On the other hand, it is possible that the cerebellum is especially vulnerable during development and thus serves as a useful marker of neuropathology, even though it may not contribute in a causal manner to the disorders. Indeed, distinct regions within the cerebellum are associated for autism, schizophrenia, and ADHD, perhaps providing hints as to the time at which prenatal developmental goes awry (Altman & Bayer, 1985). Between these two extremes is the possibility that the relationships between the cerebellum and these disorders arise from independent factors, and correspondingly, the cerebellum may contribute in a causal manner to one disorder but not another.

Also included among the developmental disorders associated with cerebellar dysfunction is dyslexia. As with the psychiatric disorders, it is possible that cerebellar problems evidenced by this population are independent of their language problems. In fact, the known relationship between cerebellar dysfunction and dyslexia is not as direct as those in the psychiatric studies noted above; the current evidence is based on indirect behavioral assays (Nicolson et al., 1995). Nonetheless, it is important to explore functional hypotheses that might account for a causal relationship between the cerebellum and dyslexia. To approach this problem, we will review two lines of evidence regarding the role of the cerebellum in cognition. We will begin with a discussion of the idea that the cerebellum operates as an internal clock, summarizing the supporting evidence and showing how the timing idea may be relevant to studies of language. We will then turn to the question of a more general involvement of the cerebellum in a distributed network supporting language functions, and specifically, how disruption in this network might be linked to dyslexia.

THE CEREBELLUM AS AN INTERNAL CLOCK

The integrity of the cerebellum is essential for coordinated movement. Despite the recent emphasis on cognitive functions, the hallmarks of cerebellar dysfunction are most pronounced in the motor domain. Patients with cerebellar lesions have difficulty maintaining posture, exhibit a tremor when reaching for objects, and have problems controlling both smooth and saccadic eye movements. The afferent and efferent pathways linking the cerebellum with the cerebral cortex, brainstem, and spinal cord put this structure in the center of the motor pathways. Based on neurophysiological, behavioral, and computational evidence, a number of theorists have emphasized a central role for the cerebellum in controlling the temporal aspects of movement.

Consider the difficulty patients with unilateral cerebellar lesions have in reaching for an object. Unlike patients with apraxia or optic agnosia, cerebellar patients are able to comprehend the goal of the desired action and accurately localize the object. They are even able to perform the complex computations for determining the trajectory, initially activating the selected muscles in an appropriate manner. The coordination problems, however, arise when the required muscular events must be precisely timed (Hore et al., 1991). These problems are especially apparent when the movement is made ballistically. Here, precise timing between the agonist and antagonist muscles is essential to ensure that the movement is terminated at the object. With cerebellar damage, this temporal pattern is frequently disrupted; the timing of the antagonist no longer appears to programmed such that the rapid movement is terminated in a predictive manner. Rather, the onset of the antagonist is delayed and becomes reactive, setting the limb into a series of oscillations, or what is called an intentional tremor.

Our neuropsychological studies have been designed to provide more direct tests of the timing hypothesis. We have used a repetitive tapping task in which the participants are asked to produce a series of evenly timed intervals. At particular rates, the patients have little difficulty maintaining the target interval. Our focus has been on the consistency of these movements, measured by the standard deviation of the inter-tap intervals. In comparison to patients with other motor disorders of central origin, patients with cerebellar lesions show a consistent increase in variability (Ivry & Keele, 1989). Moreover, using an analytic model that partitions the overall variability into two sources, one associated with the timing of the successive movements, which we call "clock" variability, and the other associated with the implementation of the responses, which we call “motor" variability, we have found that patients with lesions of the lateral cerebellum specifically exhibit an increase in "clock" variability (Ivry et al., 1988; Franz et al., 1996). These behavioral results converge with the anatomy of the cerebellar output nuclei. The output from the lateral regions of the cerebellum is part of ascending pathways that innervate premotor and motor cortex. As such, this region is positioned to be part of the system involved in motor planning and programming. Our hypothesis is that the cerebellum is critical for regulating the temporal aspects of movement, whereas other structures contribute to the establishment of other parameters such as muscle selection.

Timing, Learning, and Skill

A striking example of the importance of the cerebellum in internal timing is found in the literature on sensorimotor learning. One well-studied form of Pavlovian learning is eye blink conditioning. In this paradigm, a neutral stimulus such as a tone (CS) is repeatedly paired with an unconditioned stimulus such as an air puff (US). Over time, the animal comes to blink in response to the tone, thus attenuating the aversive effects of the air puff. Lesions of the cerebellum disrupt eye blink conditioning in humans and other species, either by abolishing the conditioned response or preventing the acquisition of the conditioned response (reviewed in Woodruff-Pak, 1997). We have proposed that the cerebellum is essential for this form of learning because it is only adaptive if the timing between the CS and the US is represented (Ivry & Keele, 1989). In support of this hypothesis, the precise timing of the conditioned blink is disturbed following focal lesions of the cerebellar cortex (Perrett et al., 1993) even though the response itself is still produced if the lesions leave the cerebellar nuclei intact. This suggests that an association between the CS and the US may occur at multiple levels of the system, but that the cerebellar cortex imposes the temporal delay between the onset of the CS and the conditioned response. In a related manner, Their et al. (2000) have recently argued that the population of Purkinje cell activity encodes the duration of saccadic eye movements, and recalibration of this population is the basis for motor learning.

