Brain and Cognition **48,** 117–132 (2002)
doi:10.1006/brcg.2001.1308, available online at http://www.idealibrary.com on IDEAL®

Temporal Control and Coordination: The Multiple Timer Model

Richard B. Ivry and Thomas C. Richardson

University of California, Berkeley

We consider the psychological and neurological mechanisms involved in timed behaviors, motor or perceptual tasks that emphasize the temporal relationship between successive events. Two general models for representing temporal information are described. In one model, temporal information is based on the oscillatory activity of an endogenous pacemaker; in the other model, temporal information is interval-based with distinct elements devoted to representing different intervals. We incorporate the interval hypothesis into a process model, the multiple timer model, to account for the timing and coordination of repetitive movements. The model accounts for the patterns of temporal stability observed within each effector and offers a novel account of between-effector coordination. Finally, we consider how timing and temporal coordination may be instantiated in the nervous system.

A striking feature of many human behaviors is their temporal consistency and flexibility. We automatically adopt a fairly constant pace when walking and yet remain sensitive to deviations from this pace. For example, we can readily detect that a friend is walking at a faster pace than we would prefer, and make the necessary adjustments so that we do not fall behind. To throw a ball accurately, the opening of the fingers to release the ball must occur within a narrow temporal window with respect to the extension of the arm (Hore, Ritchie, & Watts, 1999). The timing of these events must be altered if we wish to throw the ball farther or harder. How such control is achieved has been the subject of considerable study. In this article, we explore the question of how temporal information is represented, both from psychological and neurological perspectives. Moreover, we consider how such representations are integrated and utilized by a more general system required for the control of coordinated action.

The focus here will be on tasks that can be described as involving event timing (Schoener, 2001, this volume). Repetitive movements are perhaps the most studied example of a task involving event timing. In finger tapping, these movements involve contact with an external object. But they can also occur without such external constraint, with the events defined as points of maximum extension and flexion. The events not only define a series of periodic actions, but in many studies, the experimenter specifies a target rate at which these movements should occur. Under such conditions, temporal information must, at a minimum, be incorporated into the repre-

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Address correspondence and reprint requests to Richard Ivry, Department of Psychology, MC 1650, University of California, Berkeley, CA 94720. Fax: 510-642-5293. E-mail: ivry@socrates.berkeley.edu.

This work was supported by grants from the National Institute of Health (NS30256, NS2778) and the National Science Foundation (ECS-9873474). The authors are grateful to Joern Diedrichsen, Eliot Hazeltine, Gregor Schoener, and Andras Semjen for many discussions on the issues raised in this article.

0278-2626/01 $35.00

sentation of the goal of the action. The achievement of this goal may involve some type of direct manipulation of a temporal representation. Alternatively, adjustments in the timing may be achieved in a more indirect manner; for example, by adjusting the stiffness of the limb or varying the rate at which forces are generated.

Event timing can also be investigated in perceptual tasks. There are several different temporal attributes we can consider when comparing different events. Do the events occur simultaneously? If not, which event came first? Judgments of simultaneity and temporal order, however, do not require a metrical representation of time. To study the sense of time, researchers generally focus on the perception of duration. In such tasks, the target interval is either marked by the duration of a stimulus or by an empty interval marked by two stimulus events. Unlike motor tasks in which temporal properties may be emergent, perceptual tasks would seem to require the explicit representation of temporal information.

Central to the study of event timing has been the question whether we need to posit a psychological construct dedicated to temporal processing. Put simply, is there an internal clock that provides a representation that is isomorphic with elapsed time? Such a clock could, in principle, be used to meter out the intervals (or regulate the onset of movements) required for the motor events or provide a representation for comparing the duration of different perceptual events. Evidence in support of the internal clock hypothesis comes from various sources (see Ivry, 1997). For example, measures of temporal variability are significantly correlated across motor tasks involving different effectors (e.g., Keele, Pokorny, Corcos, & Ivry, 1985; Franz, Zelaznik, & Smith, 1992) as well as between motor and perceptual tasks (e.g., Keele et al., 1985; Ivry & Hazeltine, 1995).

CHARACTERIZING THE INTERNAL CLOCK

In attempting to characterize an internal process that represents time, it is instructive to consider two general metaphors for a clock mechanism (Ivry, 1996; Schoener, 2001, this volume). First, the representation of time might be derived from the operation of an endogenous oscillatory process, or pacemaker. Such models generally assume that different intervals require the linkage of the pacemaker with some type of counting device. For example, if the pacemaker were operating at 40 Hz, a 300-ms interval would correspond to a sum of 12 units in the counter, whereas a 400-ms interval would correspond to a sum of 16 units in the counter. In this instantiation, the pacemaker is assumed to operate at a fixed speed. It is, of course, possible that the pacemaker frequency can be adjusted based on task demands (Treisman, Faulkner, & Naish, 1992) or even that there exists a bank of such oscillators, with different intervals resulting from their interactions (Church & Broadbent, 1991; Miall, 1996). But an essential feature of this model is that the representation of events is based on a reproducible oscillatory period.

The second metaphor is that of an hourglass, or what we will refer to as an interval timer. At a microscopic level, one could say that there is an oscillatory process involved in the hourglass—the falling of the grains of sand through the funnel. But this mechanism is fundamentally different than the pacemaker model in that an hourglass, when activated, is preset to represent a specific interval. As such, the representation of different intervals will require a set of hourglasses, each tuned to a different duration. Moreover, an interval timer does not oscillate. To represent the same interval repeatedly, a reset process is required to trigger the measuring process each time.

