

A model of synchronization of motor acts to a stimulus sequence

I. Timing and error corrections

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Abstract. A closed-loop timing model is proposed that accounts for several phenomena observed in tasks which require production of a sequence of motor acts in synchrony with a sequence of stimuli. In contrast to the previous models, variables available to the central nervous system of a subject (internal variables) and externally measurable variables are distinguished, and several physiologically justifiable internal variables are included. The model assumes the existence of (a) an internal timekeeper producing a reference interval that is used in a motor-control unit for timing of the next motor command; (b) an intrinsic (subjective) synchrony that relies on some a posteriori (feedback) information about the already executed onset of the motor act. A two-way error-corrective mechanism is hypothesized: (1) period (inverted frequency) corrections - the reference interval (period) is set at the beginning of the task according to the interstimulus-onset interval (s) and later corrected for differences" between its duration and the actual duration of s ; (2) phase corrections – internal synchronization errors (i.e., time gaps between the central temporal availability of internal representations of stimuli and of some feedback aspect of responses) are corrected for directly in the motor-control unit. Objectively measured systematic asynchrony of responses and stimuli is determined by the internal delays in information transduction. Finally, the model is used for making predictions of a subject's performance in some other experimental settings of the synchronization task.

1 Introduction

Human time perception and temporal organization of behavior in general has been studied for centuries

(e.g., Lashley 1951; Pöppel 1978). Nevertheless, there are still some questions to be answered about the processing (perception and production) of temporal information in the central nervous system, and about the integration of internal temporal processes with external timing signals (Hary and Moore 1985). One of the areas connected with the "problem of time" is the temporal control of subsequent elements in a stream of motor acts (serial timing) and/or synchronization of these acts with external events (stimuli). In the latter case, the relations between the temporal structure of the stimuli and that of the associated responses are of interest. The aim is to find out more about the underlying control mechanism that enables both information integration between and appropriate timing of the motor and perceptual systems. Synchronization of finger tapping with repetitive stimuli is one of the experimental paradigms used to study sensorimotor timing mechanisms (e.g., Woodrow 1932; Michon 1967; Fraisse 1978, 1982; Kolers and Brewster 1985; Hary and Moore 1985, 1987a; Najenson et al. 1989; Peters 1989; Vos and Ellermann 1989; Mates et al. 1992). Common to most of these experiments (though of varying amounts under different conditions) is the observed preceding (negative phase shift) of the subject's response onsets with respect to stimulus onsets for interstimulus-onset intervals up to a few seconds. This temporal discrepancy will henceforth be called the sychronization (phase) error.

Human timing-control abilities during the synchronization of motor acts with external events are influenced by external factors (physical and perceptual aspects of the stimuli), as well as by random fluctuations (precision) and systematic errors (accuracy) of the involved (internal) control and executive mechanisms. The accuracy of synchronization should be considered as being influenced by the limits of sensory systems (preventing the subject from perceiving the asynchrony), by the limits of the motor system (preventing the subject from correcting sufficiently the perceived asynchrony), as well as by the inaccuracy of the corresponding temporal intervals reproduced by an internal time-keeping mechanism in a sequence of

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responses. Several questions are then of principal importance: (1) What is the source of the regular advance in time of a response related to a stimulus? Is this advance necessary for the subjective feeling of simultaneity of the response and stimulus events? Which induced sensory events or events related to the brain activity are internally synchronized to give this subjective simultaneity? (2) How can one explain the influence of different stimulus and response-feedback sensory modalities on the amount of synchronization error ?

Not only static precision and accuracy of timing, but also dynamic (sequential) relations between the durations of various temporal intervals measured in synchronization tasks should be investigated, as well as the rules of their generation by the internal timing mechanism. A significantly negative auto-correlation between successive interresponse-onset intervals during a self-paced periodic motor responding was observed, and given some independence assumptions, this phenomenon was explained in the model of Wing and Kristofferson (1973). An extension of this explanation to the reproduction of tonal sequences was discussed by Vos and Ellermann (1989) and Mates (1991). By means of auto- and crosscorrelation analysis, Hary and Moore (1985, 1987a) documented sequential dependencies between various temporal parameters of synchronization performance. Hary and Moore used these dependencies as the main criterion for fitting their synchronization model to the experimental data. But the question of what are the rules responsible for such sequential relations in a synchronization task has not sufficiently been answered yet.

2 Goal

Enough experimental data have already been accumulated to develop an explanatory mathematical-system model for the simulation and analysis of the mechanism by which the motor acts synchronized with sensory events are controlled in time. Such a model could contribute to the explanation of experimentally observed phenomena, to the understanding of the underlying processes, and to the verification of the hypotheses about them. Several models of synchronization performance have already been proposed (Michon 1967; Voillaume 1971; Hary and Moore 1987a, b; Vos and Helsper 1992; Vorberg and Wing 1993). They all are (more or less) based on the assumption that one cycle in the human strategy consists of two principal components. (1) The process of establishing a *reference interval* for timing of a next response: in this (dynamic) process, necessary information from the stimulus-response history is used; (2) selecting an event that serves as the time moment from which the "internal clock" starts to measure out the reference interval: this clock-restarting moment is called the *reset moment.* After the reference interval has elapsed, the next response is placed, and the whole procedure is repeated in the following cycle. This assumption will be retained in the present investigation as well.

The models mentioned above are, however, oriented more to an explanation of particular phenomena or even to a pure mathematical description of them. Some of the models even fail when confronted with results from other experimental settings, and none of them explains the source of the systematic response advance observed. Further, the models mentioned aim at the description of a control mechanism internal to the subject, but they are almost without exception based on variables detectable in the laboratory frame of reference. A more general model is required to comprise the following features: (1) description and explanation of the experimentally observed pattern of synchronization (i.e., of the systematic preceding of responses with respect to stimuli); (2) preservation of the character of dynamic relations of different temporal intervals in a sequence of responses; (3) distinction between objectively measurable variables and subjectively available ones; (4) a universal structure allowing the fit of results from different experimental tasks *(not* necessarily with identical model parameters!); (5) stability of the response process; (6) reflection of some phenomena observed in other experimental paradigms pointing to perceptual temporal aspects that might be connected with the problem of sensorimotor synchronization. The aim of this investigation is to propose such a model, in which new, physiologically plausible variables are also included.