Neurologists have long believed that the cerebellum is especially important for the performance of skilled movements. One idea is that with practice the requisite neural representations shift from a cortical to a subcortical locus. The timing hypothesis offers an alternative perspective. A hallmark of skilled behavior is that the it is performed in a consistent manner. When the cerebellum is damaged, a learned action can still be produced, but the movement appears fractionated into a series of poorly connected subunits. Precise timing allows the successive gestures to be integrated smoothly into a coordinated whole.

Perceptual Manifestations of the Cerebellar Timing System

The eye blink literature also emphasizes difficulties with defining the domain of cerebellar function. As argued above, the cerebellar cortex helps shape the topography of the conditioned response through its representation of the interval between the conditioned stimulus and the unconditioned stimulus. These are, of course, sensory events, which would suggest that the timing capabilities of the cerebellum are not strictly limited to motor processes. Moreover, the properties of an internal clock appear similar when investigated in either production or perception tasks (Keele et al., 1985; Ivry & Hazeltine, 1995). Given these considerations, we tested the generality of the timing hypothesis with non-motor tasks that require the precise representation of temporal information. In our initial study, we compared the performance of various patient groups on two psychophysical tasks. For both tasks, the participants were presented with two pairs of tones. In one task, they had to judge whether the interval between the second pair of tones was shorter or longer than the interval between the first pair. Thus, they had to judge the duration of a temporal interval. In the second task, the participants judged whether the second pair of tones was softer or louder than the first pair. Here, the psychophysical discrimination is based on non-temporal properties of the stimulus events. As predicted, the patients with cerebellar lesions were selectively impaired on the duration discrimination task (Ivry & Keele, 1989). Patients with Parkinson's disease or cortical lesions performed comparable to age-matched control participants.

Subsequent studies have found that these latter groups may also be impaired on perceptual timing tasks (Harrington et al., 1998a,b). However, successful performance on the duration discrimination task likely involves many other mental operations. When we apply a component analysis akin to that used in our tapping studies, the results suggest that whereas the cerebellar problem is specific to timing, cortical lesions may produce impairments due to problems with working memory or attention (Casini & Ivry, 1999; Mangels et al., 1998). Combined with the motor control and learning results described above, the evidence strongly suggests a specialized role for the cerebellum in representing the temporal relationship between events in the milliseconds range.

The timing hypothesis provides a general characterization of cerebellar function. Recent work has begun to address the important question of how the cerebellum operates an internal timing system, looking at the mechanisms through which temporal representations might be achieved. One way in which timing information could be represented is through an oscillatory process that provides a recurrent elemental unit of time, as in a pacemaker. However, temporal representations do not require pacemaker mechanisms. Alternatively, the cerebellar cortex might be viewed as a bank of hour glass timers, with a range of intervals represented across a set of cortical ensembles (Ivry, 1996). Computational studies have tended to favor the latter approach, demonstrating how relatively slow physiological processes within the cerebellar cortex could provide the mechanisms for forming precise temporal associations (Buonomano & Mauk, 1994; Fiala et al., 1996). For example, in the eye blink paradigm, the representation of the conditioned stimulus must be sustained until the onset of the unconditioned stimulus or following learning, the onset of the conditioned response. One would expect that such real-time representations are limited in duration, or at a minimum, need to be linked with memory systems in order to represent longer intervals. Thus, the range of the cerebellar timing system is likely on the order of a hundreds of milliseconds or so, a temporal range that would seem appropriate for a system primarily involved in the control of coordinated movement. For tasks requiring longer intervals, other neural systems are engaged, perhaps in concert with the cerebellum (e.g., forming a clock-counter system).

CEREBELLAR TIMING IN SPEECH PRODUCTION AND PERCEPTION

Speech disorders are observed with many neurological disturbances. Given the role of the cerebellum in skilled movement, it is not surprising that patients with damage to this structure frequently exhibit speech disorders, or what is referred to as cerebellar dysarthria. Their speech can be irregular in rate and stress, and their phonation erratic. Some patients will tend to garble their words; others may speak with a very loud voice in which each sound is individually enunciated. This articulation is irregular, however.

