Timing, Clocks, and Dynamical Systems

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Theoretical and experimental issues for our understanding of the timing of motor acts are reviewed, contrasting stochastic and dynamic timing models. It is argued that the theory of dynamical systems and, in particular, of limit cycle attractors, provides a unified framework within which these issues can be appreciated. The strength of stochastic timing models in the domain of absolute timing is contrasted with the strength of dynamic timing models in the domain of relative timing, the unification of the two domains being currently under way. It is further argued that accounts of timing must examine the interrelation between timing and other levels of processing involved in movement generation, in particular, the representation of spatial aspects of movement and the control of movement. The emergence of discrete event structure in timing skills is discussed from a dynamical systems perspective. Finally, the understanding of the timing structure of discrete movement is raised as a further challenge for future work.   © 2001 Elsevier Science

1. INTRODUCTION

All actions take place in time. But not all actions are ''timed.'' Timed actions are, for instance, rhythmic movements such as during locomotion, dancing, chewing, or speech production. Nonrhythmic movements may be timed such as when moving objects are tracked or caught, or simply, when a reaching act is performed. Actions that are not typically timed include, for instance, the displacement during ambulatory locomotion (no particular time to arrive at a particular point), or the small movements around postural states. Timed movements are thus motor acts, whose temporal form is reproducible and stable in the face of varying environmental conditions or perturbations. From an experimental point of view, one would say that a movement is timed, if a perturbation that either holds up or accelerates the movement is compensated for subsequently such as to restore as much as possible the movement time. One may ask, for instance, if the hand during reaching will accelerate to compensate for the longer movement path imposed by an obstacle or perturbation and contrast this with how the trajectory of a person ambulating in a cluttered environment is adjusted when obstacles are avoided. Timing may play a role in perception, such as when durations or event times are perceived. This review of different theoretical approaches to timing will, however, focus primarily on the timing of actions.

Our first topic will be to define ''timing'' more theoretically and to look at different

ways of conceiving of ''timers.'' Broadly speaking, we shall distinguish between ''stochastic'' and ''dynamic'' timing models, and the discussion of the relationship between these two classes of timing models will be a recurrent theme throughout the article. A short review of basic concepts of the theory of dynamical systems will be inserted to support the argument that in an abstract, general sense all timing models are limit cases of limit cycle oscillators and thus have certain dynamical properties. Arguing from the two different theoretical perspectives we examine the basic experimental fact that the variance of timing increases with increasing cycle time (temporal distance between timed events; Wing & Kristofferson, 1973).

The difference between timed and not timed actions becomes particularly clear when relative timing, or coordination, of multiple subsystems is considered. Here, the issue is if changes to the time course of one component affect the time courses of other components. Thus, the second topic will be the contrast between absolute and relative timing.

Next we ask how timing systems can be decomposed (analyzed). In other words, how can different contributions to timing be dissected? This will involve discussing the relationship between central versus distributed timing systems, as well as, more generally, the notion of different levels of processing and control that may potentially affect timing. Two more specific contrasts, between event timing versus continuous timing and between timing in rhythmic versus discrete motor acts, close the article.

2. TIMERS

In terms of physics, there are two basic ways of measuring time. The first method is based on calibrating an observable that evolves monotonically in time to measure durations (such as the amount of sand that has accumulated in the lower section of an hourglass). This conception is alluded to in our domain in the form of an ''activation'' level that increases linearly in time (Fig. 1), so that particular threshold levels of activation mark particular moments in time (Ivry, 1996). The other method consists of preparing a stable, reproducible oscillation (a ''clock''), and measuring time by counting the number of oscillatory cycles of such a mechanism. This notion is today the basis of time measurement in physics, optimized by choosing the shortest possible cycle time yielding maximal temporal resolution. Clocks as devices that generate periodic timing events are a common notion in our domain as well.

These two conceptions are intimately connected, of course. A necessary ingredient of an ''activation'' timer is some way to start time measurement. An initial reference level of activation defines the beginning of the time measurement. (An hourglass must be first ''set'' by turning it upside down.) An elementary time measurement includes, therefore, both the initialization of activation and the detection of a thresh-
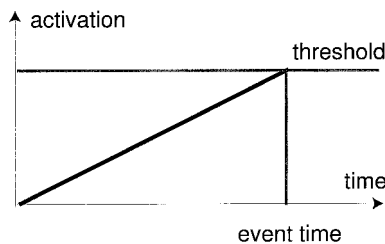

FIG. 1. A timer can be conceived of as an activation variable that evolves as a reproducible monotonic (here linear) function of time. Particular levels of activation indicate particular temporal events. A timer is functional, however, only if it can be started in a controlled fashion.
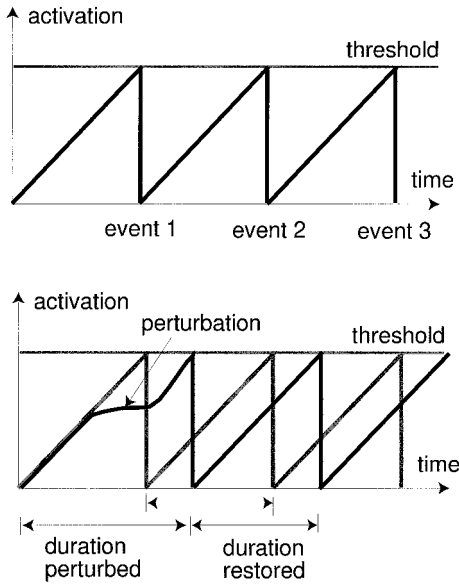
FIG. 2. (a) A clock can be conceived of as a timer, which is restarted (or reset) each time that an event was detected. (b) The notion of a clock contains, however, an implicit stability assumption: Whenever a timing cycle is perturbed, this clock mechanism returns to unperturbed periodic operation within one or several cycles.

old event. Such a timer becomes a clock if the read-out event simultaneously "resets" the activation level (Fig. 2). (An hourglass must be turned exactly when all sand has flowed into the bottom compartment in order for it to serve as a clock.)

