Human Factors and Behavioral Science:

Central Control of Movement Timing

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How do people control the delay between successive finger movements? A reaction-time experiment suggests that the delay is controlled by setting an internal "alarm clock."

I. INTRODUCTION

A fundamental concern of behavioral science is to understand how we control the movements of our bodies. This paper examines the timing of body movements: As we walk, talk, or type, how are the delays between the phases of these various activities controlled?

A popular means of approaching this question has been to consider two extreme views of how movements might be timed. One view holds that delays between the phases of a movement sequence are controlled by using feedback from each phase to trigger the next. Since the feedback can arise from receptors in the peripheral nervous system—within the muscles, joints, and skin—this view is often referred to as the "peripheralist" theory.\(^1\) The other view holds that movement timing is controlled by plans or "programs" that allow sequences to be performed without the aid of feedback. This view is often called the "centralist" theory.\(^2\)

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Two main arguments have been leveled against the peripheralist position. One argument is that times between successive movements may often be shorter than the time needed for feedback from one movement to be used to trigger the next.³ The other argument is that animals and people in whom peripheral feedback is physiologically disrupted can often perform movements effectively.^{4,5} Both of these observations indicate than when feedback cannot be relied on, central programs may be used. What the observations do not resolve, however, is whether central programs are also used when feedback is available. The experiment reported here was meant to answer this question. The experiment was also meant to provide detailed information about the nature of the programming of movement sequences when it appears that programming is used.

II. THE EXPERIMENT

The experiment, which has been reported in detail elsewhere, ^{6,7} used a simple procedure (see Fig. 1). The subject's task was to perform a sequence of two responses, made with the left and right index fingers, in such a way that the produced interresponse interval approximated a target interval. Feedback given at the end of each trial indicated whether the produced interval was longer or shorter than the target interval and by how much. In addition to producing the specified

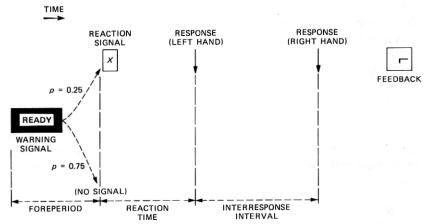


Fig. 1—Overview of the experimental procedure. "Catch trials," in which no signal was presented and no response was allowed, were used to discourage anticipation responses. The warning, reaction, and feedback signals were displayed on a CRT screen. The feedback signal consisted of a vertical line that pointed up if the produced interval was too long and down if the produced interval was too short, where the length of the line indicated the size of the proportional error; the length of a horizontal line indicated how much the Reaction Time (RT) exceeded a target of 130 ms. The foreperiod was fixed at 0.5 second, the reaction signal remained on the screen until the last required response was made, and the feedback signal came on 0.5 second after the offset of the reaction signal and remained on the screen for 2.5 seconds.

interresponse interval, the subject was also required to make the first response as quickly as possible after the onset of a visual reaction signal.

The rationale for the experiment can be understood by noting that several investigators have found that RTs are longer for the first of two responses, performed approximately simultaneously, than for single finger responses.⁸⁻¹⁴ If it is assumed that the lengthening of RTs for response doublets results from the demands associated with coordinating two responses, the question that arises is how long the delay between two responses must be before the RT for the first response is as short as the RT for a single, isolated response. According to the peripheralist theory, one would expect the RT for the first of two responses to equal the RT for a single, isolated response whenever the delay between the two responses equals or exceeds the time required to use peripheral feedback from the first response to trigger the second response. Thus, if it takes 200 ms to use peripheral feedback from one response to trigger the next, the peripheralist theory would predict that, whenever the delay between the two responses is greater than or equal to 200 ms, the RT to initiate the two responses in series should be no longer than the RT to initiate the first response alone. By contrast, according to the centralist theory, the RT to initiate the two responses in series should be longer than the RT to initiate the first response alone, even if the delay between the two responses exceeds the feedback loop time; for according to the centralist theory the availability of peripheral feedback does not suffice to control the onset of the second response relative to the first.

Figure 2 shows the results from the main experiment designed to test these predictions. In this experiment, the target interresponse intervals ranged (in a blocked design) from 0 to 1050 ms. In the control condition no second (right-hand) response was required, so the target interval was effectively infinite (∞). The data are averaged over three adult female subjects. In the "stringent" condition, the length of the vertical feedback line was directly proportional to the deviation of the produced interval from the target (nonzero, finite) interval such that the line reached the edge of the CRT screen for deviations exceeding 100 percent of the target interval. In the "relaxed" condition, the scale factor relating the size of the deviation to the length of the vertical feedback line was reduced by a factor of 25 so that generally subjects could only see whether their produced interresponse intervals were too long or too short. About 1300 observations contribute to each point in Fig. 2.