The Control of Inter-Articulatory Timing

Can the timing hypothesis also account for the symptoms associated with cerebellar dysarthria? One way in which this question has been addressed is to examine how well these patients can produce speech contrasts that require precise coordination among different groups of articulators. Consider the distinction between voiced and voiceless stop consonants. In terms of articulation, for voiced consonants the onset of vocal cord vibration, or voicing, is essentially synchronized with the release of airflow at the oral articulators. For example, to produce the labial /b/ sound in the initial position as in *bay*, the airflow commences with the parting of the lips. To produce a voiceless sound such as /p/ in the word *pay*, the onset of vocal cord vibration is delayed by approximately forty to sixty milliseconds. This delay is termed the voice-onset time, or VOT. Thus, precise timing is required in terms of the coordination across different sets of articulators.

For normal speakers, the distributions of VOT for voiced and voiceless stop consonants do not overlap. Ackermann and Hertrich (1997) measured VOT for a variety of initial-position stop consonants in eight patients with cerebellar dysarthria. For five of the patients, significant overlap was present in the VOT distributions; some of the voiced sounds were produced with abnormally long VOT and some of the voiceless sounds were produced with abnormally short VOT. Similarly, Ivry and Gopal (1992) reported that while the mean VOT for voiced and voiceless stop consonants was comparable between control participants and patients with cerebellar dsyarthria, the patients’ productions were much more variable.

As might be expected, this increased variability has perceptual consequences. In the Ivry and Gopal study, the patients were asked to articulate four consonants, /ba/, /pa/, /da/, and /ta/. Control participants listened to a tape of the productions and labeled each sound. Interestingly, the perceptual errors were always along the voicing continuum. For example, /ba/ might be perceived as /pa/ or vice-versa. None of the errors were because the place of articulation (labial or aveolar) was misidentified, as in /ba/ versus /da/.

This dissociation suggests that cerebellar dysarthria is specific to a deficit in temporal control of the articulators. The patients are accurately able to configure the oral articulators, but lack the ability to temporally coordinate inter-articulator actions. However, this conclusion is weakened by the fact that there are no reports of the opposite pattern of deficits at present. We are unaware of any reports of patients who produce speech errors in terms of place of articulation rather than voicing.[1] Indeed, overlapping VOT distributions have been associated with speech disorders that do not involve the cerebellum (see Ravizza, under review). Thus, it may be that the temporal measures of speech control are more sensitive to neurological disturbance.

The Use of Temporal Cues in Speech Perception

The speech production data are consistent with the hypothesis that the cerebellum is essential for controlling the precise timing involved in multi-joint actions. In this manner, the cerebellar role in speech production is another manifestation of its general contribution to coordination. A similar question can be asked in terms of speech perception. Is the cerebellum essential for extracting temporal information that might be required to distinguish one phoneme from another? As with the production data, the focus here has been on the voicing contrast. In an initial study (Ivry & Gopal, 1992), we found that patients with cerebellar lesions performed similarly to control participants in categorizing syllables in which the VOT ranged from -10 ms, an example of /ba/ to +70 ms, an example of /pa/. However, there are multiple acoustic cues that can distinguish voiced from voiceless stop consonants in the initial position. For example, these sounds differ in terms of the presence or absence of energy in the region of the fundamental frequency at onset. They also differ in the duration of the formant transitions.

In contrast, for medial stop consonants, the duration of the occlusion phase may be a more essential temporal cue. Ackermann et al. (1997) tested this idea in a categorical perception task with a continuum based on two bi-syllabic German words, *boden* and *boten*. They recorded a speaker saying *boden*, a sound in which there is a brief occlusion of about ten ms of the airflow prior to the onset of the second syllable. By extending this silent period in successive ten-ms steps, they created a continuum of sounds between *boden* and *boten*. Patients with cerebellar dysarthria were severely impaired in categorizing these stimuli. Across the entire continuum, they were essentially unable to distinguish the two words. Thus, it appears that the cerebellum does contribute to speech perception when the critical information requires the utilization of a precise temporal cue.

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[1] A double dissociation is not logically required to conclude that separate processes are involved in controlling the configuration of the articulators and their timing. A process involved in configuration might also select the timing pattern, and thus damage to such a process could result in both VOT and place errors. However, the literature contains many examples of patients with VOT irregularities and considerably fewer examples of place irregularities.

Note that the results of Ackermann et al. (1997) challenge the view that speech perception involves a set of dedicated modules (e.g., Liberman & Mattingly, 1985). While phonological representations have an important status for humans in terms of their importance for communication, the computational machinery for analyzing speech sounds appears to use similar processes as are involved in other types of auditory perception.

THE CEREBELLUM AND LANGUAGE

The timing hypothesis provides a parsimonious account of one way in which the cerebellum may contribute to language. Speech production is perhaps the quintessential skill exhibited by humans, and as with other motor skills, the ability to control the timing of the muscular events required for smooth articulation appears to involve the cerebellum. Similarly, certain aspects of speech perception may also involve the representation of the temporal relationships contained within the acoustic signal.