Since synchronization as such occurs in several areas of behavior (music performance, simultaneous motor actions, etc.), a closer insight into the underlying timing mechanisms could help to understand possible disturbances in these human activities. For example, Najenson et al. (1989) described the possibility of quantitatively measuring by the synchronization task the deficits of predictive timing abilities in patients with brain injury.

3 Definition of external variables

The temporal data from a synchronization task are represented either by event variables ("readings of a dock") or by interval variables (temporal differences between two events). For event variables, capital symbols are used throughout the text; lower-case symbols are used for interval variables. Time series of values of any variable x (or X) measured in a performance sequence is denoted as $\{x(k)\}\$ (or $\{X(k)\}\$ respectively), $k \geq 0$ represents an order index in such a sequence (time cycle). Of interest are the variables depicted in Fig. 1, upper part, and described in Table 1. For these variables which are measurable in the laboratory frame of reference the adjective *external* is used.

The criterion of stimulus-response synchronization accuracy (synchronization error, e) is defined as

$$
e(k) = R(k) - S(k) \tag{1}
$$

that is, if the kth response comes in advance of the stimulus $[R(k) < S(k)]$, the error is assigned a negative value $\lceil e(k) \rceil$.

4 Constituent experimental phenomena

4.1 Sensorimotor synchronization

4.1.1 Static characteristics. Stimuli of auditory, visual, and tactile modality in a tapping-synchronization paradigm with stimulus interval $s = 1, 2, 3$, or 4 s were used by Najenson et al. (1989) in a group of patients and in an age-matched group of healthy subjects (older than 55 years). Subjects produced in all cases delayed responses, but the average error was "closer to zero" for auditory than for visual and tactile stimuli, the difference being of the order of 50 ms. The errors for the latter two modalities were of comparable magnitude. Results from experiment 1 by Kolers and Brewster (1985; $s = 400$, 500, or 600ms) show that the weighted average errors for auditory, tactile, and visual stimuli were about -57 , -37 , and -13 ms, respectively (values estimated from Fig. 8, p. 159, in the cited study). Both these studies indicate that responses intending to synchronize to visual stimuli are performed objectively later with respect to stimulus than are responses to tactile stimuli, and these later than responses to auditory stimuli.

The sensory modality of feedback information from the executed onset of the motor response influences the synchronization error as well. In their experiment 2, Kolers and Brewster (1985) used visual stimuli and additional visual feedback (differing only in color), and they observed a larger variability of performance in this case than in tasks in which no additional feedback was provided. No differences in the average values were found between the two conditions in the above study. Other results (Aschersleben 1992; Mates et al. 1992) show that with an acoustical feedback signal derived from subjects' taps, the average error was smaller than under conditions when tactile-kinesthetic feedback only was available. It should be mentioned that in all the above experiments the tactile-kinesthetic feedback was always present.

Further, a larger anticipatory error in synchronization performed by foot rather than by finger was observed (Fraisse 1982; Aschersleben 1992). In the study by Bard et al. (1992) concerning a different task requiring synchronization of two different self-paced movements, a precession of heel raising over finger extension was observed. Both these studies indicate that also the type of motor effector influences the timing of performance.

4.1.2 Dynamic characteristics. In synchronization to stimulus sequences containing unexpected stepwise changes in stimulus-interval duration, resynchronization as soon as in the cycle $j + 1$ immediately following the tempo change was observed (Michon 1967, experiment 4, Fig. 19; Vos and Helsper 1992, p. 294, Fig. 3). Experimentally observed response-interval trajectories ${r(k)}$ in this case indicate that the tempo step-difference Δ applied in the cycle j is overcompensated with a factor always greater than 1 and mostly close to 2 [i.e., $s(j) < r(j+1) > r(j) + \Delta$. A sample of such an $\{r(k)\}\$ trajectory is shown later in Fig. 2E.

In a sequence of repetitive responses, a significant negative auto-correlation between successive (time lag 1) interaction intervals was observed several times (Michon 1967; Peters 1989; Vos and Ellermann 1989). Since such an auto-correlation is given by the intrinsic sequential properties of the response sequence that follow from the timing model by Wing and Kristofferson (1973; also Vorberg and Hambuch 1978; Mates 1991), an empirical negative auto-correlation cannot exclusively be attributed to the possible interventions of an errorcompensating mechanism.

A significant negative cross-correlation at lag 1 between stimulus intervals $\{s(k)\}$ and delay intervals $\{d(k)\}\$, that is $cor[s(k), d(k + 1)] < 0$, was observed in a synchronization task by Hary and Moore (1987a). They used subliminal random changes of s duration. Autocorrelation of $\{d(k)\}\$ at lag 1 was positive and significant as well (i.e., $cor[d(k), d(k + 1)] > 0$). Between $\{s(k)\}$ and response intervals $\{r(k)\}\$, no significant crosscorrelations at all were detected by Hary and Moore, in contradiction to the observation by Michon (1967, experiment 6), who found a significant positive crosscorrelation at lag 1 (i.e., $cor[s(k), r(k+1)] > 0$). It should, however, be noted that changes in s duration in the study by Hary and Moore (1987a) were random, with a standard deviation equal to 1.7% of the mean s (s = 704 \pm 12 ms), while the standard deviation of {s(k)} used by Michon (1967) was almost 10% (s = 600 \pm 58.6, $1200 + 117.2$, $2400 + 234.4$ ms). This difference might explain the above correlational discrepancy. Moreover, it has been found that a difference in duration of serially presented empty intervals is detected if it is at least 20 ms (Rammsayer and Lima 1991). Most values of the difference used by Hary and Moore (1987a) were thus below this threshold.