Given the ubiquity of oscillatory processes in the nervous system, research on internal timing has generally adopted the framework of the pacemaker metaphor. Indeed, pacemaker-like mechanisms have been identified at various levels of the nervous system, providing elegant models for a range of behavior such as invertebrate locomotion, digestion, and circadian rhythms. However, it is unclear if the pacemaker metaphor can adequately capture the flexibility of human motor control. For example, with seemingly equal proficiency, we can produce repetitive movements at any experimenter-defined rate. This is not to deny that people will exhibit preferred rates of movement. But these are likely to result from biomechanical factors (e.g., Turvey, Rosenblum, Schmidt, & Kugler, 1986). Voluntary movement is certainly constrained by such factors, but we are also capable of altering our behavior to meet task requirements.

Pacemaker models would also suggest a continuity of temporal performance over a wide range of intervals. There is no inherent reason why a pacemaker-counter mechanism would have an upper bound (other than that the counter might ‘‘overflow’’). Interval timers are, on the other hand, likely to be limited in terms of their range. Assuming that the duration of each hourglass results from variation in the time course of excitatory and inhibitory physiological processes (e.g., Buonomano & Mauk, 1994; Fiala, Grossberg, & Bullock, 1996).), the range over which these could operate would likely be relatively limited. The literature suggests that there may be discontinuities in temporal performance. For example, when events are separated by more than a couple of seconds, we lose the sense of temporal continuity and connectedness that underlies the perception of a rhythm (Fraisse, 1963).

A few studies have attempted to directly contrast the pacemaker and interval timer models. The logic of these studies has been similar, based on the assumption that a pacemaker-based system should be capable of continuing to generate beats to sustain a representation of an entrained interval. Consider a duration perception task in which the standard duration is presented as a set of isochronous intervals. The comparison duration can then be presented in which the critical events either exploit subsequent beats or are misaligned with these beats (Fig. 1). The beat-based version of the pacemaker model would predict a perceptual advantage in the former condition. An interval timer model predicts no difference between the two conditions if the reset process is assumed to be arbitrary. Across a variety of experimental conditions, the evidence suggests minimal, if any advantage when the critical events occur on the induced beats (Keele, Nicoletti, Ivry, & Pokorny, 1989; Pashler, in press; Schulze, 1978).

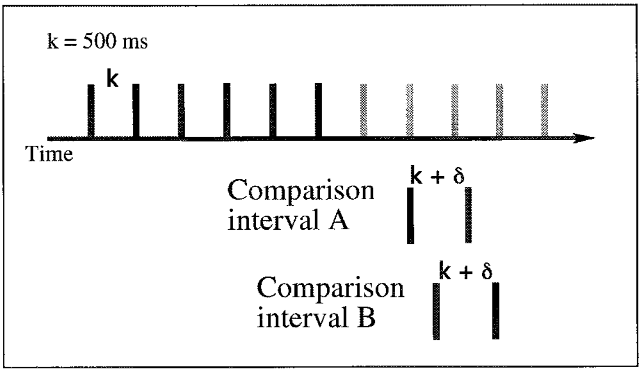

FIG. 1. Comparison of intervals falling on the beat and off the beat. The dark vertical lines on the top figure represent a set of 5 isochronous intervals. The grey lines represent the continuation of the beat over time. Comparison interval A is presented in alignment with the beats. Interval B is presented in misalignment with the beats.

THE MULTIPLE TIMER MODEL

Earlier we noted that correlational studies have demonstrated that perception and action shared a common timing system. When we consider the implications of this hypothesis in greater detail, an obvious question is what do we mean by ‘‘common.’’ Is there a unitary process that can generate abstract representations of time across a range of tasks? When we judge a visual stimulus to last 500 ms, are we accessing the same timing elements as when we tap on a response key every 500 ms? Or is there specificity within this system such that the representations used in perception and production engage different elements, with the commonality reflecting similar noise properties.

The question of specificity has received little attention in the literature on temporal processing. One exception is a study by Wright, Buonomano, Mahncke, and Merzenich (1997) looking at the effects of training on a time discrimination task. The training task was to judge whether 1000-Hz auditory tones were shorter or longer than 100 ms. After extensive practice on this task, the participants were tested on a variety of transfer conditions. In a temporal transfer condition, the target interval was increased to 200 ms, with the pitch of the auditory signal still set to 1000 Hz. In a pitch transfer condition, the target interval was still 100 ms, but the auditory signal was now 4000 Hz. Transfer was near perfect in the pitch transfer condition. In contrast, little evidence of transfer was found in the temporal transfer condition. Training with a 100-ms signal did not generalize to performance with a 200-ms signal, suggesting that the effects of practice were limited to the trained interval. This form of specificity suggests that the elements of an internal timing system have a form of temporal tuning, similar to the orientation tuning in visual cortex or frequency tuning in auditory cortex.

We have taken a different approach to investigate the specificity issue. In our initial studies on the neural mechanisms of an internal timing system, we had tested patients with unilateral cerebellar lesions on a repetitive tapping task. All of the patients were more variable when tapping with their impaired, ipsilesional hand (Ivry, Keele, & Diener, 1988). However, when we applied the two-process model of Wing and Kristofferson (1973; see Wing, 2001, this volume), the increase in variability was attributed to the ‘‘clock’’ component for those patients with damage in the lateral, hemispheric regions of the cerebellum. Implicit in this finding is the idea that, at the very least, there must be separate timing systems for the two sides of the body. Indeed, our more recent work (see below) indicates that each effector is associated with a unique set of timing elements.