Inspection of Fig. 2a reveals that none of the two-response sequences had mean RTs less than or equal to the mean RT in the control condition, as was confirmed statistically. Since the larger interre-

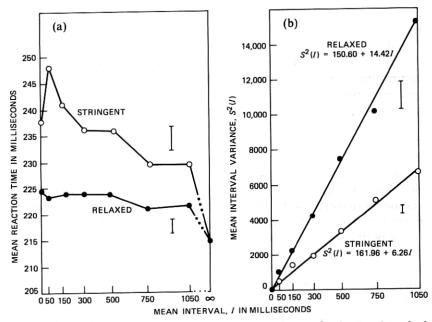


Fig. 2—Results of the experiment. (a) Mean reaction times and estimates of standard error (\pm SE) for the two accuracy conditions. (b) Mean variances of produced interresponse intervals, fitted linear functions, and estimates of \pm SE. The zero intercepts of the fitted linear functions for the two accuracy conditions were not significantly different from one another. (Estimates of \pm SE are based on mean squares from fits of mean functions to individual subject data.)

sponse intervals were certainly large enough to allow for the use of peripheral feedback, ¹⁵ this result is consistent with the centralist prediction and inconsistent with the peripheralist prediction.

Given that control of the interresponse interval was apparently not based solely on peripheral feedback, what was the nature of the central activity that allowed for control of the intervals? A plausible hypothesis is that the interresponse intervals were controlled by a kind of hydraulic system in which the amount of energy made available to the second response increased as the time until its occurrence decreased. If the total energy available to the two responses was fixed, then the amount of energy available to the first response would decrease as the desired interresponse interval decreased, leading to an inverse relationship between RTs and interresponse intervals. This is a response competition model. (For a more general discussion of response competition, see Ref. 16.)

An alternative hypothesis is that the interresponse interval was controlled by a central clock that was set just before the production of the first response (i.e., during the RT). If the time needed to set the clock depended on the precision of setting, which in turn was reflected

in the variability of the interresponse interval, this alarm clock model predicts that RTs could depend on interval variability rather than interval size.

To test these predictions, we manipulated the analog feedback that subjects received concerning the accuracy of their interresponse intervals. Recall that the analog feedback took the form of a vertical line that pointed up if the produced interval was larger than the target interval and down if the produced interval was smaller than the target interval. By changing the scale factor relating the length of the line to the proportional difference between the produced and target interresponse interval, we could impose stringent or relaxed accuracy requirements on the subject's timing performance. When the scale factor was small, a large error resulted in a small error line ("relaxed" condition), but when the scale factor was large, even a small error resulted in a large error line ("stringent" condition). The relaxed-stringent manipulation was a within-subject variable, which we introduced to get subjects to alter the variability of their interresponse intervals while keeping the means of the intervals constant.

As is seen in Fig. 2a, mean RTs in the relaxed condition were essentially constant over the range of finite intervals. However, mean RTs in the stringent condition were longer than in the relaxed condition and decreased as intervals increased for targets 50 ms or greater. [The discontinuity in the stringent mean RT function at the 0-ms target confirmed subjects' reports that control of the intervals in this condition was qualitatively different from the other conditions (e.g., because the fingers and wrists were kept stiff when simultaneous responses were attempted). Sequences begun with the right hand, which were only permitted in the 0-ms condition, did not have shorter RTs than sequences begun with the left hand.] Thus, Fig. 2a shows that mean RTs were not simply related to mean intervals, contrary to the prediction of the response competition hypothesis. Instead, mean RTs were related to the required precision of the intervals, consistent with the alarm clock model.

The question that now arises is whether the actual precision of the intervals was affected by the differential precision requirements imposed by the stringent-relaxed manipulation. If the actual precision was affected, such that greater precision was achieved in the stringent condition, the evidence would be stronger for the hypothesis that during the RT an internal alarm clock was set to varying degrees of precision. In Fig. 2b variances of produced intervals are plotted against their corresponding means. As is seen in the figure, variances were larger in the relaxed condition than in the stringent condition. That the interval means were approximately equal in the two conditions is demonstrated by the approximately vertical alignment of the filled

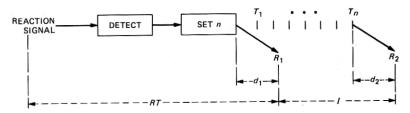


Fig. 3—Overview of an alarm-clock model for performance in the experiment.

and empty points corresponding to each target interval. As is also seen in Fig. 2b, the mean interval variances were well fit by linear functions. Linear regression accounted for 99.7 percent and 99.9 percent of the variance among the mean variances (averaged over subjects) in the stringent and relaxed conditions, respectively. The linearity of the variance functions allows for a simple elaboration of the alarm clock model, which is discussed below.