However, a broader role of the cerebellum in language has been hypothesized. The theoretical motivation for this work has come from evolutionary considerations (e.g., Leiner et al., 1993). Compared to our closest phylogenetic relatives, the neocerebellum appears to have undergone a disproportionate increase in size, especially those parts that send ascending pathways to the cerebral cortex via the dentate nucleus. Using novel polysynaptic tracing techniques, anatomists have found that these outputs not only project to traditional motor structures such as motor and premotor cortex, but are also innervate prefrontal regions thought to play an important role in higher cognitive functions.

The Cerebellum and Lexical Retrieval

Neuropsychological and neuroimaging studies have provided additional evidence of a link between the cerebellum and prefrontal cortex. Patients with cerebellar pathology, especially that resulting from bilateral atrophy tend to perform poorly on standardized neuropsychological tasks designed to assess executive function (Appollonio et al., 1993). A high correlation between activation in lateral prefrontal cortex and the cerebellum is found in the neuroimaging literature, and many of these studies have involved linguistic tasks. Consider the seminal study of Petersen and colleagues (Petersen et al., 1989) that examined the neural bases of lexical retrieval. In the critical conditions, the participants viewed a single noun, such as *apple*, and were asked either to read the word (Repeat Condition) or to generate an associated verb, such as *peel* (Generate Condition). Given that the overt motor demands were similar in the two conditions, the researchers assumed that subtracting activation observed during the Repeat condition from that observed during the Generate condition would identify the neural systems involved in semantic memory and retrieval. These regions included lateral prefrontal cortex, including Broca's area, and the right cerebellum. This pattern has been replicated in numerous other studies (see Fiez & Raichle, 1997), although the areas of activation also have been found to include more posterior cortical language areas under certain conditions.

Of course, imaging studies are limited in terms of their utility for establishing function. Simply because the cerebellum is activated during verbal retrieval tasks does not mean this structure contributes in a causal manner to the retrieval process. The representation of the semantic associates as well as the executive processes required for selecting an appropriate response may be the sole province of the cerebral cortex. It may be that the cerebellar activation reflects the preparation of the various candidates, ensuring that once a response is selected it will be produced in a rapid and efficient manner (Ivry, 1997).

Although subject to their own limitations, patient studies offer a more direct means for evaluating functional hypotheses. Fiez et al. (1992) presented a case study of a patient who had suffered a stroke resulting in an extensive lesion of the inferior right cerebellar hemisphere. Interestingly, the connections to left prefrontal cortex likely originate in this region. Despite the fact that his post-stroke IQ was 131, the patient was very impaired on variety of generate tasks, showing little improvement across trials as well as producing inappropriate responses on a significant percentage of the trials. For example, he responded with *sharp* as a verb associate of *razor*. Similarly, he had difficulty deciding whether a word was an adjective or verb as well as identifying synonyms.

Three hypotheses might account for these results. First, the behavioral deficits might reflect dysfunction in non-cerebellar structures secondary to the stroke (Gilman et al., 1994). While this problem plagues all neuropsychological studies, the fact that the cerebellum is activated in an array of semantic tasks suggests that the deficits are directly related to the cerebellar pathology. Second, the deficits may reveal cerebellar involvement in lexical-semantic memory. Third, the cerebellum may be part of the executive processes involved in the retrieval and selection of information from lexical-semantic memory. In support of this hypothesis, activation within the cerebellum is reduced when the same words are used over successive sessions (Raichle et al., 1994). Under such conditions, the retrieval and selection demands are attenuated as the participants tend to report the same items.

Given that the study involved a single patient, it is also important to ask whether the deficits are typical of patients with cerebellar lesions. Working with a group of nine patients, we failed to replicate the results of Fiez et al. (1992) on the generate task (Ivry, Helmuth, & Shimuzu, 1997). The patients were slower than controls on the task, but they showed a normal learning function when presented with the same list over successive trials as well as a similar increase in response time when a new list was introduced.

More recently, we have examined the role of the cerebellum in the presumed selection operation entailed by these tasks. Thompson-Schill and colleagues have argued that the left prefrontal cortex is not an essential part of lexical-semantic memory. Rather, they hypothesize that this region is part of a system required for sustaining and selecting among transient representations of candidate responses. For some words, the selection process is likely to be demanding. For example, the responses *purr*, *meow*, and *claw* are all actions of approximately equal association to the word *cat*. For other words, the selection process is highly constrained: almost everyone will respond *cut* to the word *scissors*. The left inferior frontal gyrus was sensitive to the selection demands, showing greater activation for words that had many viable responses (Thompson-Schill et al., 1997). Moreover, patients with lesions that encompassed this cortical region made more errors than control participants when responding to target words that involved high selection demands (Thompson-Schill et al., 1998). In contrast, the groups performed comparably to one another on the low selection words.