2.1. Stochastic Timing Models

Stochastic timing models can be formulated within either of these two kinds of conceptions. In the activation picture (Ivry, 2001), an activation variable, $u(t)$, is assumed to grow linearly in time, but subject to noise. This can be formalized by postulating that the rate of growth, $\dot{u} = du/dt$, fluctuates around a constant mean, f,

$$\dot{u}(t) = f + q\xi(t), \tag{1}$$

where $\xi(t)$ is Gaussian white noise with zero mean and unit variance and the parameter q reflects the variance of the rate fluctuations. The Gaussian character of such noise could be thought of as resulting from the averaged effect of many independent sources of variability according to the central limit theorem (Gardiner, 1983). The solution of this equation is (Fig. 3):

$$u(t) = ft + u(0) + W(t). \tag{2}$$

Here, $W(t)$ is the Wiener process. If at time $t = 0$, the process started at (had earlier been reset to) $u(0)$, then the variance of the Wiener process and hence of activation increases linearly in time

$$\mathrm{var}(t) = qt \tag{3}$$

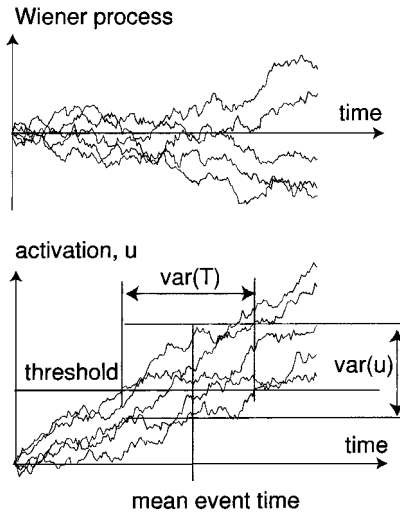(see, e.g., Introduction in Gardiner, 1983).

FIG. 3. (Top) The Wiener process has independent increments at all times, leading to linear growth in time of its variance. (Bottom) If such a process is added to a linear rise of activation, the time at which a particular activation level is reached is a random variable, which becomes the more variable, the more time it takes on average to reach the threshold event.

An event that makes such a timer observable can be defined as the reaching of a threshold level of activation. Because activation fluctuates, the time when such an event occurs is a random variable. The mean time to reach threshold, modeling the mean cycle time, depends on the rate constant, f, and the threshold level. The longer that mean time, the larger the variance of activation and thus, the larger the variance of the event time (Fig. 3). This simple model thus captures a fundamental fact of motor timing observed in tapping studies: the variance of the intertap intervals increases with increasing mean intertap interval (i.e., cycle time) (Wing & Kristofferson, 1973).

Invoking this activation picture means making the implicit assumption that the reset process is instantaneous and does not contribute to the variance of the event time. Deviation from that assumption may lead to various corrections of the predicted linear increase of event time variance. Another way of accounting for deviations from linear increase of event time variance is to assume nonlinear increase of activation in time.

In contrast to the activation picture, stochastic timing models based on the ''clock'' or ''event time'' picture do not make explicit which physical variables carry information about time. Instead, the event time (when some process is triggered and an underlying clock is reset) is directly modeled as a random variable or (discrete time) stochastic process (see Vorberg & Wing, 1996, for detailed review). For instance, Wing and Kristofferson (1973) assumed that event times characterizing the underlying clock are described by

$$T_i = T + q\xi_i, \tag{4}$$

where T_i is the ith duration of a clock interval ($i = 1, 2, \ldots$), T is the mean cycle time, and ξ_i is a family of independent equi-distributed random variables with zero mean and unit variance. No particular distributions were assumed, although the requirement that these durations are positive constrains models of such distributions (e.g., Engbert et al., 1997). In the Wing–Kristofferson model, the fundamental law of timing variability was added as an additional assumption, essentially making the

variance q increase with cycle time (e.g., $q = q_0 T$ or also $q = q_0 T^2$, cf. Vorberg & Wing, 1996, for discussion). One might think of this increase of variance as arising from a counting process, in which longer durations require more counting steps, so that imprecisions accumulate (cf. Creelman, 1962; Peters, 1989).

2.2. Dynamic Timing Models

Dynamical systems descriptions are based on the assumption that for appropriately chosen dynamical variables, their initial values uniquely specify the future evolution of the system (see Braun, 1978, or Scheinerman, 1996, for entry level text books, Perko, 1991, for more advanced treatment). Such variables are said to characterize the *state* of the dynamical system. Mathematically, this capacity to predict the future is expressed in the form of differential equations, which provide, for all possible values of the dynamical variables, a rate of change of these variables (from which the prediction arises by integration). For example, given the initial level of activation, $u(0)$, the entire evolution of activation, $u(t)$, is determined as the solution of a differential equation linking the rate of change, $\dot{u}(t)$, to the current activation level, $u(t)$:

$$\dot{u}(t) = f(u(t)). \tag{5}$$

The function, $f(u)$, thus points in the direction in which u changes, and the size of $f(u)$ indicates the speed of that change. This function is therefore called the vector field (Fig. 4).

Points at which the rate of change is zero, called *fixed points,* are invariant or constant solutions: Once these points have been reached, the state of the system no longer changes. Such points are reached when they are *stable,* so that the system converges to these points from neighboring states. In Fig. 4, the negative slope of the rate of change as it passes through the fixed point indicates that this is a stable fixed point (also called a fixed-point *attractor*): activation levels slightly higher than the fixed-point level of activation are associated with negative rates of change, so that activation falls, approaching the fixed point; activation levels slightly lower than the fixed-point level are associated with positive rates of change and activation increases, again approaching the fixed point.

The fact that the future is determined given the current state of the dynamical system has implications for what kind of state description is necessary to obtain what kind of solutions. Periodic solutions, in particular, require at least two state variables.
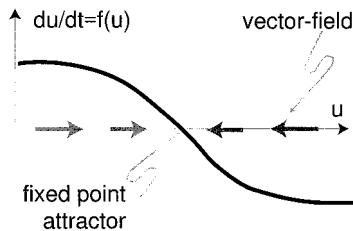

FIG. 4.   A dynamical system is defined by a functional relationship between the rate of change, $\dot{u}$, of a dynamical variable, u, and that variable itself: $\dot{u} = f(u)$. This set of rates of change is a vector field, pointing in the direction in which the solutions evolve from any initial state of the system. Zeros of this functional relationship are fixed point solutions of the dynamical system, which are stable if they attract solutions starting out from nearby states.
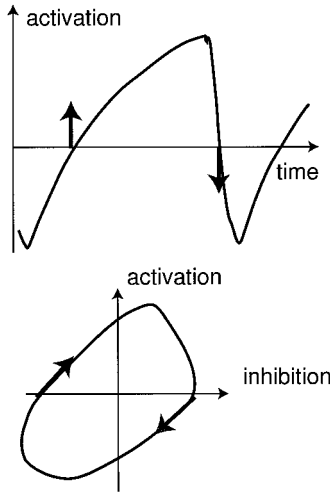
FIG. 5. (Top) A periodic evolution of an activation variable cannot be obtained as a solution of a single-variable dynamical system, because most levels of activation (here the zero level) are crossed in two different directions, so that the future is not uniquely determined by the present state of the activation variable. (Bottom) A second variable, here called ''inhibition,'' is needed to disambiguate these two events.