4.2 Related experimental paradigms

4.2.1 Order threshold. The temporal gap by which two very short intramodal stimuli have to be separated, so that humans are able to judge the order of their succession (so-called order threshold), seems to be independent of the sensory modality of the stimuli and is at least 20 ms (e.g., Hirsh and Sherrick 1961; Fraisse 1978; Pöppel 1978; Jaśkowski et al. 1990). Fraisse (1984) mentioned that the order threshold for heteromodal stimulation (click and light flash) was approximately 60 ms when the sound preceded the light, and from 90 to 120 ms when the light preceded the sound. In an intermodality temporal-order-judgement task, Jaskowski et al. (1990) found that the visual stimulus must precede the auditory one by about 28 ms in order for both stimuli be perceived as synchronous.

4.2.2 Reaction time. The asymmetrical result in intermodal order threshold just mentioned corresponds to the differences measured in simple reaction times. Pöppel et al. (1990b) reported an average difference of about 20 ms between the simple reaction times to visual and auditory stimuli. Jaśkowski et al. (1990) observed that the simple reaction time for visual stimuli was even about 40 ms longer than that for auditory stimuli; a difference of the same amount was also mentioned by Fraisse (1978).

5 Definition of internal variables

It has to be noted that the information measured in the laboratory frame of reference (defined in Sect. 3) is not identical to that available to the performing subject. Therefore, an additional class of variables has to be considered which are supposed to be internally available, in opposition to the external variables defined in Sect. 3. The adjective *internal* is used for these variables, and they will be marked throughout the paper by the subscript \tilde{I} .

According to the *perception latency* hypothesis (Fraisse 1978; Pöppel et al. 1990b), there exists a delay between the stimulus presentation and the temporal availability of its representation in the central nervous system *(temporal central availability*, Pöppel et al. 1990b). Such a delay consists not only of a simple delay in the neural transmission of sensory information, but also other possible time-consuming transformations of the information can contribute to it. These might be, for instance, some cognitive processes (see Sect. 6.2.2) or an effect of the so-called perceptual centers of stimuli (e.g., Pompino-Marschall 1991). A general term *transduction delay* will henceforth be used that comprises all those possible factors. Also, a delay in execution of the intended motor act has to be assumed (Wing and Kristofferson 1973). Therefore, three internal delay variables (parameters) are introduced in Table 1, that are physiologically justifiable.

In Table 1, further variables are introduced which characterize (in a performance-descriptive meaning) the hypothetical internal control mechanism of a subject. These internal variables can, but need not necessarily, represent any parameter of a real neural mechanism. They are used to create a source of externally measurable model behavior which is comparable with the experimentally observed human performance.

The (random) sensory transduction delays u_1 and f_I influence the temporal availability of internal representations of the corresponding input signals in the following way:

$$
S_I(k) = S(k) + u_I(k) \tag{2}
$$

$$
F_I(k) = R(k) + f_I(k) \tag{3}
$$

respectively. The (random) delay in execution of the motor act itself (motor delay, m_l) causes the overt response to occur at a time instant

$$
R(k) = R_I(k) + m_I(k) \tag{4}
$$

The relations between external and internal variables introduced are obvious from Fig. 1.

6 Hypotheses

The subject's synchronization strategy likely consists in the usage of information from the stimulus history and from the history of stimulus-response relations for the planned execution of preprogrammed movement in such a way that some expected event related to his or her

Table 1. Sensorimotor synchronization model variables

Variable	Type	Description
External variables		
S	Event	Occurrence of stimulus onset
s	Interval	Interstimulus-onset interval
R	Event	Occurence of motor response onset
r	Interval	Interresponse-onset interval
d	Interval	Delay interval (time difference between actual stimulus onset and response onset in the next cycle)
e	Interval	Synchronization error (time difference be- tween stimulus onset and corresponding response onset)
Internal variables		
u,	Interval	(Random) transduction delay of stimulus
m_I	Interval	(Random) motor delay in execution of motor act
f	Interval	(Random) transduction delay of feedback information from already executed onset of motor act
S_I	Event	Temporal central availability of stimulus
R_I	Event	Initiation of motor command
F_I	Event	Temporal central availability of feedback
e_I	Interval	Internal synchronization error (time differ- ence between temporal central availability of internal representations of some aspects of stimulus and response)
t_I	Interval	Internal timekeeper (reference) interval
C_I	Event	Reset moment
$k\geqslant 0$	Index	Stands for order index (time cycle) in a se- quence $\{x(k)\}\$ of values of a variable x

The transduction-delay variables are dependent on the sensory modality in which the corresponding mechanisms operate.

motor response will subjectively coincide in time with an event related to the expected (and predictable) stimulus occurrence. It is thus obvious that the subject's performance represents some kind of dynamic feedback control process, in which two essential subprocesses have to be distinguished: (1) timing of the next response and (2) evaluation of the previous performance. In the timing process, information available from the evaluation process is used.

6.1 Timing process

6.1.1 Corrective mechanisms generally. The goal in the synchronization task is to produce a response sequence with the same actual period (inverted frequency) as that of the stimulus sequence and with zero phase shift with respect to this sequence. It is assumed here that in an efficient error-corrective mechanism, phase differences are used for corrections of a phase shift, and period differences for corrections of the period of the response sequence. This assumption is not commonly accepted in the previous models. Any incidental phase difference in synchronization to an isochronous stimulus sequence $(s = const.)$ does not necessitate a correction of period if the response period is set correctly. If the period of stimulus sequence has changed, phase corrections only are not sufficient (see Sect. 6.1.2).