We have proposed a model concerning the organization of an internal timing system, a model we call the multiple timer model (Ivry, 1996). The model is designed to capture the two aspects of specificity described above. First, we assume that the processing units of the internal timing system have some form of temporal specificity. That is, the processing units are tuned to represent particular intervals, and a set of such units is required to represent a range of intervals. This property could be manifest as either a bank of oscillators or hourglass timers. Our working hypothesis is that the latter provides a more accurate characterization. Second, we assume these processing units are specific to particular task domains. For units linked to motor systems, the specificity might be in terms of effectors (or muscles). For units linked to perceptual systems, the specificity might be in terms of input modalities. It is, of course, possible that some elements are linked to both input and output channels, perhaps providing a basis for perception–action coupling.

The multiple timer model was motivated by the results from a series of studies involving the repetitive tapping task with bimanual movements (Helmuth & Ivry, 1996; Ivry & Hazeltine, 1999). Tasks involving repetitive bimanual movements have provided the empirical foundation for much of the theorizing involving a dynamic systems framework in the study of coordination. In those studies, the analysis has centered on the temporal coordination between the two hands. In contrast, our studies have focused on within-hand temporal variability. As pointed out in Schoener (2001, this volume), the former approach emphasizes relative timing, whereas the latter emphasizes absolute timing.

In our first bimanual study, we tested patients with unilateral cerebellar lesions (Franz, Ivry, & Helmuth, 1996). The question here was straightforward. Given that these patients exhibit greater timing variability on one side compared to the other, what would happen when they tapped with both hands simultaneously? From pilot work, we expected that the two hands would be temporally coupled. But would there be any change in within-hand performance? The results were surprising. For each patient, temporal variability for the impaired hand was significantly lower in the bimanual condition compared to the unimanual condition (Fig. 2A). We call this phenomenon the multiple effector advantage, referring to the fact that within-hand temporal variability is reduced when the movements of that hand are accompanied by the in-phase movements of another effector. When the total variability is analyzed within the context of the two-process model of Wing–Kristofferson (1973), the improvement is solely associated with a reduction in the estimate of central variability.

Our initial interpretation was that the improvement reflected a reliance on the undamaged side of the cerebellum. During bimanual movements, this side would be activated and we thought it might be providing a timing signal that could be used bilaterally. Helmuth and Ivry (1996) tested this idea by testing a group of right-handed neurologically healthy individuals on the uni- and bimanual versions of the repetitive tapping task. We hypothesized that a right-hand advantage observed during unimanual tapping would lead to an improvement in left-hand performance during bimanual tapping. Instead, the within-hand variability was reduced for both hands in the bimanual condition (Fig. 2B). As with the patient study, the reduction was again associated with the estimate of central variability. Indeed, a dominant-hand advantage was found in the estimate of motor implementation variability and this advantage remained constant in the uni- and bimanual conditions.

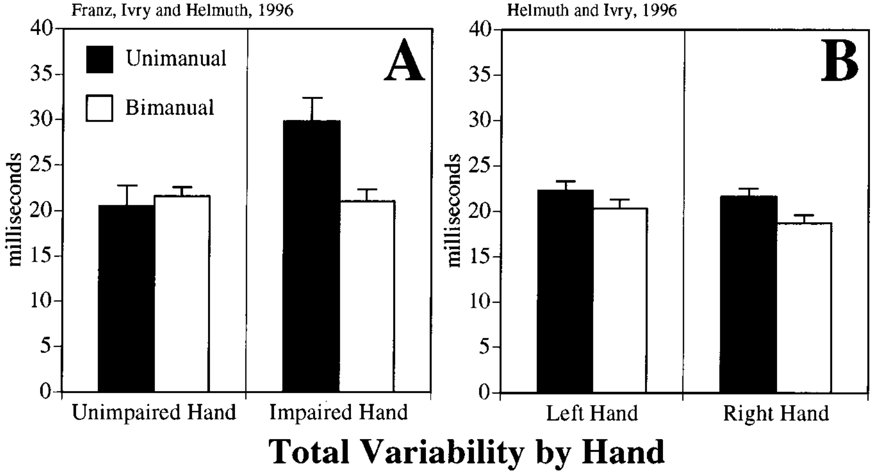

FIG. 2. Mean standard deviation of the inter-tap intervals during uni- and bimanual finger tapping. A: Results for a group of patients with unilateral cerebellar lesions. B: Results for a group of right-handed, neurologically healthy young adults.

The multiple effector advantage is a very robust phenomenon. It does not require that the two movements be produced by homologous effectors. For example, the effect is also observed when people tap with finger movements on one side of the body and forearm movements on the other side (Helmuth & Ivry, 1996). Under this condition, the improvement is only manifest in the estimate of central variability as calculated by the Wing–Kristofferson (1973) two-process model. The estimates of motor variability increase when the two limbs are of unequal mass, a result similar to that previously reported by Turvey et al. (1986). A similar pattern is found for combinations of finger and foot movements, regardless of whether the two effectors are on the opposite or same side of the body (Ivry, Richardson, & Helmuth, submitted). It also appears to be independent of skill level. We have recently tested a group of elite drummers, members of a premier drum and bugle corps in California. While the observed variances were remarkably low for this group, the multiple effector advantage persisted. When tapping unimanually at 400 ms, the estimate of central variability for this group was 8.5 ms; during bimanual tapping, this value dropped to 6.5 ms (Richardson & Ivry, unpublished).

