CEREBELLAR TIMING SYSTEMS

Richard Ivry

Department of Psychology, University of California Berkeley, California 94720

Coordinated movement requires the normal operation of a number of different brain structures. Taking a modular perspective, it is argued that these structures provide unique computations that in concert produce coordinated behavior. The coordination problems of patients with cerebellar lesions can be understood as a problem in controlling and regulating the temporal patterns of movement. The timing capabilities of the cerebellum are not limited to the motor domain, but are utilized in perceptual tasks that require the precise representation of temporal information. Patients with cerebellar lesions are impaired in judging the duration of a short auditory stimulus or the velocity of a moving visual stimulus. The timing hypothesis also provides a computational account of the role of the cerebellum in certain types of learning. In particular, the cerebellum is essential for situations in which the animal must learn the temporal relationship between successive events such as in eyeblink conditioning. Modeling and behavioral studies suggest that the cerebellar timing system is best characterized as providing a near-infinite set of interval type timers rather than as a single clock with pacemaker or oscillatory properties. Thus, the cerebellum will be invoked whenever a task requires its timing function, but the exact neural elements that will be activated vary from task to task. The multiple-timer hypothesis suggests an alternative account of neuroimaging results implicating the cerebellum in higher cognitive processes. The activation may reflect the automatic preparation of multiple responses rather than be associated with processes such as semantic analysis, error detection, attention shifting, or response selection.

0074-7742/97 $25.00

I. A Modular Approach to Coordination

The human brain can be described as an evolutionary device geared to make our interactions with the world more efficient. Although we have elaborate mechanisms for perceiving and learning about complex patterns, this information is only useful if we can respond to it in an appropriate manner. Action is the ultimate goal of cognition, and action systems are designed to allow us to achieve our goals in a coordinated and flexible manner.

Given this, it is not surprising that so many parts of the brain are implicated in motor control. A wide variety of neurological disorders can disrupt the production of coordinated behavior. In some of these disorders, such as apraxia, a loss of knowledge about the goal of behavior can be observed (Heilman *et al.*, 1981). However, in most movement disorders, the problem is a loss of coordination. The action may still be purposeful, but the control and execution of the action are disturbed. From this we can create a list of the neural systems involved in coordination and skilled movement. This list would include the motor cortex, the basal ganglia, various brain stem nuclei, and, of course, the cerebellum. But such a list would only provide a description of the functional domain of a neural structure. It would tell us little about how a particular structure contributes to the overall computations required to achieve coordinated behavior.

Research since the mid-1980s has focused on developing a psychological and neural model of the components of coordination (see Helmuth and Ivry, 1997). From this perspective, we would acknowledge that coordinated movement requires the normal operation of a number of different brain structures. However, the emphasis would be on identifying the specific contribution of these different structures. That is, we have worked from a starting assumption that there is a basic modularity to the organization of the motor system. Different neural structures contribute to movement by providing distinct computations, the sum of which will determine whether a particular action is coordinated or not. This modularity notion has been widely applied in the realm of perception. It has not been as well advanced in the motor domain. This is not to say that many, or any, researchers would argue that the basal ganglia and cerebellum perform the same function. Nonetheless, there has been a persistent tendency to describe the functional domain of motor structures in terms of tasks rather than computations. For example, the cerebellum may be described as essential for the production of well-learned movements whereas the cortex is essential for the acquisition of new movement patterns. A modular perspective, however, might emphasize that both structures are involved in both skilled and unskilled movements, but their relative contributions change in accord with varying computational demands.

Figure 1 provides an overview of some of the modules required for the performance of sequential movements. For each neural structure shown on the left side, a component operation is listed on the right side. For example, this overview characterizes the premotor cortex as playing a critical role in movement selection (Deiber *et al.*, 1991; Rizzolatti *et al.*, 1990). Thus, if one is to pick up a glass of water, the premotor areas will determine whether that gesture is made with the right or left hand. The specification of when that movement should occur and the fine tuning of the kinematics of the particular gesture, however, are assigned to other neural structures. For example, the basal ganglia may play a critical role in the switching from one action state to another (Hayes *et al.*, 1995; Robertson and Flowers, 1990).