Variable:

Fig. 1. Time scheme and definition'of externa! *(upper part)* and internal *(lower part)* temporal parameters (variables) of the sensorimotor synchronization process and time diagram of the hypothesized mechanism of subjective synchronization. For the definition and description of the variables, see Table 1. Possible reset-moment events available to the control unit (see discussion in Sect. 8.2.2) are S_I , R_I , or F_I only. In the time cycle k (left group of *events*), a nonzero internal synchronization error $e_1(k) = F_1(k) - S_1(k)$ is detected. An error-corrective mechanism improves the timing of the motor-command initiation (R_1) in the time cycle $k + 1$ in order to achieve internal synchrony, given by $S_I(k + 1) = F_I(k + 1)$ (right group of events). For this ideal case in the figure, all delay variables are drawn as being constant.

6.1.2 Ideal corrector. For identification of the dynamic structure of the model, a stepwise change in stimulus interval duration s will be considered. Assume that an ideal subject is perfectly synchronized until a time cycle $k = j$ [i.e., $e(k) = 0, k \le j$] at which the s duration changes from a value $s(k) = s_0$, $k < j$, to a value $s(k) = s_0 + \Delta$, $A \neq 0, k \geq j$. This change causes a sychronization error $e(j + 1) = -\Delta$. An ideal causal corrective mechanism would produce a response trajectory $\{r(k)\}\$ in which the resynchronization is completed in the time cycle $j + 1$. In this trajectory, an $r(j + 1) = s_0 + 2\Delta$ completely compensates the asynchrony induced by the stimulus interval change in the time cycle j , and the synchrony is maintained with a new $r(k) = s_0 + \Delta, k \geq j + 2$.

A complete compensation for $e(j + 1) = -\Delta$ only would give an $r(j + 1) = s_0 + \Delta$ and thus would result in a systematic synchronization error $e(k) = -4, k \ge j + 1$. If the discrepancy on which the ideal subject's corrections are based were the phase error $e(j + 1)$ only, the ideal subject would have no reason to overcompensate this error by factor 2, which is required to reestablish the synchrony in the cycle $j + 1$ (unless he or she had been informed in advance that a stepwise change will occur). Since such an overcompensation has been observed experimentally (see Sect. 4.1.2), there must be another source of information available on which the additional compensation is based. This information is contained in the other discrepancy which occurs in the time cycle j, that is, the difference between the $s(i)$ and $r(j)$ (period difference), *r(j)* being an external manifestation of an internal timekeeper template $t_I(j)$. An ideal corrective mechanism thus compensates not only for the phase error $e(j + 1) = -\Delta$, it also changes the duration of the internal timekeeper interval according to the period difference between $t_1(j) = s_0$ and $s(j) = s_0 + A$. Such a pair of corrections produces $r(j + 1) = s_0 + 2\Delta$, while from the cycle $j + \overline{2}$ onwards, $r(k) = s_0 + \Delta$ and $e(k) = 0$, $k \geq i + 2$. The response of this strategy is equivalent to the response of the "linear predictor model" by Michon (1967), but it is based partially on the correction of synchronization errors. The ${r(k)}$ trajectory of such a correction is identical to that later shown in Fig. 2A.

6.2 Evaluation process

6.2.1 Internal synchrony. The objectively measured systematic asynchrony of motor response and stimulus, mentioned in the Introduction, does not necessarily mean that these events are asynchronous in the brain. On the contrary, subjects in previous experiments did not report the task difficult to fulfil nor to perceive the systematic synchronization error. The existence of an intrinsic ("subjective") synchrony is assumed, that is, a synchrony at some level in the central nervous system. Such an assumption about a possible distortion of objective mutual temporal relations of external events in their corresponding internal representations has already been made by Hary and Moore (1985). Of course, the internal synchrony need not be defined as an occurrence at exactly the same time instant, but it can be understood in a broader sense. For example, according to Pöppel et al. (1990b), these events may fall in one "temporal window", of nonzero length, given by the neuronal oscillator system state (Pöppel 1970), onto which different time events can be loaded and in which the temporal "before-after" relationship is not defined. The analogous hypothesis of "psychological moment" (Fraisse 1978) can be considered, too.

It is very probable that S_t is the input information that is in the central nervous system actually synchronized with some aspect of the motor act. Which aspect of the motor act is decisive, however, is not clear (Kolers and Brewster 1985). Nevertheless, if any response aspect which occurs before the objectively detected motor act (like initiation of the motor program or initiation of the movement itself, etc.) were synchronized, it would lead to objectively delayed responses (positive errors). It follows, however, from the mostly observed negative errors that the response aspects (events), which may be considered as synchronized with the stimulus by the subject, are those coming into the central nervous system (or produced in it) after the motor response onset detected in the laboratory frame of reference, that is, after the objectively measured contact of a response key. These events are thus in some sense feedback ones, carrying information about the already performed onset of the motor act.

6.2.2 Perception latencies. It has been pointed out that the findings mentioned in Sect. 4.2 could be explained by differences in perception latency (transduction delay) for different sensory modalities (Fraisse 1978; Pöppel et al. 1990b). Assuming synchronous temporal central availability of the internal representations of the stimulus and of some feedback from the tap

$$
S_I(k) = F_I(k) \tag{5}
$$

it follows from (2) and (3) that

$$
e(k) = R(k) - S(k) = u_I(k) - f_I(k)
$$
 (6)

If the transduction delay of the stimulus is shorter than that of the feedback sensory pathways $[u_I(k) < f_I(k)]$, the response observed from outside has to be in advance as related to the stimulus $[e(k) < 0]$. Only in such a case can the delayed feedback information be detected at some level in the central nervous system as being synchronous with the information about the stimulus. The above assumptions are analogous to those by Fraisse (1984), who stated that "It is difficult not to attribute these anticipations to the fact that the tactile stimulus must precede the sound in order to be perceived as simultaneous by the brain ..." (p. 6). The basis of the hypothesis was put forward by Fraisse (1980), who refers to Paillard (1949); independently also by Pöppel et al. (1990a). A recent theoretical study of it is found in Prinz (1992). As mentioned in Sect. 4.1.1, there is some experimental evidence supporting this hypothesis.