To see this, imagine a periodic time course of activation (Fig. 5). All levels of activation (except at the turning points) are then passed through in two directions, once at increasing and once at decreasing activation. Thus, such activation values do not uniquely specify the future. A second variable, here called ''inhibition,'' is needed, to disambiguate the future: each activation level is passed through once at a smaller and once at a larger level of this second variable. Thus, clocks cannot be built as dynamical systems in terms of activation alone!

Stable periodic solutions, to which the system is attracted from nearby states are called *limit cycle attractors.* An example of a dynamical system supporting limit cycle attractors of an activation–inhibition pair of variables is

$$\tau \dot{u} = -u + h_u + w_{uu} f(u) - w_{uv} f(v) \tag{6}$$

$$\tau \dot{v} = -v + h_v + w_{vu} f(u), \tag{7}$$

equations first analyzed by Amari (1977). The first two terms of each equation describe two linear uncoupled dynamical systems, each with a stable fixed point at the resting levels of activation, h_u, and of inhibition, h_v. A sigmoid function,

$$f(u) = \frac{1}{1 + \exp[-\beta u]}, \tag{8}$$

makes the system nonlinear in terms of ''self-excitation'' (w_{uu}) and of coupling between activation and inhibition variables (w_{uv}, w_{vu}). For appropriate choices of these parameters, a limit cycle attractor emerges (Fig. 6). The stability of the periodic solution manifests itself by attraction of neighboring states toward the limit cycle. The activation-based stochastic timer model emerges as the limit case, in which the vector field is structured such that a period of graded activation growth is followed by a more rapid phase of activation decay (Fig. 6b). In fact, abstractly speaking, any clock is a limit cycle attractor of a dynamical system (see, e.g., Andronov, Vitt, & Khaikin,
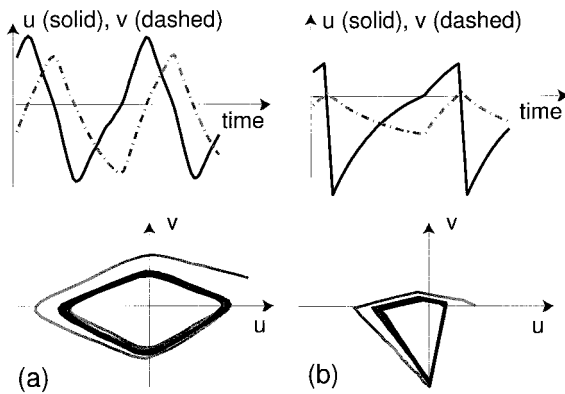
FIG. 6. (a) A stable periodic solution (top) for activation (black) and inhibition (gray) variables emerges from the dynamical system Eqs. (6) and (7). The phase plane portrait illustrates how nearby states are attracted (gray trace in bottom panel) toward the limit cycle (black trace in bottom panel). (b) By different choice of model parameters, the oscillation becomes asymmetric, a slow rise followed by a sharp reset of activation.

1966, Chap. III.4). The dynamic formulation captures the implicit assumption of stability, illustrated in Fig. 2 (bottom): Whenever a clock cycle is lengthened or shortened by some perturbation, the clock returns to normal operation and, hence, to the stable cycle time over the next (or the next few) cycle.

Stochastic dynamical systems are defined in analogy to deterministic dynamical systems by the postulate that the present predicts the future (see Arnold, 1974, or Gardiner, 1983, as text books). Roughly speaking, knowing the initial probability distribution of the dynamical variables specifies the future evolution of the probability distribution of these variables. Mathematically, under some mild assumptions, such stochastic dynamical systems can be described as differential equations containing a stochastic noise source, ξ_t, which is Gaussian and white. The Gaussian nature can be thought of as arising from the averaging of many stochastic sources of perturbation through the central limit theorem. The whiteness of the stochastic perturbations expresses the assumption that all temporal correlations have been captured by the deterministic part of the dynamical system, so that the stochastic part is uncorrelated in time. The lowest order approximation takes into account stochastic perturbations only as additive contributions to the vector field. This expresses the assumption of regularity, according to which the noise sources do not depend on the current state of the dynamical system. Higher order corrections involve multiplicative noise, not considered here.

Adding such noise sources to Eqs. (6) and (7) leads to fluctuating periodic solutions of the activation and inhibition variables. To examine the consequences of such fluctuations on the statistics of the cycle times, we measure discrete event times (defined here as times at which the activation variable peaks[1]). The time intervals between these events times is an estimate of the cycle time. Figure 7 shows the variance of this cycle time as a function of mean cycle time, which was varied by changing the values of the model parameters such as to vary the period of the limit cycle. The observed increase of variance within increasing mean cycle time shows that the dynamical systems model of timing captures the fundamental property of human motor timing.

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[1] This is slightly different from defining event times based on an activation threshold that must be reached, but leads to the same results and is adopted for simplicity.
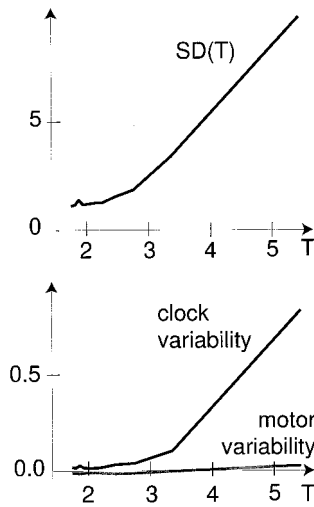
FIG. 7. The dynamical timing model with noise is simulated at different parameter values leading to different mean cycle times, T. The variability of the resultant cycle times ($SD(T)$ is plotted as a function of mean cycle time on top. The clock (CV) and motor variance (MV) was computed as $CV = c(0) + 2c(1)$ and $MV = -c(1)$, where $c(i)$ is the lag-i autocorrelation of cycle time (Wing & Kristofferson, 1973). These measures are shown on bottom for increasing mean cycle time. The increase of timing variability with increasing cycle time is modeled successfully, but no lag-one autocorrelations are detected, leading to flat, near-zero motor variance. The exact functional forms of these dependencies depends on the details of the dynamical equations.

The discrete time structure of events can be used to directly model the dynamics of clocks. The Poincaré section of a dynamical system is obtained by recording the intersections of the solutions of the dynamical system with a hypersurface that has one dimension less than the original space. Figure 8 illustrates this for the case of a two-dimensional phase space, with the hypersurface (the u axis) defined by $v = 0$. Only when the surface is pierced in the same sense are events registered. Given an intersection point, u_i, all future intersection events (both states and times) are uniquely determined. The result is therefore a discrete time dynamical system:

$$u_{i+1} = g(u_i). \tag{9}$$

Stable fixed points of such discrete time dynamical systems correspond to limit cycle attractors of the original system.