In this conceptualization, the cerebellum is proposed to play a critical role in establishing the temporal patterns of muscular activation. This chapter reviews some of the evidence that supports the idea that the cerebellum plays a unique role in representing temporal information. A central theme to be emphasized is that this computational capability may be exploited in a variety of task domains. That is, the cerebellum can be viewed as an internal timing system that not only regulates the timing of muscular events, but is also used whenever a precise representation of temporal information is required. This computational demand may arise in percep-

Brain Region		Computations required for sequential movement
Frontal Lobes	•	Goal Development
Parietal Cortex	•	Spatial Representation and Planning
Premotor and Supplementary Motor Area	•	Movement Selection
Movement Specification and Initiation		
Cerebellum	•	Temporal patterns of activation
Basal Ganglia	•	Switching between different patterns
Motor Cortex	•	Movement Execution

FIG. 1. Overview of modules required for performance of sequential movements.

tion and learning, and as such, the cerebellum will be implicated in these nonmotor tasks. But this does not mean that the essential function of the cerebellum has changed. Rather, the domain of cerebellar function has become generalized because these other tasks utilize its timing capability (see Ivry, 1993).

II. Cerebellar Contribution to Movement Timing

While there has been much interest in nonmotor functions of the cerebellum, it is important not to lose sight of the lessons that have been garnered from a century of neurological observation. The foremost signs of cerebellar dysfunction involve a loss of coordination (Holmes, 1939). The springboard for the timing hypothesis stems from consideration of the unique movement problems that result from cerebellar lesions.

Figure 2 depicts the electromyographic (EMG) record associated with a series of movements produced by a patient with a unilateral cerebellar lesion (Hore *et al.*, 1991; see also Hallett *et al.*, 1975). As would be expected with this pathology, the patient's problem were restricted to the ipsilesional side, and thus the nomal records are from movements produced by the same

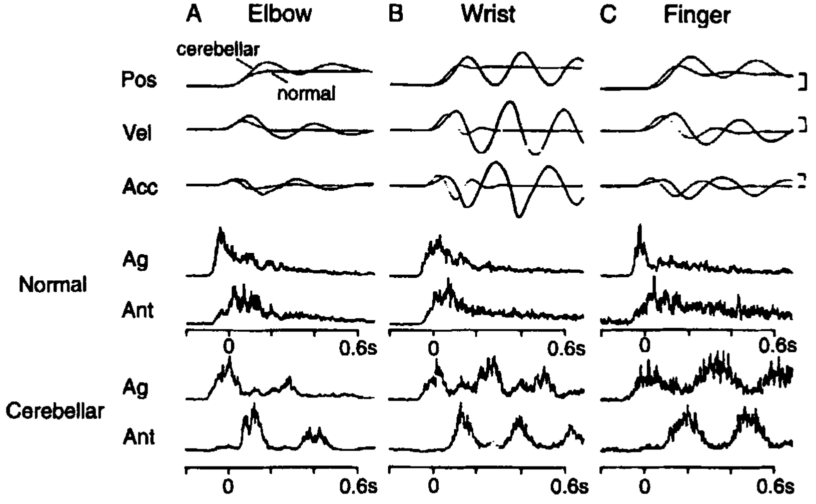

FIG. 2. Kinematic (top) and EMG (bottom) records from single-joint movements produced by a patient with the contralesional hand (Normal) or ipsilesional hand (Cerebellar). From Hore *et al.* (1991), with permission.

patient when using muscles on the contralesional side. On the unimpaired, normal side, the EMG record shows a biphasic pattern, with the antagonist muscle becoming active near the peak of the agonist activity. The antagonist provides the necessary braking force that will allow the movement to terminate at the target location. A different pattern emerges when we look at performance on the impaired side. Here the onset of the antagonist is delayed and fails to brake the movement. The patient ends up being hypermetric, i.e., overshooting the target. In addition, there is an intention tremor as the person hones in on the final goal of the movement, with the delayed antagonist activity producing a series of overshoots. Thus, the disruption of the temporal pattern of muscular events leads to both hypermetria and intention tremor. Other work has indicated that the problem is primarily in the timing of the muscle patterns. For example, these patients can scale the agonist burst when producing movements of different amplitudes (Hore *et al.*, 1991). Thus, while the timing hypothesis does not exclusively account for these results, it does meet the basic criterion of providing a consistent account of the coordination problems observed following cerebellar pathology.