The hypothesis can be depicted by the time diagram of an internal synchronization process shown in Fig. 1, lower part, where for the time being the dynamic part of the closed-loop control system (timing and motor control unit) is considered as a "black box". It follows from Fig. 1 that an externally measurable synchronization error e is produced with a nonzero bias equal to the mean difference in transduction delays $u_I - f_I$ according to (6). At the same time, the mean value of the internally available synchronization error (e_i) is maintained by the correction mechanism at the zero (unbiased) level, allowing a subject to feel sufficiently in synchronization and causing no corrections of the externally detected asynchrony.

On the other hand, Fraisse (1978) mentioned the fact that "... if two stimuli are presented, the stimulus to which attention is given seems to precede the other... this attentional bias can reach 46 ms... (p. 213). The spontaneous attentional state of a subject affects the transduction of sensory information in such a way that an attentional focus to one stimulus probably causes a relative increase of the delay of the internal representation of the other stimulus. The influence of directed attention on the speed of transduction of sensory information has been documented, for instance, by Stelmach and Herdman (1991). If the stimulus with which the motor act should synchronize is the "more important" signal, the theoretical precise synchrony $R = S$ would always result in the subjective feeling of delayed response. Therefore, the feedback information from the tap would have to enter the control system earlier than the stimulus, to maintain the feeling of their synchrony. This attentional bias would thus require the measured motor response to be in advance of the stimulus even if the residual (i.e., uninfluenced by attention) neural transmission delays of stimulus and response-feedback were equal. Thus, a persistent negative error would be observed probably independently on involved sensory systems.

7 The model

An ideal corrector (see Sect. 6.1.2) requires a two-way corrective mechanism that makes both phase corrections (corrections for synchronization errors $\{e_i(k)\}\$ and period corrections (corrections for differences between the duration of timekeeper interval t_l [reference template] and the duration of stimulus interval s). Since $e_l(k)$ may be caused by a variability in the executive motor system as well, it does not necessitate a correction of $t_1(k)$ until

Fig. 2A-E. Response trajectories $\{r(k)\}\$ of pure deterministic variants (i.e., without any source of random variability) of different models to a stepwise change of s duration at the time cycle j. A An ideal corrector. B Hary and Moore's model, reset moment $C(j) = S(j)$. **C** Hary and Moore's model, $C(j) = R(j)$. **D** The proposed model (7), (8), in which phase-correction gain $\alpha = 0.8$ and period-correction gain $\beta = 1$. In **B** and **C**, *r* durations are displayed up to the time cycle $j + 1$ only, since from this cycle onwards, the model would continue with a random selection of $R(k)$ or $S(k)$ as the reset moment $C(k)$, $k \ge j + 1$. In all cases, perfect synchrony until the time cycle j was assumed. E A sample of experimentally observed data (taken over from Michon 1967). On the y-axis a relative scale is used: 0 corresponds to the interval duration until the step change, 1 corresponds to the amount of the step change applied. *Solid lines,* r durations; *dashed lines, s* durations

an inappropriate duration of $t_I(k)$ is detected. Therefore, corrections for synchronization (phase) errors $\{e_i(k)\}\$ are suggested to be made directly on the timing of motor output and are independent of corrections for period errors (much more conservative, if anything) made to $\{t_i(k)\}\$ due to the discrepancies in interval durations. The proposed model is described by the following recurrence equations:

$$
t_I(k) = t_I(k-1) - \beta(t_I(k-1) - [S_I(k) - S_I(k-1)]) \quad (7)
$$

$$
R_I(k + 1) = R_I(k) + t_I(k) - \alpha e_I(k)
$$
 (8)

where β and α are (constant) *period-correction gain* and *phase-correction gain,* respectively (i.e., multiplication factors, by which the period and phase errors, respectively, are weighted for corrections). The difference $S_I(k) - S_I(k-1)$ represents the internally detected duration of the external stimulus interval $s(k - 1)$. The internal variables are related to their external equivalents by (2) - (4) . The model is a linear one; a possible existence of a nonlinear process in the subjective acquisition of the internal synchronization error $e_I(k)$ is discussed in detail in Part II (Mates 1994).

The response of the system (7), (8) to a stepwise change in $\{s(k)\}\$ is for phase- and period-correction gains $\alpha = \overline{\beta} = 1$ the same as that of the ideal corrector (shown in Fig. 2A). A sample response of the proposed model (7), (8) for phase-correction gain $\alpha = 0.8$ and period-correction gain $\beta = 1$ is depicted in Fig. 2D. This is comparable with the experimental responses reported by Michon (1967), a sample of which is shown in Fig. 2E. Further simulations are made in Part II.

Consider $\{s(k)\}\$ randomly fluctuating around a mean duration s_M . It can be shown that the proposed structure of the model can produce a negative correlation $cor[s(k), d(k + 1)]$, even with an error-compensating mechanism. Assume that $t_1(0) = s_M$ and period-correction gain $\beta = 0$. This means that the subject has correctly extracted the mean s duration, has established the internal reference interval equal to it, and does not make any corrections to it (only ${e_I(k)}$ are corrected for, phasecorrection gain $\alpha > 0$). Since $t_1(k + 1) = s_M$, $m_1(k + 1)$ and $m_l(k + 2)$ are independent of $s(k)$, then we get from (4), (8)

$$
cov[s(k), d(k+1)] \approx cov[s(k), e(k+1)] \tag{9}
$$

the right term being negative as follows from the definition of variables in Fig. 1 [shorter *s(k)* causes larger $e(k + 1)$ and vice versa].