We have proposed the multiple timer model to account for the improved temporal consistency of each effector during multieffector tapping (Fig. 3). The model rests on three critical assumptions. First, we assume that independent temporal representations of the desired target interval are generated for each effector. This form of timing is event-based. The signals might correspond to the desired onset of each response or they may represent the desired time of the next tap (Billon, Semjen, & Stelmach, 1996). In either case, these signals correspond to the ‘‘clock’’ signals in the Wing–Kristofferson model. Central to our model, we assume that separate signals are generated for each effector. Thus, in bimanual tapping, two temporal representations are activated, one associated with the right hand and one associated with the left hand.

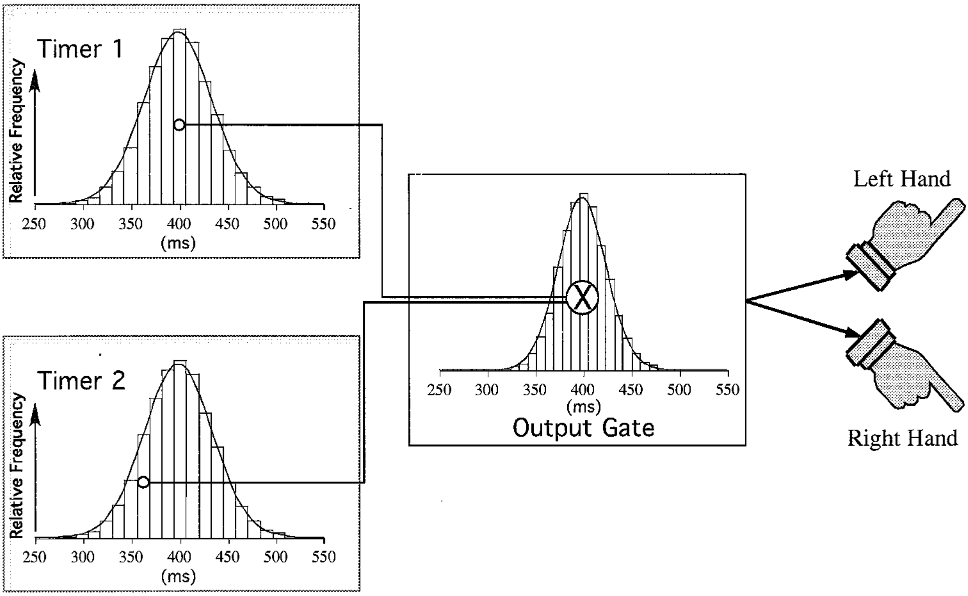

FIG. 3. The multiple timer model. Left column: Separate temporal representations (Timers 1 and 2) are generated for each hand during bimanual tapping. These representations are depicted as samples from a normal distribution (circles). Middle column: An output gate determines when movement commands are sent to the effectors. The gating process must combine independent timing signals when more than one effector is used (X). Right column: Central commands from the gate are issued to both hands simultaneously, although the taps may not be perfectly synchronized due to peripheral noise.

Second, we assume that these signals do not have direct access to their associated effectors. Rather, we postulate the existence of a central gating process that provides the link between central control commands and the motor periphery (see Vorberg & Wing, 1996, for a related model in which timing and control operations are separated). For bimanual tapping, central commands to the periphery are updated for all selected effectors simultaneously. Thus, the gating process ensures that the two hands remain in phase during bimanual tapping. We do not make strong claims regarding the nature of this gating process. It may reflect a structural limitation of action systems. An output gate of this nature may help ensure that selected actions are implemented in a coordinated fashion and reduce competition between different candidate actions in an efficient manner. Or it may reflect task constraints: In our bimanual studies, the participants are asked to move their limbs in synchrony with one another. However, the difficulty people have in temporally uncoupling their limbs suggests that the gating process may reflect a fundamental constraint in human performance.

The third assumption addresses the dynamics that arise during multijoint movements. It is possible that the multiple effector advantage results from interactions between the two hands that result from the integration of the various feedback sources associated with bimanual tapping, for example, proprioceptive and tactile cues indicating asynchronies between the taps of each hand or the sounds generated by the depression of the response keys. While there is little empirical data to evaluate this hypothesis (but see, Ivry & Hazeltine, 1999), simulation studies indicate that feedback models in which the asynchronies are used to adjust subsequent intervals fail to reduce within-hand temporal variability (Helmuth & Ivry, 1996).

As an alternative, we assume that timing within the multiple timer model is primarily open-loop, similar to the foundation assumption of the Wing–Kristofferson model of unimanual tapping (Wing, 2001, this volume). The timing signals for each hand reflect the operation of an internal timing system that is initially set in motion by some external signal (e.g., the pacing signals from a metronome). Once initiated, the timing system is cyclically engaged to produce the signals corresponding to a representation of the next interval. The open-loop nature of these signals results from the fact that they are not triggered by feedback from the actual responses (although such feedback could be used if sufficiently salient, see Pressing, 1999; Repp, 1999). Rather, each cycle of the internal clock is triggered by the output from the previous cycle. In the multiple timer model, the triggering process is associated with the output of the gate. Thus, the gating process not only initiates the responses of each effector, but also triggers the next timing cycle. This constraint ensures that the two effectors remain temporally coupled, despite the fact that they are associated with independent timing elements. Given this assumption, the multiple timer model is a form of a coupled oscillator model, but one with rather unique dynamics given that the interactions between the oscillators are rather discrete (see Schoener, 2001, this volume).