In our research, we have looked for more direct evidence of a cerebellar involvement in timing. We began with a simple motor task in which patients with a variety of neurological disorders were tested on a timed tapping task (Ivry and Keele, 1989). Each trial began with a synchronization phase in which the subject tapped along with a series of computer-generated tones separated by 550 msec. After about 6 sec, the tones were terminated and the subject was instructed to continuing tapping, trying to maintain the target pace. Tapping continued until the subject had produced 30 unpaced intervals. Each subject completed at least 12 trials in this manner.

Overall, the patients tend to approximate the target interval in a consistent manner. The primary focus was on the standard deviation of the intertap intervals. Patients with either cerebellar or cortical lesions were more variable than control subjects on this task (Ivry and Keele, 1989). Although this result is not surprising given that all of the patients were selected because of their motor problems, this crude measure still proved sufficient to differentiate between the patient groups. In particular, patients with Parkinson's disease, a disorder of the basal ganglia, performed comparably to the control subjects.

There are many reasons why an individual may be inconsistent on the timed tapping task. Variability would, of course, be inflated if an internal timing system was damaged, creating noise in a process determining when each response should be initiated. However, a central timer might be intact, but its commands may be inconsistently executed due to problems in the motor implementation system. Wing and Kristofferson (1973) developed a formal model which partitions the total variability observed on this tapping task into two component parts. One component is associated with variability in central control processes including an internal timer. The second component is associated with variability arising from implementation processes. A description of this model and empirical justification for its primary assumptions can be found in Wing (1980). Ivry and Keele (1989; also Ivry *et al.*, 1988) describe neurological evidence in support of the model.

The Wing and Kristofferson model was used to analyze in detail the performance of patients with unilateral cerebellar lesions (Ivry *et al.*, 1988). This group was chosen because the patients could serve as their own control, i.e., their performance could be compared with the impaired, ipsilesional hand against that of their unimpaired, contralesional hand. In this analysis, the cerebellar group was separated into those with medial lesions and those with lateral lesions. Motivation came from consideration of the anatomy of the cerebellum (see Ghez, 1991). The output from the lateral regions is primarily ascending, ending up in the motor and premotor cortex. The output from the medial regions is primarily descending, ending up in brain stem nuclei or synapsing directly on spinal circuits.

The results showed a double dissociation (Fig. 3). When tapping with their ipsilesional hand, the increased variability in patients with lateral lesions was attributed to the central component (Ivry *et al.*, 1988). In contrast, the increased variability for the patients with medial lesions was attributed to the implementation component. This dissociation, coupled

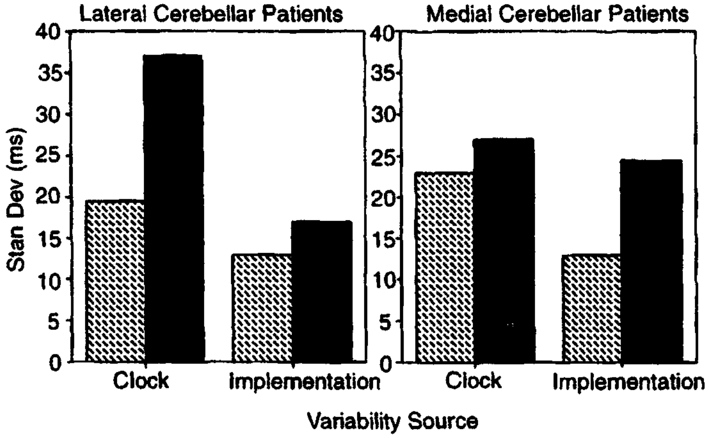

FIG. 3. Estimates of clock (central) and implementation variability on the repetitive tapping task. Hatched bars, unimpaired hand; solid bars, impaired hand. Modified from Ivry *et al.* (1988).

with the following perception results, led to the proposal that the lateral cerebellum plays a critical role in controlling the timing of these periodic movements. This does not exclude the possibility that the medial cerebellum is also involved in timing. Its contribution to coordination may also be time based, but in a manner that anticipates and corrects ongoing movements (e.g., efference copy) rather than one that initiates new motor commands (see Keele and Ivry, 1991).