8 Relation to existing models

In order to assist the reader's easier orientation and to put the proposed model into a broader context, a brief overview of some existing models is given in Table 2, and the models will be discussed briefly.

Table 2. Overview of some existing synchronization models

8.1 Overview

8.1.1 Michon (1967). The "linear predictor model" is able to fit response-interval trajectories $\{r(k)\}\$ from experiments with a stepwise change in stimulus intervals $\{s(k)\}\$ (cf. Michon 1967, experiment 4); its response to a stepwise input is shown in Fig. 2A. Nevertheless, since there are no corrections made due to sychronization errors $\{e(k)\}\$, the model requires as a basic assumption that the performance starts at perfect synchrony $[e(0) = 0]$. Any initial $e(0) \neq 0$ (caused, for instance, by unknown or improper estimates of motor and transduction delays, see Fig. 1) is not eliminated in the model at all and stays systematic until the end of a sequence.

The model-predicted cross-correlations for a random sequence $\{s(k)\}\$ are $cor[s(k), r(k + 1)] > 0$, *cor*[s(k), $r(k + 2)$] < 0. The former cross-correlation was confirmed by Michon's own experimental data (see Sect. 4.1.2); the latter one, however, was not. The only tapping strategy that was claimed to account for the correlational results was the strategy of pure copying of the previous s duration [i.e., $r(k + 1) = s(k)$]. Exclusive usage of such a strategy without compensation for $\{e(k)\}\)$, however, would lead to a further systematic lag between the responses and stimuli as well, due to an insufficient correction after a stepwise change in s duration (see Sect. 6.1.2).

8.1.2 Hary and Moore (1987a). In the definition equations in Table 2, α is a multiplication factor by which the synchronization error e contributes to the correction of the reference interval t_i ; sources of random fluctuations are not included. The model equations for the reset moment $C(k) = R_I(k)$ resemble the model (7), (8), but in (8) $t_I(k)$ and $e_I(k)$ are used instead of $t_I(k - 1)$ and $e(k - 1)$.

 T is the so-called "internal" tick, representing the hypothesized internal rhythm

^b In fact $\{S(k)\}\$ serve as reset moments, see Sect. 8.1.3.

The model was developed for isochronous stimulus sequences

As has been shown by Hary and Moore (1987b), if $\{C(k)\} = \{R(k)\}\$ (tap-reset strategy) in their model, an unstable model behavior (cumulation of e) would result, even if an error-corrective mechanism were used. On the other hand, if $\{C(k)\} = \{S(k)\}\$ (metronome-reset strategy), a zero correlation *cor* $[s(k), d(k + 1)]$ would be observed if no error corrections were made; if errors were corrected, this correlation would be positive, in contradiction to the experimentally observed negative one (see Sect. 4.1.2). A random selection between the two possible events (S, R) was therefore chosen. Given the observed systematically negative e, the usage of the random-mixture reset moment strategy in the internal timekeeper yields to the paradoxical feature that the internal reference interval is not even asymptotically equal to the mean s duration (Hary and Moore 1987a). This means that a subject would have to establish his or her own reference different from the perceived external clock source.

There is a second-order delay in the feed-forward path of the model (cf. Table 2). It means that a correction due to $e(k)$ is not made before the reference interval $t_l(k + 1)$, thus not earlier than in the timing of $R(k + 2)$. It is suggested that the necessary information [i.e., an erroradjusted reference interval $t_I(k)$] for the placement of $R(k + 1)$ should be available at the reset moment $C(k)$ regardless of whether $C(k) = S(k)$ or $C(k) = R(k)$. Once a reset moment has been passed, no corrections are made in the timing of the following response. In their theoretical study, Hary and Moore (1987b) also considered a model in which $e(k)$ was used for corrections of $t_I(k)$ (such a model was originally proposed by Voillaume 1971), but on the basis of their experimental results, they rejected that solution.

Due to the second-order dynamic delay, if $C(j) = R(j)$, a stepwise change in the stimulus-interval duration in the time cycle *j* is reflected in the simulated sequence $\{r(k)\}$ not earlier than from cycle $j + 2$ onwards (i.e., with a lag of two cycles; see Fig. 2C), thus contradicting the experimentally observed responses (see Sect. 4.1.2). The stepwise input change could be reflected in $r(j + 1)$, if and only if $C(j) = S(j)$, which represents at least an exception with respect to the strategy of a random choice of reset moments finally suggested by Hary and Moore (1987a). Moreover, even in the latter case and for correction gain $\alpha = 1$, the response trajectory does not correspond to the empirical data (see Fig. 2B).

The second-order dynamic structure of the model does not exactly correspond to the auto- and cross-correlograms derived from the data by Hary and Moore (1987a, Fig. 2, p. 308), since these do not exhibit any significant correlation at lags greater than 1, which the modeled correlograms do (Fig. 4, p. 309 in the same study). It reflects the fact that a lot of older information preserved in $t_I(k)$ is not updated by the actual $e(k)$. Further, the very low gain $\alpha = 0.05$, required from simulations by Hary and Moore (1987a), might be a consequence of the fact that too old information (from the time cycle $k - 2$) is used for corrections. Moreover, the small value of α would represent almost autonomous performance, very conservative toward the correction of errors.This seems not to reflect the real subject's strategy in the range of stimulus-interval durations, where voluntary (more controlled) behavior is assumed (Peters 1989).