III. AN ALARM CLOCK MODEL*

The elaborated alarm clock model is shown in Fig. 3. It says that the size of the delay between the first and second response $(R_1 \text{ and } R_2, \text{ respectively})$ depends on the number, n, of pulses of an internal clock, where the value of n is set during the RT interval. The model assumes that the interval, I, between R_1 and R_2 equals the sum of the times, T_1, T_2, \cdots, T_n for the n clock pulses, plus the difference between the motor delays, d_1 and d_2 , of R_1 and R_2 , respectively. That is,

$$I = T_1 + \cdots + T_n + d_2 - d_1. \tag{1}$$

It is also assumed that the times for the successive clock pulses fluctuate randomly about a mean and are stochastically independent. Hence, as n increases, the variance of the cumulative pulse time increases linearly.^{17,18}

The model affords two plausible ways of explaining the difference in slopes for the fitted variance functions in the stringent and relaxed conditions. One possibility is that the variability of interpulse times was greater in the relaxed condition than in the stringent condition. The other possibility, which will be pursued here because of its interesting ramifications for the proposed clock-setting process, is that the variance of n was greater in the relaxed condition than in the stringent condition. It is possible to express precisely how the variance of n in the relaxed condition would be related to the variance of n in the stringent condition, given that the slopes (but not the zero intercepts) of the variance functions differed in the two conditions. Let the

^{*} This is a greatly simplified version of a model presented in Ref. 6.

random variable N be the number of clock pulses between the triggering of response 1 and 2. Let the time between pulses i-1 and i, for $1 \le i \le n$, be a random variable T, where the random variables T_i are independent of N and identically distributed as a random variable T with finite mean and variance. Allowing the random variable D to represent the difference $d_2 - d_1$, and assuming T, N, and D are mutually independent, it is possible to use the expression for the variance of a random sum¹⁹ to obtain

$$Var(I) = E(N)Var(T) + Var(N)E^{2}(T) + Var(D).$$
 (2)

Assuming that the only terms in (2) that differ in the relaxed and stringent conditions are Var(I) and Var(N), and using subscripts R and S for the relaxed and stringent conditions, respectively, we can subtract $Var_S(I)$ from $Var_R(I)$ and rearrange terms to obtain

$$\operatorname{Var}_{\mathbf{R}}(N) - \operatorname{Var}_{\mathbf{S}}(N) = [E^{2}(T)]^{-1} \cdot [\operatorname{Var}_{\mathbf{R}}(I) - \operatorname{Var}_{\mathbf{S}}(I)]. \tag{3}$$

Since $Var_R(I)$ and $Var_S(I)$ were found to be linear functions of I with what are assumed to be identical zero intercepts, and since $E^2(T)$ is assumed to be a constant, eq. (3) becomes

$$Var_R(N) - Var_S(N) = kI,$$
 (4)

where k is a constant greater than 0. Equation (4) shows that $\operatorname{Var}_{\mathbb{R}}(N)$ and $\operatorname{Var}_{\mathbb{S}}(N)$ are related in a simple way. As is seen below, however, the relationship can be shown to be even simpler.

Consider how the variance of N changes with I within the stringent or relaxed condition. Relying on the fact that we found Var(I) and I to be linearly related, and noting that

$$E(N) - [E(I) - E(D)]/E(T),$$
 (5)

eq. (2) can be rewritten to solve for Var(N) as

$$\operatorname{Var}(N) = \frac{\alpha + \beta \cdot E(I) - \operatorname{Var}(D) - \left[\frac{E(I) - E(D)}{E(T)}\right] \operatorname{Var}(T)}{E^{2}(T)}. \quad (6)$$

All the terms in eq. (6) are constant except for Var(N) and E(I). Therefore, eq. (6) can be rewritten

$$Var(N) = u + vE(I), \tag{7}$$

where u and v are constants. Since the clock presumably would not be used (i.e., N would not be set) when E(I) = 0, u can be set to 0, leaving

$$Var(N) = vE(I). (8)$$

On the basis of the simple relation shown in eq. (8), we can indicate how Var(N) in the stringent condition, $Var_S(N)$, is simply related to

Var(N) in the relaxed condition, $Var_R(N)$. Let $Var_R(N) = rE(I)$. As we saw in eq. (4), $Var_R(N) - Var_S(N) = kE(I)$. It follows, then, that $Var_S(N) = (r-k)E(I)$. Thus, $Var_R(N)$ and $Var_S(N)$ differ with respect to the size of the proportionality constant relating each of these quantities to E(I).