Given the similar patterns of activation within left prefrontal cortex and the cerebellum on semantic generation tasks (but see Desmond et al., 1998), we tested a group of 11 patients with focal cerebellar patients on the same task (Ivry, Thompson-Schill, & Middleton, unpublished). The results were clear-cut: the patients rarely made any errors on the task. On almost every trial, the patients were able to generate an appropriate verb associate. They were slower to respond to the high selection items, but this increase was comparable to that seen in the controls. Thus, our results challenge the idea that the cerebellum is part of a distributed network involved in the selection of items from lexical-semantic memory.

The Cerebellum and Verbal Rehearsal

The preceding discussion addressed one hypothesized role for the cerebellum in executive functions that are essential for fluent linguistic competence. A different functional hypothesis concerning cerebello-cortical interactions can be developed by consideration of other components of the executive operations involved in language tasks. Again, the starting point is in the neuroimaging literature. Cerebellar activation is not only prominent in verbal generation tasks, but it is also frequently observed in two tasks that place heavy demands on verbal working memory. First, during delayed response tasks, verbal information must be held in working memory for subsequent retrieval (Paulesu et al., 1993; Fiez et al., 1996; Awh et al., 1996; Desmond et al., 1997; Jonides et al., 1998). Secondly, during N-back tasks, the current contents of working memory must be constantly modified (Awh et al., 1996; Schumacher et al., 1996). These experiments also have shown that Broca's area, the supplementary motor area, and portions of the parietal lobe are associated with verbal working memory tasks.

This distributed network of activation has been considered within the framework of the working memory model proposed by Baddeley (Baddeley & Hitch, 1974; Baddeley, 1986). In this model, working memory is divided into three components: a central executive that coordinates information processing in all modalities and two specialized systems, a visuospatial sketchpad and a phonological loop. The specialized systems are designed to maintain domain-specific representations. The phonological loop is further divided into two subsystems: a phonological short-term store (STS) and an articulatory rehearsal mechanism (Figure 1). The phonological STS is the locus of the phonological representations whereas the rehearsal process is required to refresh information in the store. In attempts to link this model to the neuroimaging data, the parietal lobe activation has been thought to correspond to the phonological STS (e.g. Awh et al., 1996; Jonides et al., 1998; but see Fiez et al., 1996; Becker et al., 1999). Similarly, processing in Broca's area, SMA, and the cerebellum are thought to correspond to the articulatory rehearsal mechanism (e.g. Paulesu et al., 1993; Fiez et al., 1996; Awh et al., 1996; Desmond et al., 1997).

The psychological evidence for separable components associated with phonological short-term memory and articulatory rehearsal comes from studies that have manipulated phonological similarity and word length (Baddeley et al., 1984). When no additional articulatory task is required, phonologically similar words are more difficult to remember than phonologically dissimilar words (the phonological similarity effect). Additionally, words with many syllables are more difficult to remember than words with fewer syllables (the word length effect). However, when articulatory suppression is added, as for example when the participant must count repeatedly from one to three while also perceiving and rehearsing the verbal stimuli, the word length effect disappears regardless of whether or not the words are read or heard. In contrast, the phonological similarity effect disappears only when the words are read.

To account for this dissociation, it is proposed that *spoken* words are automatically represented in the phonological STS. In this representation, they are susceptible to interference from words that are phonologically similar. To maintain the fidelity of the phonological representations, an articulatory rehearsal process is engaged. Because of the motor demands associated covert rehearsal, the articulatory mechanism is time dependent and errors will be more pronounced for longer words. The rehearsal process is disrupted when the articulatory mechanism is occupied by the additional task of counting and therefore the advantage for short words over long words diminishes. The processing of *written* words is similar to that of spoken words, with the exception that the articulatory rehearsal mechanism must be available to convert them from orthographic to phonological representations before the information can be processed in the phonological STS. When rehearsal is not available, as during articulatory suppression, the advantages typically found for both shorter and phonologically dissimilar words is attenuated. Neuroimaging evidence also supports the idea that orthographic representations are first translated into phonological representations before entering the verbal working memory system (Schumacher et al., 1996).

The Cerebellum and Dyslexia

With these ideas in hand, we can now turn to the central topic of this volume, dyslexia. Building on the neuroimaging literature, we assume that a cerebellar contribution to language is as part of a system involved in articulation, silent or overt. This notion is consistent with current theories of motor control that assume that covert or mental “actions” engage the same processes as those involved in overt movement (Ryding et al., 1993). Within the context of verbal working memory, articulatory rehearsal plays an important role in reading, supporting the conversion from orthographic to phonological representations. As such, the cerebellum would be seen as one part of a network required for articulatory rehearsal.