Formally, stochastic timing models in the ''event'' picture with ''feedback'' corrections (Engbert et al., 1997; Pressing, 1999; Semjen, Schulze, & Vorberg, 2000) are discrete time dynamical systems, e.g.,
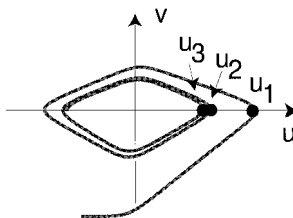

FIG. 8. Illustration of a Poincaré section in two dimensions, using the u axis as a hypersurface. The points $u_1, u_2, u_3, \ldots$, correspond to intersection events 1, 2, 3, $\ldots$, occurring at times, $T_1, T_2, T_3, \ldots$.

$$x_{i+1} = \delta_{i+1} - k \tanh(\alpha(x_i - \delta_i)), \qquad (10)$$

where $x_i = T_i - T_{i-1}$ is the interval between the two event times T_i and T_{i+1}. These models use duration itself as the variable representing the state of the dynamical system. This makes them a different class of dynamical systems, which cannot be obtained from a conventional dynamical system through Poincaré section. Their ''lifting'' to continuous dynamics leads into the category of delay (or functional) dynamical systems, which have an infinite number of variables (see Hale & Lune, 1993, for an introduction).

3. ABSOLUTE VERSUS RELATIVE TIMING

Many different effectors can be recruited to perform timed acts. In many instances, more than one effector is involved simultaneously. Establishing and maintaining stable temporal relationships between different effectors (coordination) or between effectors and perceived timed events (action–perception coupling) or even between different trains of timing within an effector (unimanual polyrhythms) is thus an aspect of such timing skills. Such *relative timing* is not necessarily supported by the same mechanisms or governed by the same principles as the aspect of *absolute timing* discussed hitherto. Two effectors may, for instance, perform a highly variable rhythm (near unstable absolute timing), while maintaining a very tight timing relationship (highly stable relative timing). This is schematically illustrated in Fig. 9.

3.1. Stochastic Timing Models

Within the framework of stochastic timing models, relative timing relates to the issue of how multiple clocks or activation-based timers fuse their timing information. Referring to the activation picture, Ivry proposed that two timers add or average their activation levels. This provides an account for reduced variability of cycle time in coordinated two-handed tapping compared to single-handed tapping (Helmuth & Ivry, 1996). While at first sight, this appears to be an account in which the information of different timers is simply combined, it actually implies true mutual coupling of the two timers. This is because the two timers must be reset when the combined, not
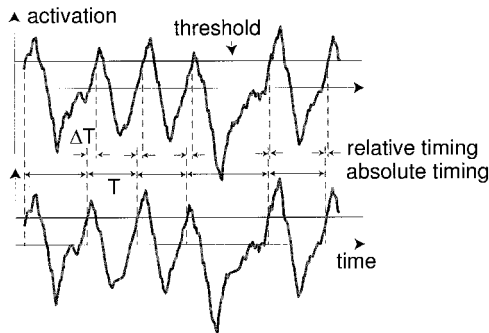

FIG. 9. The absolute and the relative timing of two periodic activation functions do not necessarily have the same stability properties. As shown here, the processes may have highly variable absolute timing (assessed by the variance of cycle times) while maintaining precise relative timing (assessed by the variance of latencies). The moments in time when each activation variable pierces a threshold are marked by dashed lines. The time intervals between two such events, the cycle times, T, reflect absolute timing while the latencies between matching events of the two activation functions, ΔT, reflect relative timing. *Relative phase* is latency expressed in percentage of cycle time: $\phi = \Delta T/T$.
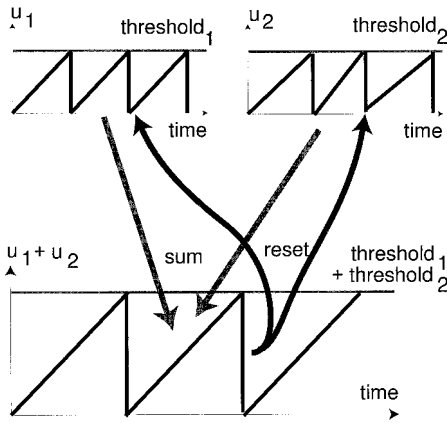
FIG. 10. Combining two activation levels by adding or averaging (gray arrows) leads to a fused timing signal with reduced variability. This is true, however, only if the two individual timers are reset or restarted in response to the threshold event of the combined signal (black arrows). This amounts to coupling between the two timers.

when the individual, signals reach threshold (Fig. 10). If this was not done, in the presence of even the most minute source of noise, the two timers would drift away from each other leading to a combined signal with a different frequency and variable amplitude, which may no longer reach threshold. Once the reset of the timers is driven by the combined signal, fluctuations in one timer, affecting the event time of the combined signal, affect the other timer upon reset, and vice versa, leading to mutual coupling of the two timing processes. Dynamic systems ideas are thus implicit in this account.

In the event picture, averaging of the outputs of stochastic timers is an abstract, formal solution to the coordination problem. The combined event time must, in general, occur earlier than one of the averaged component events. Thus, the future is somehow assumed to affect the present. This illustrates that the event timing approach lacks a description of the physical substrate by which timing is supported (as do delay dynamical systems). (But see Engbert et al., 1997, for a proposal to use estimation of upcoming durations to solve this problem.) Moreover, like the activation picture, this conception too requires that the individual clocks are mutually coupled to avoid qualitative changes of rhythm occurring when timers drift against each other (again because in nervous systems noise must always be reckoned with). Thus, a dynamic description is likewise implicit in this formulation.

Related conceptual problems arise when polyrhythms are conceived of in terms of the combination of multiple timers running at different frequencies (see Krampe et al., 2000, for the most sophisticated study along that line to date). In terms of the activation picture, there are obvious problems with normalization of the summed signal (the amplitude of which would strongly vary within the overall cycle) as well as the same implicit assumption about mutual coupling. That assumption applies to the event picture as well, in which the different clocks, running at different frequencies (typically forming simple ratios) must remain phase-locked for the resultant rhythm to display the desired structure. Such coupling may come about by the faster clock being reset by events from the slower clock or the combined event, or also by processes such as waiting for the other clock to emit a signal before starting to count. In all cases, concepts such as coupling, and hence of stability, are required to make sense of such notions. By contrast, event-based stochastic models with feedback

(Engbert et al., 1997; Pressing, 1999; Semjen et al., 2000) deal explicitly with coupling, albeit within the framework of delay or functional dynamical systems.