It is essential to consider how the gate operates in the multiple timer model. We have explored various computational models for how the gating process might function given the situation in which the input consists of two timing signals (see Helmuth & Ivry, 1996; also Ivry et al., submitted). The model that provides the best account of the multiple effector advantage is one in which the two timing signals are averaged. In a formal sense, the averaging idea constitutes a situation that simply exploits the central limit theorem. In unimanual tapping, a single sample of the target is generated for each trial by the internal timing system. In bimanual tapping, two samples are generated for each trial, one associated with each effector. The output from the gate will represent the average of these two samples. Over a series of trials, the variability of the observed intertap intervals will be reduced because of this averaging process.

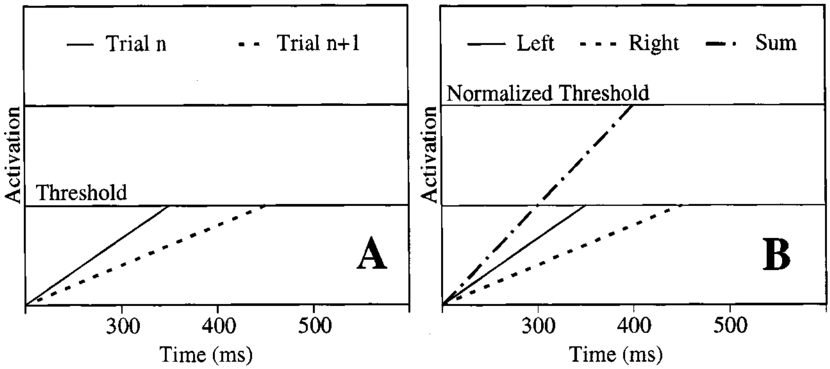

FIG. 4. Activation process within the output gate. The gating process is depicted as a threshold mechanism. Activation arises as a consequence of the input from the timing signals. Panel A: Operation of the gate on two successive trials. The movement is triggered when the threshold is reached from the input of a single timer. Panel B: Operation of the gate on a single trial with two independent timing signals. The two timing signals are summed and the normalized threshold is reached at a time corresponding to the average of when the signals would have reached the standard threshold. The firing at threshold provides a central command to initiate movement(s) and restarts the timing process for the next cycle (not shown).

At first blush, the idea of temporal averaging seems nonsensical. How does the gate know when the later input signal will occur in order to produce an output at the average time? This problem, however, only exists when the input signals from the timing mechanisms are considered as discrete events. If the inputs are treated as activation functions (Fig. 4), the idea of averaging becomes more plausible. Figure 4A shows the operation of a gating mechanism for two successive intervals in a unimanual condition. The variability in the intervals produced by the gate reflects noise in the input signals (and could also reflect noise in the gating process itself, i.e., fluctuation in the threshold level). During bimanual tapping (Fig. 4B), the two input signals occur on a single trial and the thick line represents their sum. Assuming the threshold is normalized to reflect the increased input, the summed signal will reach threshold at a point corresponding to the average of when the individual signals would have reached threshold. While linear activation functions are depicted in the example, a similar result would also occur with alternative functions.

In a recent study (Ivry et al., submitted), we have confirmed a number of predictions derived from the multiple timer model. First, the multiple effector advantage is not limited to the timing of repetitive movements. It is also observed when the participants produce a series of individual intervals, with a random gap between each production. This observation is in accord with our hypothesis that even under such conditions, representations of the target interval for each hand must be generated. The reduction in temporal variability does not appear to reflect some sort of entrainment process that occurs when a person is moving two effectors in a stable pattern.

Second, the notion of averaging predicts that the magnitude of the improvement will be multiplicative rather than additive. This prediction builds on the well-established observation that the variability of the internal timing system is proportional to the interval being represented. When the target duration is varied, the standard deviation of the produced intervals is a linear function of duration, a form of Weber's law in the temporal domain. Given that the increase in variability is attributed to processes associated with the internal clock, the size of the multiple effector advantage should increase as variability increases due to the averaging operation. Ivry et al. (submitted) tested this by having 10 participants tap at four different durations,