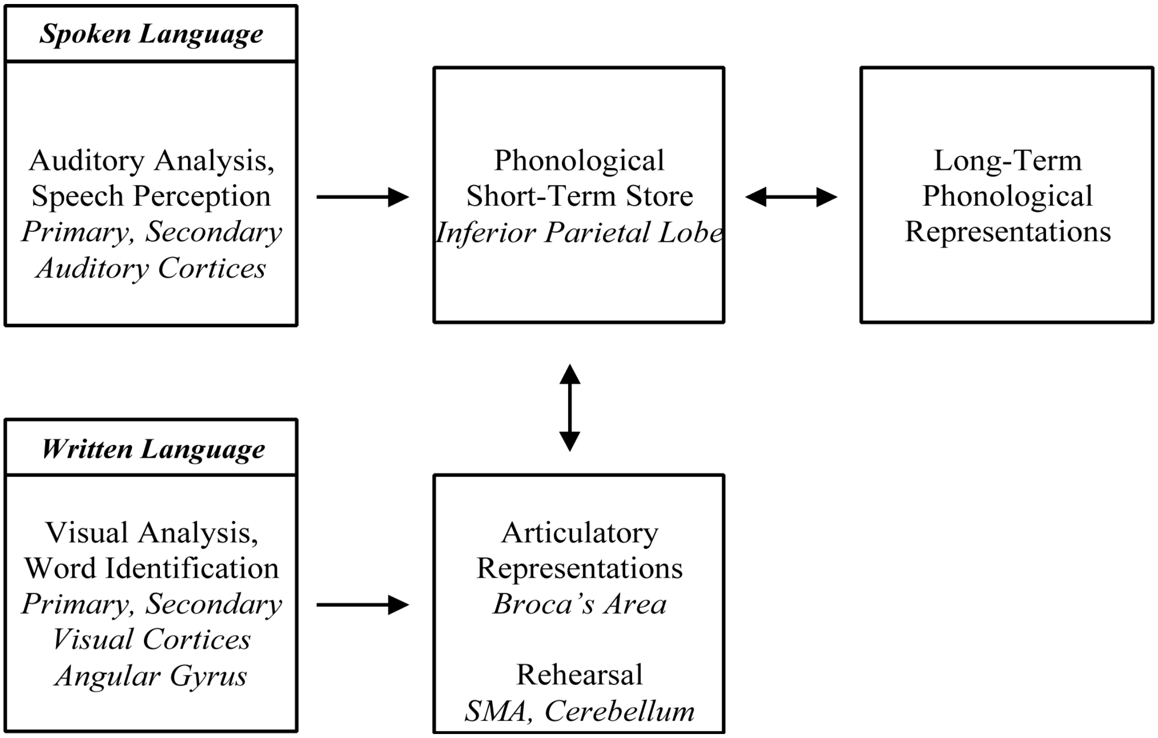

Figure 1: Spoken and written language processed in verbal working memory, as suggested by the Baddeley phonological loop model and neuroimaging evidence. Each box represents a stage in the working memory algorithm along with the hypothesized locus of neural implementation. (Adapted from Baddeley, Gathercole, and Papagno, 1998)

If the cerebellum is part of a covert rehearsal system, then an association between cerebellar pathology and reading problems would be predicted regardless of whether or not one advocates an input-based (acoustic) or output-based (motor) kind of phonological representation. Assuming Baddeley's model, input-based representations in the phonological STS must be preceded by the operation of the articulatory rehearsal mechanism during reading. Even with well-developed input-based phonological representations, the conversion to those representations would be handicapped with cerebellar abnormalities.

However, the motor theory of speech perception (e.g. Liberman and Mattingly, 1985) would predict further developmental problems for children with cerebellar abnormalities. If speech is represented as abstract motor commands associated with articulatory gestures, then cerebellar abnormalities may not just diminish the accessibility of otherwise good phonological representations, but may also interfere with the normal development of those phonological representations in the first place. While this problem might also be expected to be manifest in auditory language, it should be especially marked with written language given the demands of mapping abstract symbols onto the articulatory-based phonological representations (Liberman, 1997).

The link between the cerebellum and salient phonological representations is consistent with the argument that the primary function of the phonological loop is that of a language learning device, allowing for the long-term representation of novel phonological input (Baddeley, Gathercole, & Papagno, 1998). There is strong evidence that the phonological loop mediates the long-term representation of new vocabulary in children, especially when the new words have an unfamiliar phonological structure. Moreover, the phonological similarity effect and word length effect are more pronounced when the phonological forms are unfamiliar and cannot rely on information represented in long-term memory. Thus, the rehearsal mechanism is seen as an important way in which a short-term phonological store could modify long-term phonological representations.

Note that this hypothesized functional relationship between the cerebellum, rehearsal, and dyslexia is independent of other ways in which cerebellar dysfunction could contribute to this disorder. For example, Stein (this volume) develops the idea that, in the dyslexic population, the cerebellum may operate on noisy sensory signals, and thus lead to a variety of sensorimotor and oculomotor deficits. Given that different types of dyslexia hay have very different etiologies, it is possible that the cerebellum contributes in multiple ways to variations in reading ability.