III. Perceptual Deficits in the Representation of Temporal Information

The domain of the cerebellar timing system extends beyond motor control. One line of support for this hypothesis is that patients with cerebellar lesions are also impaired on perceptual tasks that require precise timing. This work was motivated by correlational studies showing that a common timing system was used in motor and perceptual timing tasks (Keele *et al.*, 1985; Ivry and Hazeltine, 1995). In our patient work, we employed a simple duration discrimination task (Ivry and Keele, 1989). On each trial, two pairs of two tones were presented. The first pair was separated by 400 msec; this provided a standard, reference interval. The second pair of tones formed an interval that was either shorter or longer than 400 msec. The subject made a two-alternative forced choice response. An adaptive psychophysical procedure was used to determine the difference threshold required for each subject to be accurate on approximately 72% of the trials (Pentland, 1980). For a control task, a similar stimulus configuration was used, but here the intensity of the second pair of tones was varied. The subject judged if the second pair was softer or louder than the first pair, and the same adaptive procedure was used to determine the difference threshold for loudness perception.

The results in this study provided a second double dissociation (Fig. 4). Only the patients with cerebellar lesions were impaired on the duration discrimination task (Ivry and Keele, 1989). Patients with Parkinson's disease were as accurate as controls and, more importantly, so were the cortical patients. In fact, the latter group was found to be impaired on the loudness discrimination task, perhaps because some of the lesions extended into the temporal lobe. While we were not particularly interested in the neural basis of loudness perception, the fact that the cortical group was selectively impaired on this task provides further weight to the claim that the cerebellar deficit on the duration discrimination task reflected a specific deficit in time perception.

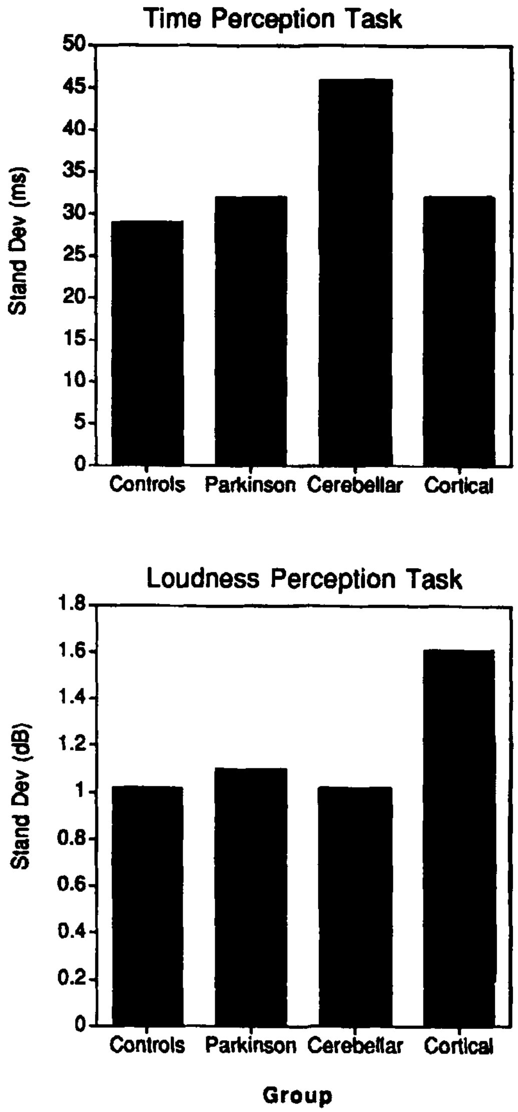

FIG. 4. Perceptual acuity on two psychophysical tasks, duration (top) and loudness (bottom), for four groups of age-matched subjects (Stand Dev, standard deviation). Modified from Ivry and Keele (1989).

Converging evidence for a role of the cerebellum in time perception comes from a positron emission tomography (PET) study (Jueptner *et al.*, 1995). The experimental task in this study was essentially the same as that used in the patient study of duration discrimination. For their control task, the subjects simply listened to the stimuli and made alternating finger responses to control for motor output. Significant increases in blood flow were observed bilaterally, with the foci centered in the superior regions of the cerebellar hemispheres.

Patients with cerebellar lesions are also impaired in their ability to judge the velocity of a moving visual stimulus (Ivry and Diener, 1991). In these studies, the subjects viewed displays consisting of a series of dots that swept across the screen. As a dot reached the end of one side of the screen, a new dot appeared at the other end. This configuration was adopted to minimize tracking eye movements. The subjects were required to judge in which of two successive displays the dots moved fastest. A control task used a similar procedure, but here the location of the dots was adjusted in the vertical plane and the perceptual judgment was position based. The patients were significantly impaired only on the velocity task. This finding has been replicated in another laboratory (Nawrot and Rizzo, 1995), and similar velocity perception deficits have been found with somatosensory stimuli (Grill *et al.*, 1994).