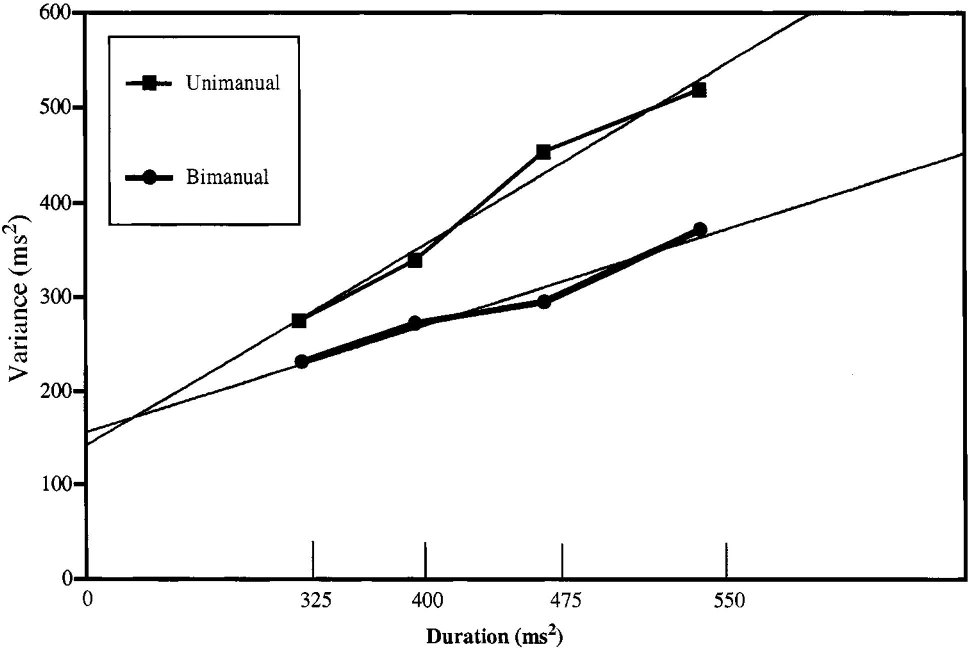

FIG. 5. Temporal variability as a function of target duration during uni- and bimanual tapping. Following Ivry and Hazeltine (1995), the data have been plotted as a function of the mean produced interval squared.

325, 400, 475, and 550 ms, under uni- and bimanual conditions. As predicted, the slope of the function relating variability to duration was shallower during bimanual tapping (Fig. 5).

Perhaps most striking, we have also found that the multiple effector advantage is even greater when three effectors are moved in synchrony. In this experiment, participants were tested under three conditions: tapping with the right hand alone, tapping with the right hand and right foot, and tapping with the right hand, right foot, and left hand. The estimate of central variability for the right hand for the one-, two-, and three-effector conditions was 17.8, 16.0, and 15.1 ms. Moreover, the estimate for the right foot was 17.1 and 15.0 ms for the two- and three-effector conditions, respectively. Following the logic of the multiple timer model, we assume that with each additional effector, a new representation of the target interval is generated and becomes part of the averaging operation. Thus, with three effectors, the gating operation has three inputs, resulting in an even better estimate to the target interval due to the statistical consequences of averaging. As an aside, the multiple timer model offers a novel perspective on why musicians like to move their bodies in time with the beat. We propose that, as each effector is recruited, temporal stability is improved due to the recruitment and integration of additional temporal elements representing the target intervals.

PSYCHOLOGICAL AND NEUROLOGICAL CONSIDERATIONS

The multiple timer model provides an explicit description of the component processes associated with both timing and temporal coupling during bimanual movements (or movements involving any set of effectors). The model attributes the control of timed actions to an internal system that provides the requisite representations for when the movements should occur (Semjen & Ivry, in press). Temporal coupling, on the other hand, arises from the operation of the gating process. At an abstract level, timing and temporal coupling are conceptualized as separate entities in this model. In this section, we address some important issues that must be considered when evaluating the computational and biological merits of this approach.

Consider the timing component of the model. Building on our previous work concerning the neuropsychology of coordination, we assume that the cerebellar cortex plays a critical role in providing the requisite representations for event timing (Ivry, 1997). In bimanual repetitive movements, this representation would support the task demands to produce a series of isochronous movements with the two hands. Our working hypothesis is that these representations reflect the operation of an interval timing system composed of elements that have specificity in terms of both input/output linkages and duration (Ivry, 1996). Fundamental to the model is the idea that separate temporal representations within the cerebellum are generated for each hand during bimanual tapping. Similarly, we expect that different regions of the cerebellum would be engaged if the movements were made with the feet or if event timing was required for perceptual judgments. While this hypothesis is at odds with the construct of an amodal internal clock, it does seem more plausible from a biological perspective. Not only is the effector-specificity hypothesis consistent with physiological evidence showing multiple somatotopic maps across the cerebellar cortex (Oscarsson, 1979), but also it would seem difficult to wire a system that supported generic access to the output of an amodal clock.

The timing elements are also assumed to have duration specificity. Thus, tapping with both index fingers at 2 Hz would require the recruitment of timing elements that generate intervals of around 500 ms and send outputs that are linked to the index fingers. If tapping were at a different rate, such as 4 Hz, we assume that a different set of timing elements would be recruited. We do not, however, want to imply that there needs to be strict temporal tuning. Our notion of a ‘‘timing element’’ is not intended to correspond to single neurons. We expect that individual neurons or ensembles of neurons would have rather broad temporal tuning properties and the emergence of a particular interval would reflect the weighted contribution of coarsely coded signals. Ideas along these lines have, of course, been widely applied in the study of many perceptual systems. The multiple timer model extends this idea to the temporal domain.

The organization of such a network of temporally tuned neurons remains to be seen. It is possible that such an organization is found at a structural level. That is, there may be some form of chronotopic map (or more accurately, maps, given the effector specificity) across the cerebellar cortex. At present, our hypothesis is more applicable at a functional level: We expect that across the population of neurons, a range of optimal tunings would be observed. Various theories concerning the function of the cerebellar cortex have entertained the idea that this neural region may be suited to representing a range of temporal intervals, building on the idea that a range of delays can be created by relatively slow physiological processes (e.g., Buonomano & Mauk, 1994; Fiala et al., 1996).

Sensorimotor learning could entail a process of learning via selection (i.e., biasing the system toward those units that provide the appropriate temporal representation) or tuning (i.e., changing the timing of the input–output function of recruited units). Seen from this perspective, one can understand the deficits observed following cerebellar damage in the production of skilled movement. The cerebellar cortex may not be essential for forming the fundamental associations required for producing a particular action. Rather, it may provide the fine timing that allows such actions to be performed in the most efficient and optimal manner (Ivry, 1997). In a related manner, the cerebellar cortex could learn the temporal relationship between successive external events, supporting a more general role in event timing and prediction (Tesche & Karhu, 2000).