A Preliminary Study of Verbal Rehearsal and the Cerebellum

Central to the preceding discussion is the hypothesis that the cerebellum is part of an articulatory rehearsal process. This hypothesis is consistent with the neuroimaging evidence associating the cerebellum and language. However, there is little direct evidence on this issue. We have begun to evaluate these ideas by testing patients with cerebellar lesions on verbal working memory tasks, applying the manipulations developed by Baddeley and his colleagues. As noted previously, the word length effect is thought to reflect the operation of an articulatory rehearsal process. In normal individuals, this effect is attenuated by the demands of a secondary rehearsal task. Correspondingly, we would expect to find an attenuated effect of word length in patients with cerebellar damage. Such a result had been observed previously in a single cerebellar case study (Silveri et al., 1998). We wished to extend these results to a larger group of cerebellar patients, testing for the word length effect using a set of abstract low-frequency English words, which were either two-syllables or four-syllables in length (Justus & Ivry, 2000).

To date, we have tested one patient with a right unilateral cerebellar lesion, two patients with bilateral cerebellar degeneration, and four control participants matched in education and age. The participants were asked to listen to a list of words read aloud by the experimenter and then to recall the words immediately after the last item. The number of items per list was gradually increased until a moderate level of difficulty was achieved. Based on our criteria, we used four-item lists with the three patients and one of the controls and five-item lists with the other three controls. For the main experiment, one hundred lists were presented, fifty with two-syllable words and fifty with four-syllable words.

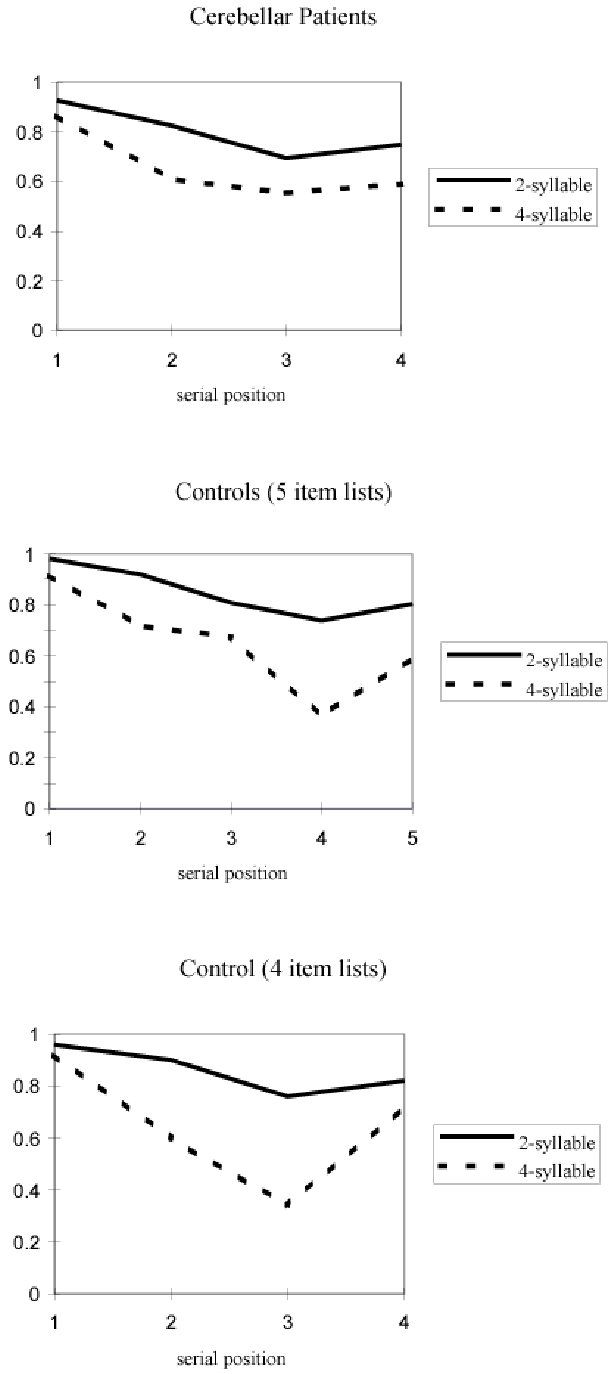

Figure 2: Results of a verbal working memory study comparing the word length effect in cerebellar patients and controls. Each graph shows the probability of recalling an item as a function of its syllable length and serial position for a) three patients with lesions or degeneration to the cerebellar hemisphere(s) tested with four-word lists, b) three control subjects tested with five-word lists, and c) one control subject tested with four-word lists. (Justus and Ivry, 2000)