3.2. Dynamic Timing Models

Coupling is the central concept for understanding relative timing within dynamic timing models. Mathematically, two dynamic timers, (u_1, v_1) and (u_2, v_2), are mutually coupled if the dynamic variables of one timer contribute to the dynamic equations of the second and vice versa. For the Amari oscillator model presented earlier [Eqs. (6) and (7)], for instance, a simple form of mutual coupling is generated by the terms carrying the coefficient, c, in these equations:

$$\tau \dot{u}_1 = -u_1 + h_u + w_{uu} f(u_1) - w_{uv} f(v_1) \tag{11}$$

$$\tau \dot{v}_1 = -v_1 + h_v + w_{vu} f(u_1) + c f(u_2) \tag{12}$$

$$\tau \dot{u}_2 = -u_2 + h_u + w_{uu} f(u_2) - w_{uv} f(v_2) \tag{13}$$

$$\tau \dot{v}_2 = -v_2 + h_v + w_{vu} f(u_2) + c f(u_1) \tag{14}$$

These are only two out of a great variety of possible coupling terms. They generically generate phase locking, so that the two oscillators adopt identical frequencies and align matching parts of their activation trajectory (Fig. 11). This relative time order is stable; that is, when the two oscillators start out with differently aligned trajectories or are perturbed away from the stable alignment, then the dynamics drives the timers back to the stable timing relationship.

A characterization of relative timing independently of the underlying activation states is possible through the concept of *relative phase*. Its empirical definition is based on reference events (here the moments in time when activation pierces a threshold leading to a motor event such as a tap). The latency between matching events of two activation functions divided by the current cycle time of either of the activation functions is the relative phase, $\phi = \Delta T/T$ (Fig. 9). (Relative phase may be normalized

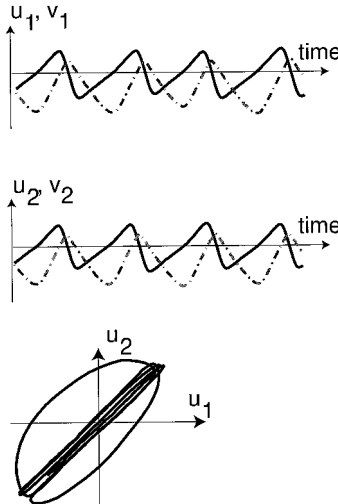**FIG. 11.** Two coupled dynamic timers [Eqs. (11), (12), (13), (14)] generically adopt a stable pattern of relative timing called phase-locking (here near in-phase). Activation variables are in solid black, inhibition variables in dashed gray. (Bottom) The two activation variables are plotted against each other. Except for noise-induced fluctuations, the two variables covary, indicating phase-locking.

to vary between 0 and 1, or, by multiplication, to vary between 0 and 2π or 360 degrees.)

The stability of relative timing can often be studied somewhat independently of the stability of the absolute timing pattern by postulating that relative phase is governed by an autonomous dynamical system, which has an attractor at the emergent stable phase relationship. Mathematically, models like

$$\dot{\phi} = -\alpha \sin(\phi - \phi_0) + q\xi_t \tag{15}$$

(illustrated in Fig. 12) can be fitted to experimental observations of relative timing patterns based on three mappings between experiment and model (Schöner, Haken, & Kelso, 1986): (a) The mean relative phase, $\bar{\phi}$, is an estimator of the attractor position: $\bar{\phi} = \phi_0$. (b) The variability of relative phase, $(SD(\phi))$, is an estimator of the ratio between the noise strength and the stability of the attractor: $SD(\phi) = q/(2a^{1/2})$. (c) The relaxation time (τ_{rel}: time constant of exponential decay of the perturbed relative phase to the stable state) is an estimator of the attractor stability: $\tau_{rel} = 1/a$. Noise sources are again modeled as Gaussian white noise, ξ_t.

The deterministic part of similar relative phase dynamics can be derived from models of coupled oscillators in the limit case of weak nonlinearity, in which these oscillators have approximately harmonic solutions. Such models have been proposed (e.g., by Haken, Kelso, & Bunz, 1985) to describe the kinematics of limb movement, although the link between observed and modeled kinematics is not close (e.g., Kay, Saltzman, & Kelso, 1991; see also Beek, Peper, & Daffertshofer, 2001, for extensive discussion of the Haken–Kelso–Bunz model and its support).

Because the relative phase dynamics has few parameters, but many observables, it is a powerful version of a dynamic account of relative timing. In the coordination of rhythmic bimanual movement, for instance, in-phase and anti-phase are the two spontaneously stable patterns of relative timing (Kelso, 1984; Schöner & Kelso, 1988a). Models of the type of Eq. (15) describing locally around either pattern the dynamics of relative timing have provided a quantitative account for experimental observations, including instances of quantitative prediction (predicting, for instance, ratios of variances from ratios of relaxation times, cf. Kelso & Schöner, 1987).

Relative phase dynamics identified in tasks in which spontaneously stable patterns of relative timing are encouraged provide constraints from which performance in related relative timing tasks can be predicted. When, for instance, particular relative phase values are imposed experimentally (through metronome information or feedback, by learning, or intentionally, cf. Yamanishi, Kawato, & Suzuki, 1980; Tuller & Kelso, 1989), then the observed dynamics of relative phase change, reflecting additional contributions that attract to the required relative phase values. The ''intrinsic'' dynamics, identified when no particular relative phase values are imposed, continue
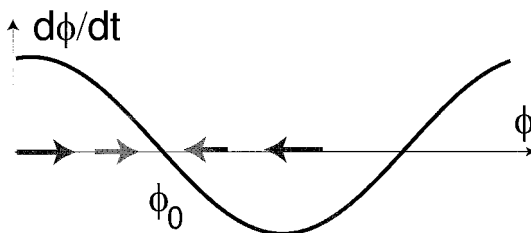

FIG. 12. The dynamics of relative phase Eq. (15) is illustrated. It models the relative timing dynamics close to a stable state, ϕ_0.

to affect relative timing, however. This manifests itself in two characteristic ways: When the required relative phase is close to one of the two spontaneously stable patterns in-phase or anti-phase, both constant and variable error are small. When the required relative phase is at a distance from either in-phase or anti-phase, systematic bias toward the nearest spontaneously stable patterns is accompanied by increased variability of relative phase. In terms of relative phase dynamics, this signature results from the way the two contributions to the dynamics agree or conflict with each other (Fig. 13; Schöner & Kelso, 1988b). In the first case, they attract to coinciding values of relative phase, which leads to enhanced stability. In the second case, they attract to conflicting relative phase values, leading to an attractor at an averaged relative phase value (hence the bias) and reduced stability. In the worst case, this may lead to instability.