Ivry and Diener (1991) hypothesized that a faulty representation of the velocity of a moving stimulus, a time-based computation, may underlie some of the occulomotor problems observed in these patients (see Leigh and Zee, 1991). For example, in order to generate an appropriate saccade, it is necessary to have an accurate representation of the future position of a moving stimulus. By measuring eye movements, Ivry and Diener (1991) showed that the perceptual deficit was not an indirect consequence of a motor problem. Patients who were able to maintain fixation were as impaired as those who were unable to suppress intrusive eye movements.

IV. Timing Requirements in Sensorimotor Learning

Summarizing to this point, we have consistently observed impairments in patients with cerebellar lesions on tasks designed to require precise temporal processing. The timing hypothesis not only provides an account of the motor problems faced by these patients, but also leads to predicted perceptual deficits. A further source of evidence for this hypothesis comes from a very different paradigm: research showing that the cerebellum is involved in certain types of sensorimotor learning. This work also underscores the usefulness of thinking about brain structures in terms of their component operations rather than in terms of their task domains.

A large literature has been assembled since the mid-1980s demonstrating that the cerebellum plays a critical role in eyeblink conditioning (for reviews, see Thompson, 1990; Yeo, 1991, this volume; Woodruff-Pak, this volume). In the standard eyeblink conditioning paradigm, a tone is used as the conditioned stimulus and precedes an airpuff to the eye by a fixed interval such as 400 msec. Although the animal will make an unconditioned response to the airpuff, learning centers on the fact that, over time, the animal comes to make a conditioned response in anticipation of the airpuff.

A number of studies have demonstrated that animals with cerebellar lesions fail to learn the conditional response. Moreover, learned responses may be abolished following cerebellar lesions. The deficit does not appear to be a motor problem in that the same animals continue to produce the unconditioned response. Similar results have been reported in human literature. Patients with bilateral cerebellar lesions show a severe impairment in eyeblink conditioning (Daum *et al.*, 1993; Topka *et al.*, 1993). Patients with unilateral lesions are more severely disrupted on the side ipsilesional to the lesion (Woodruff-Pak *et al.*, 1996).

Much of the research with this paradigm has focused on identifying the neural circuitry that is critical for this simple form of learning. Our interest in this phenomenon centers on the computational characteristics of eyeblink conditioning. In particular, one critical aspect is the need for a precise representation of the temporal interval between the conditioning stimulus and the unconditioned stimulus. The animal learns to make an anticipatory conditioned response. The fact that the response is anticipatory is what makes it adaptive: by blinking before the airpuff, the animal is able to attenuate the aversive consequences of the airpuff. Equally important, the conditioned eyeblink must be appropriately timed. The animal should not blink too soon or the blink may be finished before the airpuff is delivered. Thus, this paradigm demands that the animal learn not only to associate the two stimuli, but learn the precise temporal relationship between the tone and the airpuff. The evidence that they do just this is shown by the fact that the timing of the learned response is always just prior to the airpuff, regardless of the interstimulus interval (Kehoe *et al.*, 1993; Wickens *et al.*, 1969).

Thus, it could be argued that the cerebellum is not essential for eyeblink conditioning because of some general role in classical conditioning. Rather, the essential reason is because this type of learning requires precise timing and the cerebellum is uniquely suited for providing this type of computation. Classical conditioning of other responses that do not show the same temporal constraints do not involve the cerebellum (Lavond *et al.*, 1984).

Two other points are relevant for the extension of the timing hypothesis to classical conditioning. First, it is of interest to note that at least four computational models of eyeblink conditioning have been proposed since the early 1990s (Bartha *et al.*, 1992; Buonamano and Mauk, 1994; Desmond and Moore, 1988; Grossberg and Schmajuk, 1989). A central feature of all four models is that they contain mechanisms which can provide an explicit representation of temporal information. This feature has not been part of neural models developed for other task domains.

Second, Perrett *et al.* (1993) have observed an important dissociation between the effects of lesions of the deep cerebellar nuclei and lesions of the cerebellar cortex on the conditioned response. Nuclear lesions abolish this learned response, presumably because these lesions destroy all of the output from the cerebellum. In contrast, cerebellar cortical lesions do not abolish the conditioned response. Rather, they disrupt the timing of the responses, with many of the eyeblinks occurring shortly after the onset of the tone. It is as if the delay imposed by the cortex to ensure that the eyeblink occurs at the right point in time is abolished. In this situation, the response is, of course, no longer adaptive.