The results showed a significant word length effect for both the patients and controls (patients: *t*(2) = 6.4, *p* = .02; controls: *t*(3) = 9.7, *p* = .002; see Figure 2a, 2b). However, the size of the effect is larger for the controls compared to the patients with cerebellar damage, in particular on the second to the last item (overall word length effect: *t*(5) = 1.9, *p* = .12, ns; analysis restricted to the second to the last item: *t*(5) = 4.7, *p* = .005). The interaction is consistent with the hypothesis that the integrity of the cerebellum is essential for normal rehearsal. However, these preliminary results must be taken with caution. First, the overall interaction is not statistically significant and we need to enlarge our sample sizes. Secondly, by using our difficulty criteria (which was successful at equating the overall performance of the two groups), a difference was created between the list lengths used for the patients and most of the controls. It is noteworthy that the control participant who was tested with four-item lists showed a larger word length effect than any of the cerebellar patients (Figure 2c), suggesting that the apparent difference in word-length effect between the patients and the other controls is unlikely to result from an inherent difference between remembering four-item or five-item lists.

These preliminary results suggest that damage to the cerebellum may interfere with verbal rehearsal, complimenting the work of Silveri et al. (1998), Desmond et al. (1997) and others in suggesting a role for the cerebellum in the phonological loop. Again, given the importance of the phonological loop in creating long-term phonological representations for the native language, along with the importance for these representations for reading, this suggests a possible causal relationship between abnormalities in cerebellar development and later reading problems.

CONCLUSIONS AND FUTURE DIRECTIONS

In this chapter we have considered ways in which the cerebellum may contribute to language, and in particular, reading and dyslexia. First we reviewed the evidence for the cerebellum as a specialized structure for temporal processing in movement and perception, relating this to speech production and perception. We then reviewed some of the evidence for cerebellar involvement in two linguistic processes: lexical retrieval and verbal rehearsal. We focused on the latter process as providing a possible functional link between the cerebellum and developmental dyslexia.

To date, the links between cerebellar abnormalities and dyslexia remain rather indirect. Their clumsiness is well established, and recent evidence has indicated that cerebellar dysfunction may underlie their movement problems (Nicolson, Fawcett, & Dean, 1995). However, even if we assume that cerebellar pathology and dyslexia are correlated, it is important to consider whether a causal relationship exists. With this in mind, our goal was to present one possible chain of causal relationships linking the two. In this model, we consider three relationships: the link between the cerebellum and verbal rehearsal, the link between variability in verbal rehearsal and phonological skill, and the link between phonological skill and reading ability.

The role of the cerebellum in verbal rehearsal emerged in the neuroimaging literature and this work has inspired testable predictions for neuropsychological research. Patients with localized cerebellar lesions can help clarify the parts of the cerebellum that contribute to verbal rehearsal. Manipulations involving word length, phonological similarity, articulatory suppression, and modality of presentation should help evaluate how the cerebellum fits into the Baddeley-Hitch model and alternative models. It is important to extend this work to children with developmental abnormalities in the cerebellum, rather than focus exclusively on adults with acquired lesions.

The second relationship is that between verbal rehearsal and phonological skill. Tests of working memory capacity, such as digit span and spoken text comprehension, are predictive of reading ability (Perfeti, 1985). These correlations emphasize possible connections between specific working memory components and reading. In terms of phonological skill, the relationship has been considered from the reverse perspective, with impaired verbal rehearsal being one consequence of poor reading skills (e.g., Brady, 1997). We are suggesting the reverse causal relationship, namely, that variation in verbal rehearsal ability will contribute to variation in the quality of phonological representation, and therefore phonological skills.

Of the three connections hypothesized in our model, that between phonological skill and reading ability is the most substantiated. Phonological skill typically has been measured using two different kinds of speech tasks, categorical perception tasks and pseudoword repetition tasks, and the literature supports a relationship between both of these indices of phonological skill and reading ability (see Brady, 1997, for review). The primary unresolved issue here is the degree to which what we are calling phonological processing is specifically phonological and not part of a greater temporal processing ability (see Farmer & Klein, 1995, for review; Studdert-Kennedy & Mody, 1995; Merzenich et al., 1996).

In suggesting this connection between the cerebellum, verbal rehearsal, phonological representation, and reading, we do not mean to suggest this particular etiology as *the* potential explanation for dyslexia. Given the large set of mental processes involved in comprehending written language, it is likely that there are numerous causes for dyslexia involving developmental differences in any of these various systems. Some dyslexics may primarily have an auditory problem and others a visual problem. Some may have a specific deficit in phonological processing and others a more general auditory or temporal impairment. Not only do we caution against a single explanation for dyslexia, but we also suggest that the role of any given brain structure such as the cerebellum could contribute in multiple ways to reading. The cerebellum may not only play a role in verbal rehearsal, but is likely to participate in multiple ways through its contributions to motor control and temporal processing.

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