Instabilities of relative phase have been crucial to revealing the power of the dynamical timing models. The simplest case is the original observation that anti-phase coordination becomes unstable as the frequency of the rhythmic movement is increased (Schöner & Kelso, 1988a). That instability manifests itself by increased relaxation times, by increased relative phase variability, and ultimately, under appropriate task constraints, by switching out of anti-phase into in-phase. Although coupled oscil-
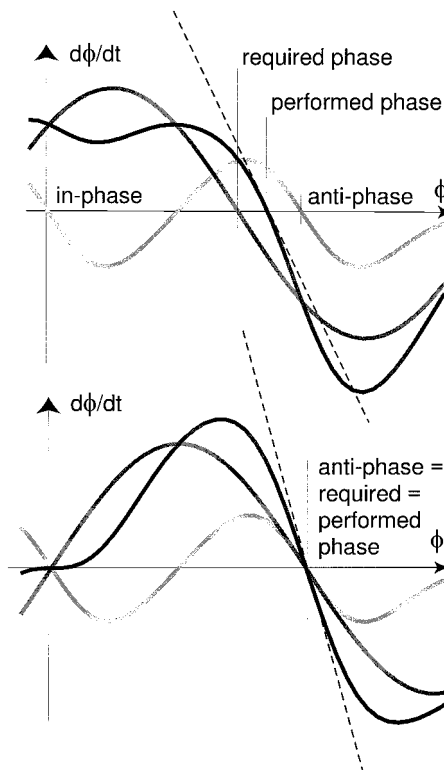

FIG. 13. Two contributions to the dynamics of relative phase are depicted. In light gray appears the ''intrinsic'' dynamics, which generates attractors at the two spontaneously stable relative phases, in-phase and anti-phase. In gray appears a contribution that reflects an imposed relative timing constraint, generating an attractor at the required value of relative phase. The sum of these contribution, depicted in black, generates an attractor at an averaged position between the nearest intrinsic pattern (here anti-phase) and the required pattern (top), which leads to bias away from the required pattern toward the intrinsic pattern. When the two contributions coincide (bottom), no averaging, and hence no bias, occurs. The resultant attractor is the more stable (steeper negative slope of dynamics at attractor, indicated by the dashed straight lines) the more closely the two contributions match.

lator models of this transition have been proposed (Haken et al., 1985), it is curious that no systematic attempt has been made to study the link between this instability in *relative* timing to the fundamental law of *absolute* timing, which predicts *decrease* of timing variability with increasing frequency. Why is anti-phase less stable than in-phase? Answers to this question must establish links between the instability and other timing phenomena. Although a few proposals have been made (Rosenbaum, 1991; Ivry, 2001), this issue remains open at the present time.

The notion of coupling reaches beyond interlimb coordination of rhythmic movement. In action–perception systems, a representation of the perceived timing of environmental events is coupled to a timer controlling an action system (e.g., Schöner, 1994a; Kelso, Delcolle, & Schöner, 1990; Carson, 1996). In polyrhythms, different timers running at different frequencies are mutually coupled, which maintains their generalized relative phases locked and thus keeps stable the rhythmic structure (e.g., Peper, Beek, & van Wieringen, 1995; Haken, Peper, Beek, & Daffertshofer, 1996). Only timers that have stability properties can be coupled: The influence on a given timer of a second timer must be one of degree that does not overwrite the state of the first timer (or else no evidence for a separate timing processes could be obtained), but does not ignore the influence of the second timer as well (or else no evidence for coordination or phase locking could be obtained). Thus, endowing timing models with the notion of stability is a necessary step to overcome the conceptual limitations of stochastic timing accounts for relative timing.

4.   DISCUSSION

Only the most salient issues surrounding theoretical accounts for timed motor acts have been sketched. Three additional contrasts are drawn in this section: (a) the issue of local vs distributed timers, which could also be conceived of as an issue of different levels contributing to timing; (b) the issue of discrete event-like timing vs continuous timing; and (c) the issue of timing in rhythmic actions vs timing in discrete motor acts.

4.1.   Local vs Distributed Timers and Levels

The observation of relative coordination, or more generally, of incomplete, or unstable coordination, provides ample evidence for the existence, in principle, of multiple timers. Neuropsychological evidence, on the other hand, points to the existence of central or unitary timers, in the sense that characteristics of timing are shared across different effectors and tasks (Ivry, 1997). The more general question is thus twofold: (a) To what extent is timing unitary and central? Which systems contribute to timing processes? (b) Which other levels of motor planning and control does timing relate to or interact with? In which way is timing a distinct aspect of the generation of movement, which can be studied separately from, for instance, control or spatial planning?

Stochastic timing models.   The Wing–Kristofferson model (1973) considered two contributions to timing errors, those arising from a clock (in the sense of an event based stochastic timing model), and those arising from a ''motor'' component, which randomly shift the motor event (e.g., tap) away from the moment in time specified by the clock. Both clock and motor errors were assumed uncorrelated in time, but because cycle times (intertap intervals) depend on the difference between two motor event times, the difference between two subsequent motor errors enters. This difference is negatively correlated in time. Intuitively, this negative correlation comes from

the fact that when a motor fluctuation delays a response to any particular clock signal, this both lengthens the time interval ended by the motor event and shortens the next interval that is initiated by that motor event. The model accounts therefore for the ubiquitous observation of negative lag-one autocorrelation in rhythmic tapping tasks.

This model has been extraordinarily influential and successful in the analysis of absolute timing error. Because the variances of the model clock and motor errors can be estimated from the variance and lag-one autocorrelation of cycle times, this model has been used to determine the contributions of different subsystems to timing error. Ivry and Keele (1989), for instance, showed that certain brain pathologies (like cerebellar lesions) affected clock, but not motor, error, and thus provided evidence for (limited) neuroanatomical localization of the processes underlying the clock component.

Curiously, the idea that correlations in time may reveal the inner structure of timing processes has not been carried over to the issue of relative timing, where such ideas were developed independently within the dynamic systems approach (but see Helmuth & Ivry, 1996). Conversely, despite the use of temporal cross-correlation to estimate relative timing stability (e.g., Fig. 4 in Kelso, Schöner, Scholz, & Haken, 1987), the dynamic systems approach to timing has ignored for a long time the issue of lag-one autocorrelations within a single effector (but see Post, Daffertshofer, & Beek, 2000).

Dynamic timing models. Dynamic timing models may generate negative lag-one autocorrelations even when only a single timer is considered (Schöner, 1994b). Those correlations do not show, however, the invariance across changes of cycle time observed experimentally. Moreover, the negative lag-one autocorrelation is not a robust property of dynamic timing models (Daffertshofer, 1998; compare Fig. 7), but occurs only under specific choice of model parameters. By contrast, a dynamic version of the Wing–Kristofferson model, in which a ''motor'' level is added to a ''timing'' level, reproduces the phenomenology of clock and motor error (Schöner, 1994b; Beek et al., 2001).