V. Characterizing the Cerebellar Timing System

The timing hypothesis provides a general description of cerebellar function. This specifies a unique computational role of the cerebellum that is not limited to motor control, but also can account for perceptual and learning deficits associated with cerebellar lesions. An important question, of course, is how to best characterize the timing properties of the cerebellum. When we think of a timing system such as a clock, our first inclination is to think about oscillatory processes such as a pacemaker. Indeed, most models of internal timing systems center on a clock-counter system in which outputs from an endogenous oscillator are stored in a counter mechanism. The full models also include various memory and decision processes, as well as a gating process that can control whether the periodic outputs of the clock are stored (e.g., Gibbon and Church, 1990).

For the most part, these models have been developed to account for behaviors that span intervals considerably longer than those studied in motor and perceptual tasks, usually on the order of at least several seconds. A general assumption in the timing literature is that these same mechanisms would apply for millisecond timing. The basic idea of a pacemaker as a periodic process, however, may not provide the best description of the cerebellar timing system. Rather, the cerebellum may be viewed as providing a near-infinite set of hourglass or interval-type timers (see Ivry and Hazeltine, 1995). Each hourglass represents a particular interval. There may be some sort of organization to these units, a chronotopic map within the cerebellum. However, computational models such as that offered by Buonamano and Mauk (1994) capture the notion of multiple timers, but with a distributed representation that can be shaped as a function of the temporal demands of a particular task.

In our initial tapping studies, each patient served as his or her own control. The tapping performance was compared between trials in which the patients used their contralesional, unimpaired hand with trials in which they used their ipsilesional, impaired hand. Patients with lateral lesions were found to have higher clock variability on the impaired side. This suggested that there are at least two clocks: a damaged one on the lesioned side and an intact one on the normal side.

More recently, the notion of multiple timers has been explored in a variant of the repetitive tapping task. Franz *et al.* (1996b) examined what would happen when patients with unilateral hemispheric lesions tapped with both hands simultaneously. The results were quite surprising (Fig. 5). In the unilateral condition, our original findings were replicated. Variability was higher when tapping with the ipsilesional hand, and when the Wing–Kristofferson model was applied, the difference was attributed to the central component. However, this difference disappeared in the bimanual condition. Now the two hands were equally consistent. Most interesting, the bad hand became better. We were puzzled as to how to interpret the results. One possibility was that the patient could somehow rely on the good timer. Perhaps it provided a more salient signal and thus dominated performance.

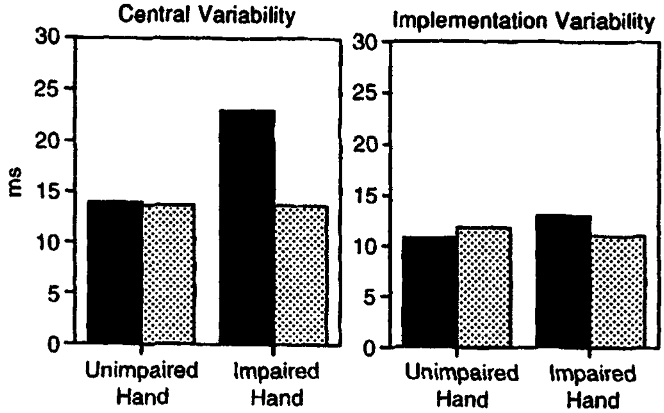

FIG. 5. Estimates of central and implementation variability in cerebellar patients during either unimanual (solid bars) or bimanual (hatched bars) repetitive tapping. Estimates are always of within-hand variability and are plotted for both unimpaired, contralesional hands and impaired, ipsilesional hands. Modified from Franz *et al.* (1996b).

However, this position was abandoned when the experiment was repeated in healthy subjects (Helmuth and Ivry, 1996). Thirty right-handed college students were asked to tap with their right hand, their left hand, or both hands. The results, in terms of total variability, are shown in Fig. 6. Two points stand out. First, subjects were slightly more consistent when tapping with their dominant hand. This effect was linked to higher implementation variability in the nondominant hand (see also Sergent *et al.*, 1993). Second, and more important, timing variability was reduced when subjects tapped with both hands at the same time, i.e., each hand became more consistent when the two hands moved together. As with data from cerebellar patients, the Wing and Kristofferson (1973) model attributed this bimanual advantage to reduced variability in central control processes.