As noted earlier, we would expect an upper bound on the range over which an interval timing system could operate. The physiological processes that can delay the consequences of a neural input for 500 ms are unlikely to extend to 5 s, let alone 5 min. We assume that the cerebellum is only capable of representing intervals (or predicting events) over a relatively short time-scale. Different timing systems might be necessary for representing longer intervals. Alternatively, the cerebellar timing system may be linked with neural systems that can provide the counter/memory functions necessary to concatenate a long interval out of a series of short intervals (Mangels, Ivry, & Shimizu, 1998).

Turning to the gating process, there are a number of computational and neurological issues that need to be explored in future research. In the multiple timer model, the gating process plays a key role in response initiation. We have hypothesized that the threshold mechanism imposes a form of response selection. Activation at the gate is likely to reflect activation across a distributed set of neural systems involved in the preparation of actions. Through either direct or indirect projections to the gate, a response will be initiated when it has accrued sufficient activation. In a task in which actions are explicitly timed, the contribution of the cerebellum might be especially pronounced. We would, though, expect this system to also contribute to many other actions, especially skilled ones where temporal control may be more implicit.

An appealing feature of the gating concept is that the computational requirements for response selection/initiation are minimal. At any point in time, it is likely that many potential actions are possible. Activation-threshold models allow for these candidates to compete in parallel with the selected action being the one that reaches threshold first. Under this scheme, it is not necessary that the threshold process have access to the contents of the different actions. It is sufficient that the process simply respond on the basis of the activation functions. Threshold schemes also impose a level of discrete control. For example, we imagine that central processes are primarily dedicated to the control of particular events (e.g., when to initiate the next tap). This is not to deny the importance of feedback. However, the utilization of this information may fall within the purview of other parts of a distributed control system rather than require continuous modification of representations related to the goal of the action.

For bimanual movements, the gating process instantiates task constraints. For example, when the movements are made in phase, the gating process ensures that both effectors are updated simultaneously. As such, the multiple timer model is a variant of a coupled oscillator model. The oscillators here are the product of the successive activations of the interval timers and the coupling arises from the gating and resetting process (Schoener, 2001, this volume).

We assume that part of the resetting process involves the inhibition of the activated response codes. This requirement ensures that the activation process will begin anew, preventing the system from perseverating and avoiding unwanted interference from the losing candidates' actions. A resetting process of this form leads to a novel conceptualization of the phase transitions that have been extensively described in the dynamic systems literature. From an event timing perspective, one would expect that particular moments within a repetitive movement have special status. For example, in the free-motion wrist oscillations studied by Kelso and colleagues (reviewed in Kelso, 1997), these events might correspond to the points of maximum abduction or adduction (see Semjen & Ivry, 2001, for an alternative characterization based on the manner in which the underlying temporal goals are represented). During in-phase movements, these events would be in correspondence for the two limbs. In contrast,

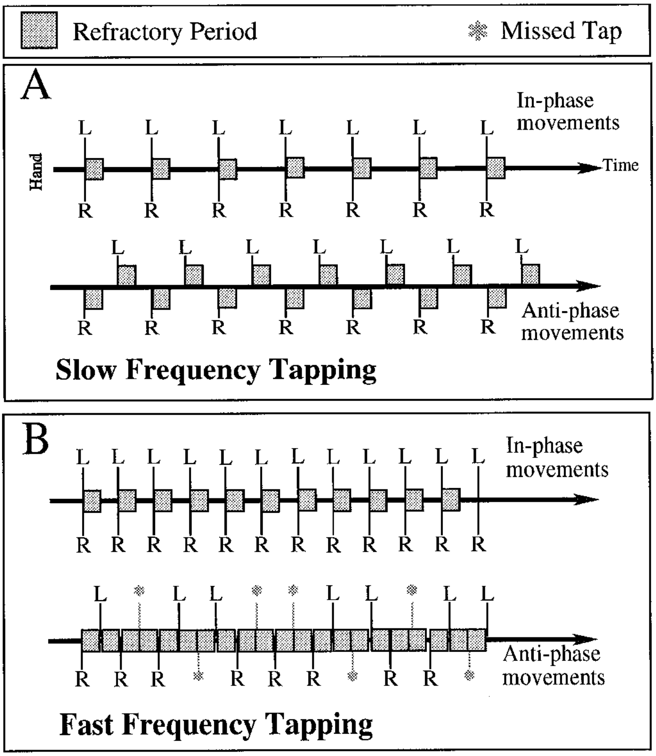

FIG. 6. Phase transitions resulting from a refractory reset period following gate activation during bimanual movements. In-phase movements are assumed to be initiated with a common gating signal. Separate initiation signals are assumed to be generated for each limb during anti-phase movements. Panel A: At slow frequencies, the refractory period does not interfere with the next initiation cycle for both bimanual modes. Panel B: At fast frequencies, the refractory period may interfere with the next initiation cycle during anti-phase movements. The resulting instability may produce a transition to in-phase movements.

for anti-phase movements, the corresponding events would be 180 degrees out of phase. Under these conditions, there might be two critical events per cycle, and correspondingly the inhibition process might occur at twice the frequency as in-phase movements (Fig. 6). At slow frequencies, this extra inhibition may cause little interference. However, as frequency is increased, a point will be reached at which the anti-phase pattern becomes unstable.