8.1.3 Vos and Helsper (1992). Despite the fact that a concept of an "internal" tick is introduced (see Table 2), the tick is a linear combination of external variables, and there is no unique sequence of the internal ticks $\{T(k)\}.$ Due to the possibly different factors a and b in the model equations, a tick $T(j) = (1 - b) S(j) + b R(j)$ used for timing of the response $R(j + 1)$ differs from the tick of the same order *j*, $\overline{T}(j) = (1 - a) S(j) + a R(j)$ used for the timing of $R(j + 2)$. The model equations from Table 2 can be put together and rewritten in the following way:

$$
R(k + 1) = S(k) + s(k - 1) + a[r(k - 1)-s(k - 1)] + (2b - a)e(k)
$$
 (10)

The model combines period- and phase-error corrections, preceding external stimulus-interval durations as timekeeper intervals, and $\{S(k)\}\$ as reset moments.

8.1.4 Vorberg and Wing (1993). The model was originally proposed to analyze stochastic characteristics of error- and response-interval sequences in synchronization with isochronous stimulus sequences. The model does not, therefore, contain any corrections to the internal timekeeper interval (period corrections). The detailed analysis done by Vorberg and Wing (1993) has proven that their model can fit quite well the variability and covariances empirically observed in the specific task. It is easy to show that the model is a limiting case of model (7), (8).

8.2 Consequences for the model

8.2.1 Model dynamics. The auto- and cross-correlations derived from the data by Hary and Moore (1987a, Fig. 2, p. 308) are not significant at lags greater than 1. Further, the experimentally observed responses to a stepwise stimulus-interval change reveal a compensation even at the time cycle immediately following the input change (Michon 1967; Vos and Helsper 1992). These responses agree well with the $\{r(k)\}$ trajectory predicted by the ideal corrector (cf. Sect. 6.1.2). All these facts support the hypothesis incorporated in the proposed model that there should be a feed-forward path in the modeled system that transfers an error from a time cycle k to the timing of the response in the time cycle $k + 1$, that is, a path with a delay of one cycle only.

8.2.2 Reset events (moments). A crucial question in the model development represents the choice of reset moments $\{C_I(k)\}\)$ from the available internal events (see Sect. 2 and Fig. 1). Since $\{S_I(k)\}\$ as internally available representations of the stimuli are only randomly delayed stimulus events, their usage as reset moments suffers from the same shortcomings as the usage of the stimuli themselves (see Sect. 8.1.2). A usage of ${F_I(k)}$ (see Fig. 1) would result, due to the nonzero delays $\{m_l(k)\}\$ and ${f_I(k)}$, in the same paradox as in the model discussed in Sect. 8.1.2, that the internal reference t_I would be shorter than the stimulus template. Therefore, the previous internal initiation of the motor command $R_I(k)$ is suggested in the model to serve as the reset moment for the timing of the next initiation $R_{I}(k + 1)$. The idea of a continuously running internal timekeeper (timer that restarts itself when the produced interval has elapsed) has been used in several timing models (e.g., Michon 1967; Wing and Kristofferson 1973; Vorberg and Hambuch 1978).

9 Discussion

To account for interindividual or intertask differences, an explanatory model of performance must be based either on a variable structure, if parameters are constant, or on variable parameters, if an invariable model structure is hypothesized. In the former case, consequently, different structures of the respective real underlying mechanism modelled would have to be assumed. If there is a unique control mechanism, a model of the latter class is more useful. Its invariable structure has to be universal enough to enable us to find such a set of values of its parameters that various data are fitted by a parameters-specific model response. In the model presented, two variable parameters are introduced: period-correction gain β and phase-correction gain α . The values of these gains and their mutual relation represent to a certain degree a subject's strategy in a task.

In the model, $\{R_I(k)\}\$ are used as reset moments, ${R_I(k)}$ are directly (with ergodic random motor delays ${m_I(k)}$ only) transformed to the stream of responses, and the mean of ${e_i(k)}$ is maintained by the error-corrective mechanism at zero. Consequently, the mean reference interval t_I and the mean of internal response-timing intervals ${R_1(k + 1) - R_1(k)}$ are asymptotically equal to the mean s duration.

The process by which the response sequence is generated in the proposed model of synchronization partially corresponds to the assumptions made by Wing and Kristofferson (1973) in the timing model of self-paced responses. The mutual independence of motor delays is preserved, but due to the error-corrective mechanisms, the internal timekeeper intervals are no longer a sequence of mutually independent variables. The proposed model structure is in a limiting case identical to the continuation model by Wing and Kristofferson (1973).

The model also provides a formal framework within which the influence of modality-specific transduction delays, in other words of unequally delayed temporal central availability, of stimuli and of additional feedback information from the already executed onset of the motor act as well as the influence of different motor effectors are comprehended. If the other experimental conditions remain identical (mainly the modality of the feedback signal), an increase in the stimulus-transduction delay u_l should cause a shift of the mean synchronization error "to the right" on the time axis. The already mentioned results from synchronization experiments with different stimulus modalities reported by Kolers and Brewster (1985) illustrate these conclusions: synchronization errors

for the visual modality were the "most to the right" on the time axis after the tactile modality and both after the auditory modality. This might reflect the order of transduction times: the longest for the visual and the shortest for the auditory modality.

Different sensory pathways (i.e., auditory, visual, or tactile-kinesthetic) also cause the feedback signals of the corresponding modality to be centrally available at different time instants. With one stimulus modality, the faster, acoustical pathway can supply the feedback information earlier, and therefore the motor command could be sent later than, for instance, with a visual feedback about the performed onset of the motor act. According to the abovementioned differences observed for different stimulus modalities, the mean of error distribution is thus expected to be shifted more to the "right in time" for acoustical than for the tactile-kinesthetic feedback and both more than for the visual feedback (e.g., Aschersleben 1992).

Differences in neural transmission times of peripheral feedback information from different motor effectors are expected to have analogous influence. The larger anticipatory error in synchronization performed by the foot rather than by the finger already mentioned (Fraisse 1982; Aschersleben 1992) can be explained by a longer neural transmission time of the afferent information from the foot. Bard et al. (1992), who used a different task, also observed an asynchrony of movements of two different effectors. They suggested that the judgment of synchrony was based upon the evaluation of afferent information. Both the above findings support the hypothesis presented in Sect. 6.2.2.