The larger question that must be confronted here is about the nature, level of abstraction, and uniqueness of dynamic timers. Are these timers dedicated exclusively to generating temporal order, separate from the generation of spatial relationships and from control? Or do they represent an integrated description of movement generation, so that the state of the dynamic timer corresponds directly to the state of the effector? Are dynamic timers dedicated neural processes or do many different components, including biomechanics or even external loads, contribute to timing? In which sense are multiple coupled dynamic timers separate entities?

Many different factors affect timing. When humans swing pendula, for instance, the preferred movement frequency and joint stiffness, as well as the precision of the coordination between two limbs, depend on the physical eigenfrequency of the pendulum (Sternad, Collins, & Turvey, 1995; Hatsopoulos & Warren, 1996). Biomechanics contributes in the sense, for instance, that the effective joint stiffness varies with movement frequency (Latash, 1992). Spatio-temporal patterns reflect an influence of spatial relationships on timing, such as in the two-thirds power law (Lacquaniti, Terzuolo, & Viviani, 1983). On the other hand, the capacity to maintain timing patterns in the face of added loads (Feldman, 1980), invariant timing under spatial change (such as in isochrony), and the observation of changes in timing stability independently of movement amplitude (Peper & Beek, 1998) underline that timing is not inseparably tied to the movement generation system.

Timing may thus be conceived of as a particular level of processing involved in generating voluntary movements. In terms of dynamical systems ideas, levels are defined in terms of what degrees of freedom they provide stability for (Schöner,
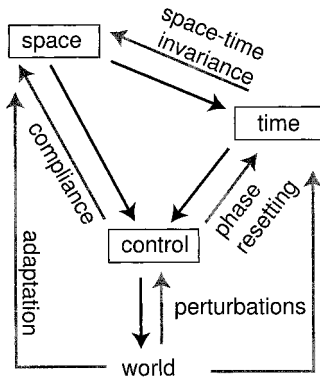
FIG. 14.   The three abstract conceptual levels of processing involved in movement generation concern *spatial* aspects of the motor act (e.g., movement amplitude and direction), *timing* (including coordination), and *control*. By definition these levels are linked in an ordered, feedforward fashion by providing information for each other (black arrows). Other links (gray arrows) introduce, however, mutual dependencies. These links are thus responsible, for instance, to the resetting of a motor rhythm by mechanical perturbations, for the adjustment of spatial aspects of a movement in response to its temporal structure (to generate spatio-temporal patterns), or the adaptation to force or timing constraints by changing the spatial extent of a movement plan.

1994b). The timing level stabilizes absolute and relative timing, assessed by the variability of timing measures as well as the relaxation process following perturbations of timing (either stochastic in correlational analysis or external such as when a metronome is abruptly phase-shifted or when one of multiple effectors is advanced or delayed in its cycle).

At least two other levels are involved in generating movement (Fig. 14). The level of control stabilizes mechanical degrees of freedom and thus deals with actual physical forces and effector constraints. The level of spatial planning stabilizes representations of spatial relationships and thus deals with perturbations affecting the relationships between different reference frames. These levels have obvious interdependencies in which, for instance, spatial and temporal information affects control. There is no unidirectional (or hierarchical) order to these interdependencies, however. The control level, for instance, couples into the timing level as observed when mechanical perturbations reset the phase of an ongoing rhythmic movement (Kay et al., 1991). Adaptation to loads or force fields reflect couplings from the control level into the level stabilizing spatial relationships as well as into the timing level. Spatiotemporal patterns necessitate adjustments of spatial trajectory planning in response to timing changes, a coupling from the timing into the ''space'' level. The discovery and detailed characterization of these interdependencies are important research tasks that must be solved in order to advance our understanding of movement generation.

4.2.   Event vs Continuous Timing

There is a theoretical tension in the field of ''timing'' research between event-based descriptions of rhythms or temporal order (often associated with the perspective offered by stochastic timing models) and continuous, trajectory-based descriptions (often associated with the dynamic systems perspective). Both the dynamical systems approach and the activation-based stochastic timing approach are based on a continuous underlying description, in which a substance (here called activation) physically represents time by varying reproducibly within a cycle and periodically across cycles. From that continuous description, threshold events, generalized in the Poincaré map,

lead to a discrete description. By contrast, event-based stochastic timing models abstract from the underlying physical support of timing, so that they are more fundamentally tied to a discrete event structure of timing. Even when such models are made dynamical systems by adding feedback, they represent a different class of dynamical systems that is not necessarily linked to an underlying continuous description (although an infinitely dimensional delay differential equation may offer such a possibility).

Experiments have begun to speak to the issue. Zanone and Kelso (1997), for instance, reported that the relative timing between two limbs in a rhythmic movement task varied strongly in stability across different portions of the cycle. During learning of a new relative timing pattern, changes of timing were again inhomogeneous across the cycle. Semjen and colleagues have likewise provided detailed evidence for differential stability (variability) and mean timing for different events within a tapping cycle in the presence of a metronome (Semjen, personal communication). The signature of such inhomogeneous timing is typically that particular ''anchoring'' events (such as peak velocity) are more tightly controlled with respect to their absolute or relative timing than the rest of the trajectory.

How can such inhomogeneous time structures emerge from underlying continuous timers? In dynamical timing models, such time structure of timing stability reflects the structure of the vector field. Figure 15 shows a sequence of simulations of the dynamic timer model Eqs. (6) and (7) in which the vector field is varied from a symmetric and weakly nonlinear form to an asymmetric and strongly nonlinear form. This leads to a change from relatively harmonic to increasingly anharmonic activation trajectories of the ramp-reset type. While the harmonic trajectories display relatively homogeneous timing within each cycle, the anharmonic trajectories have inhomogeneous time structure. This is illustrated in Fig. 16, in which the variability of cycle time is assessed either in terms of the time of peak activation or in terms of the time
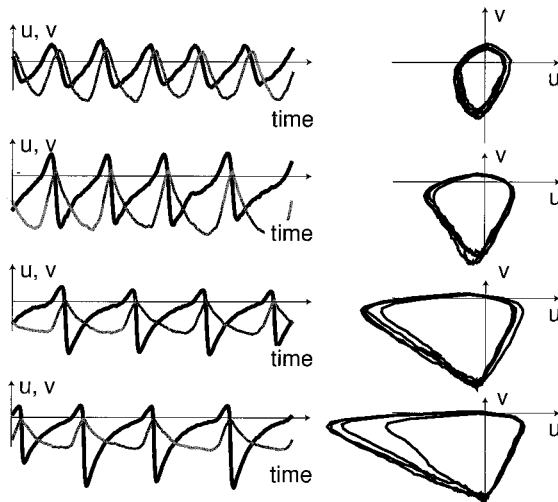