These results argue against the hypothesis that performance is determined by a single timer in bimanual tapping. If this were the case, we would not expect to see an improvement in the control subjects for both hands. Given these results, Helmuth and Ivry (1996) considered an alternative model to account for the bimanual advantage. This model centers on a simple, yet counterintuitive hypothesis. Specifically, Helmuth and Ivry (1996) postulate that there are two independent timers during bimanual movements: one associated with movements of the right hand and a second associated with movements of the left hand. The bimanual advantage emerges because of a central bottleneck that limits when central motor commands can be issued, a mechanism believed to underlie the ubiquitous

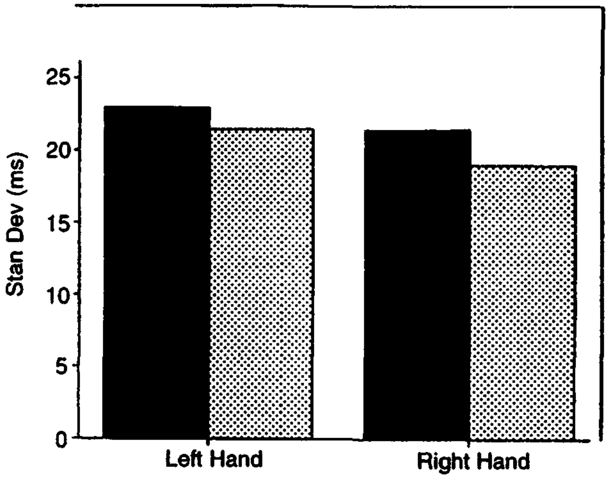

FIG. 6. Total variability in unimanual (solid bars) and bimanual (hatched bars) conditions in healthy subjects on the repetitive tapping task (Stand Dev, standard deviation). Modified from Helmuth and Ivry (1996).

temporal coupling observed in multi-effector actions. The authors propose that this bottleneck must integrate the two timing signals and issue a single command. The bimanual advantage results as a statistical consequence of this integration process (see Helmuth and Ivry, 1996). Thus, by this account, there is not a single timer in bimanual movements, but separate timers that are integrated by a constraint in terms of when central motor commands can be implemented.

As noted earlier, the timing of ipsilesional movements produced by cerebellar patients becomes less variable when accompanied by corresponding movements of the contralesional hand. Moreover, during bimanual movements, the patients show strong interlimb coupling. These two results suggest that the temporal integration process producing the bimanual advantage is not dependent on the cerebellum. Timing and temporal coupling appear to be associated with different neural systems (Franz *et al.*, 1996a).

In other work with normal subjects, a similar reduction in variability was found when subjects made simultaneous finger and foot movements regardless of whether the two limbs were on the same or different sides of the body (Helmuth and Ivry, manuscript in preparation). The generality of this effect is in accord with the notion that the cerebellum is best conceptualized as an array of a near-infinite set of timers. As long as the movements invoke nonoverlapping neural elements, the bimanual advantage will be obtained. In this sense, timing is assumed to reflect a general and unique computational capability of the cerebellum. This capability will be exploited whenever a task requires the timing function of the cerebellum, but the exact neural elements that will be activated will vary from task to task.

VI. Interpreting Cerebellar Activation in Neuroimaging Studies: A Challenge for the Timing Hypothesis?

The idea of multiple timers has potential implications beyond providing a characterization of the cerebellar timing system. It can also lead to a novel perspective on recent functional neuroimaging evidence that points to a role for the cerebellum in cognition. In these studies, the cerebellum is activated even when the experimental and control tasks are equated in terms of their motor requirements (e.g., Jenkins *et al.*, 1994; Kim *et al.*, 1994; Petersen *et al.*, 1988; Raichle *et al.*, 1994).

What do the metabolic events seen in PET and functional magnetic resonance imaging studies reflect? In the neuroimaging studies, there is a common denominator across those conditions that produce significant increases in metabolic activity in the cerebellum. This common denominator is that these conditions are invariably more difficult than the comparison conditions. That is, there seems to be a strong correlation between task difficulty and cerebellar activation. One operational definition of "task difficulty" would be to determine the possible set of responses. By this definition, difficult tasks are those associated with more response alternatives.