One avenue for evaluating the multiple timer model would be to explore the neural locus of the gating process. The limited evidence that exists suggests a subcortical locus. Across a variety of tasks, callosotomy patients continue to exhibit pronounced temporal coupling between the two limbs, regardless of whether these movements involve proximal or distal joints (Tuller & Kelso, 1989; Preilowski, 1972). The persistent temporal coupling is especially striking given the fact that the operation eliminates other sources of bimanual interference such as that associated with planning movements involving conflicting spatial trajectories (Franz, Eliassen, Ivry, & Gazzaniga, 1996) or selecting responses with incompatible stimulus–response mappings (Ivry, Franz, Kingstone, & Johnston, 1998). We have also found that callosotomy patients exhibit the multiple effector advantage (Ivry & Hazeltine, 1999). That is, they not only remain temporally coupled when making repetitive movements, but they also exhibit a reduction in within-hand temporal variability. We assume this indicates that independent representations of the target interval interact in the manner described by the multiple timer model.

At present, we can only offer a few speculations concerning the possible locus of the gate. We suspect that spinal mechanisms are not critical despite their obvious role in interlimb coordination during locomotion. Our reasoning here is based on the fact that temporal coupling seems similar for movements involving the fingers, effectors that are likely to have the greatest degree of neural independence, as with more proximal joints. Moreover, temporal coupling is found between vocal and peripheral movements, suggesting a more central locus of origin.

One interesting possibility is the basal ganglia. From a computational perspective, Berns and Sejnowski (1996) have proposed that this subcortical structure is well-suited to operate as a winner-take-all gating system within the closed-loop cortico-striatal circuits. They emphasize that the series of two inhibitory connections along the main pathway of the basal ganglia is a relatively unique feature in the nervous system and that such an arrangement provides an ideal physiological arrangement for instantiating a competitive threshold model (Fig. 7). The tonic inhibitory output from the basal ganglia to the thalamus keeps activated cortical response codes in check. Selection of a particular code is through disinhibition of one of these codes. In their view, all the other pairwise connections of two synapses fail to capture this specificity in terms of selection.

Some of the prominent symptoms associated with basal ganglia pathology are also consistent with the idea that this structure plays a role in gating central motor signals to the periphery. Patients with Parkinson’s disease have difficulty initiating movement. This might be considered a situation in which the gate is stuck. Perhaps dopamine plays a role in adjusting the level of the threshold and in its absence, the threshold rises to a high level. Under such conditions, a greater input to the gate would be required for a movement to be triggered. It is widely recognized that the akinesia is alleviated when a salient external stimulus can help cue an action. For example, we have worked with a patient who uses a cane when walking, not because of any unsteadiness in his gait, but because he finds it easier to start walking by attempting to kick the cane when placed in front of his feet. The stuck gate metaphor may also provide insight into why these patients have difficulty on certain cognitive tasks such as those requiring flexibility in attentional set (e.g., Hayes, Davidson, Keele, & Rafal, 1998). In contrast to the akinesia associated with Parkinson’s disease, other basal

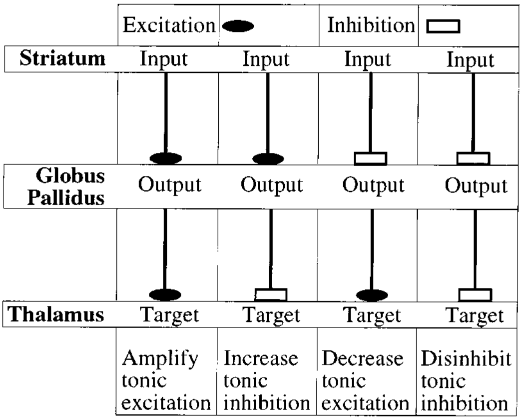

FIG. 7. Computational implications of two successive neural connections that are either inhibitory or excitatory. A series of inhibitory links is uniquely suited to act as a winner-take-all mechanism. Adapted from Berns and Sejnowski (1996).

ganglia disorders such as Huntington's disease or tardive dyskinesia result in excessive movements. The stereotypic and repetitive nature of these movements suggests a system that is unable to inhibit inappropriate action patterns. Such deficits could reflect a threshold that is too low or an inability to deactivate response codes once they have been triggered.

In discussing these diseases, we have proposed that the threshold may be set at abnormal levels. Implicit in this hypothesis is the notion that the threshold is an adjustable process. Threshold adjustment may be an important part of how the basal ganglia contribute to motor learning. Perhaps dopamine, as a reinforcement agent, modifies the threshold level associated with stimulus–response codes. In this view, the system would be biased to trigger actions that had been previously reinforced by assigning lower thresholds to their associated input patterns. In the extreme, an action would be habitual or automatic, not because a representation has developed in a distinct system, but because the triggering conditions have reached a minimal level.

CONCLUSIONS

These last speculations underscore the general framework we have adopted in developing a functional analysis of the psychological and neural processes involved in motor control. In our work on the cerebellum and timing, our approach has been twofold. Not only do we wish to determine if this structure plays a critical role in representing temporal information (e.g., a localization question), but we also seek to characterize the form of these representations. The interval-timing model, at least for event-based behaviors, appears to provide a biologically plausible functional characterization of the cerebellum. To this point, our investigations of the gating component have been restricted to its role in the production of in-phase repetitive movements. However, this process may not be limited to specific task domains but rather may reflect the operation of a more general component of coordination.

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