FIG. 15. By varying the vector field of the dynamic timing model Eqs. (6) and (7) the stable periodic activation functions may display varying degrees of harmonicity. Here, from top to bottom the vector field for positive inhibition is reduced in strength compared to the vector field for negative inhibition (compare phase plane plots in the right column). This leads to slower growth and faster decay of activation (black line in left column). During the rapid decay of activation, fluctuations are increased (see fluctuations at negative activation levels in phase plots). As shown in Fig. 16, timing is thus increasingly more variable when assessed for events in that epoch of the trajectory (e.g., the minima of the inhibition variable, which is depicted in gray in the left column).
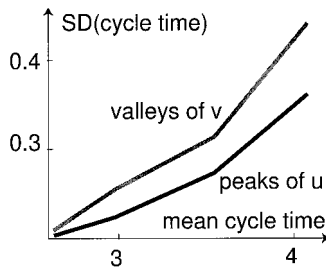
FIG. 16. The simulations shown in Fig. 15 lead to increasing cycle times as anharmonicity is increased. Here the variability of cycle time is plotted as a function of mean cycle time. Two types of events are used to assess cycle time: peaks of activation (lower line) or valleys of inhibition (upper line). For harmonic timer trajectories (at smallest cycle time corresponding to top row of Fig. 15), both events reflect the same variability of timing. For increasingly anharmonic timer trajectories (at larger cycle times) the variability of the peak activation event increases less than the activation of the valley inhibition event. Thus, peak activation events are relatively more stable than minimal inhibition events for anharmonic timer dynamics, an emergence of discrete event structure in timing.

of minimal inhibition. These two events fall into two different epochs of each cycle. For increasing anharmonicity (corresponding here to increasing cycle time), the stability of timing in the two epochs differs more and more.

Experimental evidence for continuous timing is provided whenever temporal averaging is observed. For instance, when the relative phase is biased toward intrinsic values of relative phase (Fig. 13), then those other points in time must have been able to exert an influence on the event observed. More direct evidence for continuous timing is provided when the effect of perturbations can be observed within a cycle, e.g., through gradual relaxation of relative phase toward a stable state.

It is likely that the structure of the task determines, in part, the structure of the timer dynamics. It is conceivable, for instance, that in situations in which the physical dynamics of the moving limb (or even an external load) contributes to timing, the vector field of the timing dynamics is effectively less nonlinear, smoothed by that contribution, leading to more homogenous timing. By contrast, tasks requiring intermittent release from control (such as generating complex rhythms in movement) may make use of a highly nonlinear timing dynamics, leading to inhomogeneous timing stability. This enables such a system to avoid interference and averaging with other timers.

4.3. Timing of Rhythmic Movement vs Timing of Discrete Movement

Although timing is most commonly studied in rhythmic movements, stable temporal relationships and reproducible movement times occur, of course, also during discrete motor acts. For instance, the timing of the grasp is controlled relative to the timing of the reach movement during a prehension task (Jeannerod, 1984). Only a limited amount of knowledge is available about the stability of timing during discrete movements. Perturbation experiments have provided evidence for stable relative timing: when one effector is slowed down or accelerated, other effectors may change their time course to reduce the discrepancy in relative timing (e.g., Gracco & Abbs, 1988).

Indeed, it is the coordination of discrete movement that poses the major challenge for understanding timing in those situations. Theoretical modeling (Schöner, 1989) has demonstrated that the same conceptual framework, coupling of stable limit cycles, can account for the coordination of discrete movement, if a mechanism is postulated that deactivates the limit cycle after a single (or even a half) cycle.

Additional experimental evidence for such coupling during the discrete motor act comes from action–perception patterns (e.g., table tennis drive, Bootsma & van Wieringen, 1990), in which discrete movements were observed to be accelerated (or slowed down) when movement initiation occurred late (or early) relative to a perceptual event. Thus, during the motor act there was a tendency to restore invariant relative timing of the movement and the perceptual event.

5. CONCLUSIONS

Variants of the two dominant approaches to timing may be conceived of as arising as limit cases from what could be a unified dynamical systems account: Activation-based stochastic timing models (with implicitly defined fast reset) are limit cycle attractors with a strongly nonlinear and asymmetrical vector field. Event-based stochastic timing models abstract from the physical substrate of timing. Although formally also dynamical systems (in particular, when augmented with feedback mechanisms) these models represent a separate class of systems potentially linked to delay differential equations. A number of conceptual problems (such as when future events affect the present during fusion of information from multiple timers) make these models somewhat counterintuitive. In all models, however, the notion of mutual coupling, and hence, stability, is inescapable. Dynamic timing models excel at describing relative timing, and coordination in general. Their power for addressing absolute timing has been underused.

Timing is always only one of a number of levels involved in generating movement. Discovering how these levels are interrelated and to which extent they are separate is one of the important tasks in our field still awaiting a more concerted effort. Ultimately, the difficulty of the scientific study of motor behavior may be related to this issue, as it is so much harder than in, say, psychophysics, to propose tasks or perturbations that selectively probe a single level of processing. Other interesting challenges for the future include integrating the understanding of timing with problems in serial order, as well as extending our understanding of timing into the domain of discrete movement and of movement preparation and initiation.

APPENDIX: MODEL PARAMETER VALUES

The parameters of Eqs. (6) and (7) were given the following values to generate the simulations shown in Fig. 6: $\tau = 1$; $h_u = 0.25$; $h_v = -0.5$; $w_{uu} = 0.5$; $w_{uv} = 1.25$; $w_{vu} = 1$; $\beta = 50$; $q = 0.01$. In Fig. 6b the following was changed: $\beta = 1000$, $w_{uv} = 10$.

The simulations underlying Fig. 7 used the same values except $\beta = 100$. The following parameters were varied to generate different cycle times: $h_u = 0, 0.05,$ . . . , 0.55, $w_{uv} = 1., 1.05, \ldots , 1.50$.

The simulations underlying Figs. 15 and 16 used the same values except $h_u = 0$. The following parameters were varied to generate the different degrees of harmonicity: $\beta = 20, 30, 40, 50$, $w_{uv} = 1, 3, 9, 19$.

The simulations of the coupled system of Eqs. (11), (12), (13), and (14) shown in Fig. 11 used the following model parameter values: $\tau = 10$; $h_u = 2$; $h_v = -5$; $w_{uu} = 2$; $w_{uv} = 15$; $w_{vu} = 10$; $\beta = 10$; $q = 0.01$, and $c = 1$.

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