A review of the imaging literature indicates that experiments demonstrating a role of the cerebellum in cognition confound the experimental and control tasks in terms of the number of response alternatives. Consider the seminal language study of Petersen *et al.* (1988). In the two critical conditions, the stimuli were identical, the presentation of a single concrete noun. In the control, repeat condition, the subjects simply read the word. As such, there was only a single possible response. In the experimental, generate condition, the subjects had to name a verb that was a semantic associate of the stimulus. Here, we would expect there to be many possible responses, at least in the first trial. For example, if the target word was "apple," possible responses in the generate condition would be "eat," "peel," "throw," and "boot up."

The fact that the cerebellum was more active in the generate condition, even though both conditions required the subjects to articulate a single word, is frequently cited as demonstrating a cognitive role for the cerebellum.[1] However, an alternative, essentially motoric view would be that the cerebellar activation reflects the preparation of all of the possible responses. By this logic, the increased activation in the generate condition results from the fact that there are more potential responses and that the cerebellum does its part to prepare for each one.

Is this cognition? Would the fact that the cerebellum prepares all possible movements imply a cognitive role for this structure? On the other hand, we might imagine a motor theory of cognition in which the choice about which response to make requires the ability to plan that response. As such, the cerebellar contribution would seem to be cognitive. On the other hand, the cerebellum may be viewed as a system that simply goes about the business of preparing its contribution for candidate responses. The cerebellum could be entirely unrelated to the more cognitive aspects of the task.

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[1] Fiez *et al.* (1992) have provided converging evidence based on a case report of a patient with a cerebellar lesion. This patient had great difficulty on a variety of semantic associate tasks, despite his superior performance on standard neuropsychological tests. However, Helmuth *et al.* (1997) failed to find similar deficits in a group study of cerebellar patients. The reason for this discrepancy remains unclear.

It may simply be a slave system in the sense that for any possible response generated in the cortex, the cerebellum helps prepare to make that response. Some responses will be selected, but the cerebellum need not be part of this more cognitive, decision-making process.

If this hypothesis is correct, the imaging results need not be at odds with the hypothesis that the primary function of the cerebellum involves timing. Perhaps the cerebellum faithfully goes about preparing the temporal patterning of the movements associated with all of the possible responses. The idea that each response requires its individual cerebellar activation is in accord with the hypothesis of Helmuth and Ivry (1996) regarding bimanual movements. In that work, the authors proposed that independent timers were invoked for each effector, even producing synchronous movements. In this reinterpretation of the imaging data, the authors propose that nonoverlapping motor plans are prepared for all candidate responses.

Raichle *et al.* (1994) have reported that, with practice, the cerebellar activation in the generate task diminishes. Given that subjects report the same semantic associate on successive trials, it would be expected that the number of potential responses also becomes reduced, eventually equal to that of the repeat condition (i.e., arc possible response). Reductions in cerebellar activation with practice have been observed in other PET studies (Friston *et al.*, 1992). These results are consistent with the idea that one aspect of skill automatization involves constraining the number of possible responses.

VII. Conclusions

Three main points emerge from this chapter. First, the cerebellum is part of a distributed system for motor control, and it is necessary to identify the component operations of the different structures involved in motor control. The timing hypothesis provides a specific functional role for the unique contribution of the cerebellum.

Second, this timing capability appears to extend beyond motor control into tasks focusing on perceptual processing or sensorimotor learning. As with motor function, these nonmotor tasks depend on the cerebellum when the task requires the precise representation of temporal information. This more cognitive view of the cerebellum still remains grounded in its prominent role in the motor system.

Third, within the cerebellum, time is represented in a distributed manner, with the exact elements required varying from task to task. The cerebellum performs its temporal computations whenever needed. This may include the programming of the temporal aspects for potential movements, regardless of whether that particular movement is produced.

To say that the cerebellum is involved in cognition does not propel our understanding of the system very far. We need to have specific ideas about what this contribution might be. This contribution may be timing, but timing in its many manifestations. This working hypothesis offers a concrete and testable idea about the role of the cerebellum in action, perception, and learning.

Acknowledgments

The author is grateful to Steve Keele and Scott Grafton for their comments on preliminary versions of this chapter. The preparation of this chapter was supported by NIH Grant NS30256.

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