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References

- Aschersleben G (1992) Sensumotorische Synchronisation. Max-Planck-Institut für psychologische Forschung, München, Paper 1/92
- Bard C, Paillard J, Lajoie Y, Fleury M, Teasdale N, Forget R, Lamarre Y (1992) Role of afferent information in the timing of motor commands: a comparative study with a deafferented patient, Neuropsychologia 30:201-206
- Fraisse P (1978) Time and rhythm perception. In: Carterette EC, Friedman M (eds) Handbook of perception, Vol 8. Academic, New York, pp 203-254
- Fraisse P (1980) Les synchronisations sensori-motrices aux rythmes. In: Requin J (ed) Anticipation et comportement. CNRS, Paris, pp 233-257
- Fraisse P (1982) Rhythm and tempo. In: Deutsch D (ed) The psychology of music. Academic, New York, pp 149-180
- Fraisse P (1984) Perception and estimation of time. Annu Rev Psychol 35:1-36
- Hary D, Moore GP (1985) Temporal tracking and synchronization strategies. Hum Neurobiol 4:73-77
- Hary D, Moore GP (1987a) Synchronizing human movement with an external clock source. Biol Cybern 56:305-311
- Hary D, Moore GP (1987b) On the performance and stability of human metronome-synchronization strategies. Br J Math Stat Psychol 40:109-124
- Hirsh IJ, Sherrick CE (1961) Perceived order in different sense modalities. J Exp Psychol 26:423-432
- Jaśkowski P, Jaroszyk F, Hojan-Jezierska D (1990) Temporal-order judgments and reaction time for stimuli of different modalities. Psychol Res 52:35-38
- Kolers PA, Brewster JM (1985) Rhythms and responses. J Exp Psychol Hum Percept Perform 11:150-167
- Lashley KS (1951) The problem of serial order in behavior. In: Jeffress LA (ed) Cerebral mechanisms in behavior. Wiley, New York, pp 112-136
- Mates J (1991) Extending the model of self-paced periodic responding: comments on Vos and Ellermann (1989). J Exp Psychol Hum Percept Perform 17:877-879
- Mates J (1992) Timing and corrective mechanisms in synchronization of motor acts with a sequence of stimuli. Proceedings of the 4th Workshop on Rhythm Perception and Production, June 1992, Bourges, France, pp. 43-48
- Mates J (1994) A model of synchronization of motor acts to a stimulus sequence. II. Stability analysis, error estimation and simulations. Biol Cybern 70:475-484
- Mates J, Radil T, Pöppel E (1992) Cooperative tapping: time control under different feedback conditions. Percept Psychophys 52: 691 - 704
- Michon JA (1967) Timing in temporal tracking. Institute for Perception RVO-TNO, Soesterberg, Netherlands
- Najenson T, Ron S, Behroozi K (1989) Temporal characteristics of tapping responses in healthy subjects and in patients who sustained cerebrovascular accident. Brain Behav Evol 33:175-178
- Paillard J (1949) Quelques données psychophysiologiques relatives au déclenchement de la commande motrice. Annee Psychol $48.28 - 47$
- Peters M (1989) The relationship between variability of intertap intervals and interval duration. Psychol Res 51:38-42
- Pompino-Marschall B (1991) The syllable as a prosodic unit and the so-called P-centre effect. Forschungsberichte des Instituts für Phonetik und Sprachliche Kommunikation, Miinchen 29: 65-123
- Pöppel E (1970) Excitability cycles in central intermittency. Psychol Forschung 34:1-9
- Pöppel E (1978) Time perception. In: Held R, Leibowitz HW, Teuber H-L (eds) Perception. (Handbook of sensory physiology, Vol VIII). Springer, Heidelberg, pp 713-729
- Pöppel E, Müller U, Mates J (1990a) Temporal constraints in synchronization of motor responses to a regular sequence of stimuli. Paper presented at the Annual Meeting of the Society for Neuroscience, St. Louis, Missouri
- Pöppel E, Schill K, von Steinbüchel N (1990b) Sensory integration within temporally neutral systems states: a hypothesis. Naturwissenschaften 77:89-91
- Prinz W (1992) Why don't we perceive our brain states? Eur J Cogn Psychol 4:1-20
- Rammsayer TH, Lima SD (1991) Duration discrimination of filled and empty auditory intervals: cognitive and perceptual factors. Percept Psychophys 50: 565-574
- Stelmach LB, Herdman CM (1991) Directed attention and perception of temporal order. J Exp Psychol Hum Percept Perform 17:539-550
- Voillaume C (1971) Modèles pour l'étude de la régulation de mouvements cadencés. Annee Psychol 71:347-358
- Vorberg D, Hambuch R (1978) On the temporal control of rhythmic performance. In: Requin J (ed) Attention and performance, Vol VII. Erlbaum, Hillsdale, NJ, pp 535-555
- Vorberg D, Wing A (1993) Modelling variability and dependence in timing. In: Heuer H, Keele SW (eds) Handbook of perception and action, Vol. 3. Academic, London
- Vos PG, Ellermann HH (1989) Precision and accuracy in the reproduction of simple tone sequences. J Exp Psychol Hum Percept Perform 15:179-187
- Vos PG, Helsper EL (1992) Tracking simple rhythms: on-beat versus off-beat performance. In: Macar F, Pouthas V, Friedman WJ (eds) Time, action and cognition. Towards bridging the gap, Vol 66. Kluwer, Dordrecht, pp 287-299
- Wing AM, Kristofferson AB (1973) Response delays and the timing of discrete motor responses. Percept Psychophys 14:5-12
- Woodrow H (1932) The effect of rate of sequence upon the accuracy of synchronization. J Exp Psychol 15:357-379