To summarize, the above discussion reveals that the variance of N is proportional to E(I), and that the slope of this function differs in

the relaxed and stringent conditions.

The simplicity of these theoretical results allows for the proposal and test of a simple model of the process that may have given rise to the mean RT effects shown in Fig. 2a. The model is suggested by the observation that shorter RTs were associated with larger (predicted) values of Var(N). Essentially, the model says that the time to set N increases as the range of possible values of N decreases. (A possible reason will be given in Section IV of this paper.) Let θ denote the time to set N and recall that the range of a distribution is proportional to the standard deviation of that distribution. The model says

$$\theta = \frac{\gamma}{\sqrt{\operatorname{Var}(N)}} = \frac{\gamma}{\sqrt{\delta E(I)}} = c[E(I)]^{-1/2},\tag{9}$$

where $c=\gamma/\sqrt{\delta}$ is an empirical constant and $0 < E(I) < \infty$. From the previous observation that the proportionality constant relating $\mathrm{Var}(N)$ to E(I) distinguishes the relaxed and stringent conditions, it follows that only the size of c in eq. (9) needs to differ in the relaxed and stringent conditions. Moreover, as is implied in Fig. 3, the RT is assumed to equal θ plus the time to detect the reaction signal and execute the first response. Hence, the model predicts that the RT in the relaxed and stringent conditions can be expressed as

$$RT_R = k + \theta_R$$

and

$$RT_{S} = k + \theta_{S}, \tag{10}$$

respectively, or

$$RT_R = k + r[E(I)]^{-1/2}$$

and

$$RT_S = k + s[E(I)]^{-1/2},$$
 (11)

respectively, where k, r, and s are empirical constants. Equation (11) has the appealing property that RTs increase with decreases in E(I) at a rate related to the size of the linear coefficient. Thus, changing the linear coefficient in eq. (11) produces a set of curves two of whose members look like the pair of curves seen in Fig. 2a.

For purposes of finding out how well eq. (11) actually fit the RT data, an iterative procedure was used to find the values of k, r, and s for which it was possible to minimize the sum of squared deviations of the obtained RTs from the predicted RTs. The obtained RT values used were the mean RTs in the conditions where nonzero finite interresponse intervals were required. The best-fitting values of r and s turned out to be 25 and 236, respectively, and the best-fitting value of k turned out to be 221 ms. With these estimates the fitted model accounted for 94.6 percent of the variance of mean obtained RTs. (When k was held at 216 ms, which was the mean RT in the control condition, only 67.5 percent of the variance was accounted for. Because the goodness of fit was so much poorer here, it appears that the time required for detection of the reaction signal and execution of the first response differed in the finite and infinite-interval conditions, or that some extra process, not identified in the model, in fact occurred in the finite-interval conditions.)

IV. CONCLUDING REMARKS

This paper has examined the mechanisms of movement timing. Of necessity, the experiment that has been reported involved a restricted type of movement, namely simple finger sequences. Yet the experiment appears to have fairly broad theoretical importance for our understanding of how movements are timed. In particular, the experiment suggests that even when peripheral feedback is available, central programs play a controlling role in movement timing. The basis for this conclusion is that the mean RT for the first of two responses was longer than the mean RT for a single, isolated response, even when the time between the first and second response exceeded 1 second. That the lengthening of RTs at such long delays was in fact attributable to some aspect of the control of movement timing is suggested by the fact that the lengthening of RTs was greater when the interresponse interval was controlled more precisely.

Besides supporting a general, qualitative principle about movement control, the data from the present experiment also allow for a relatively detailed model of the control of movement timing. The model likens the selection and control of an interresponse interval to the setting and running of a conventional alarm clock: First, the desired number, n, of clock pulses is selected (during the RT), and then the clock is allowed to produce the n pulses so that the first response is triggered at the time of the first pulse and the second response is triggered at the time of the nth pulse. The proposal that there is a clock-pulsing mechanism is motivated by the finding that the variance of the interresponse interval increased linearly with the interval mean, which is suggestive of a stochastic wait process (see Refs. 17 and 18) where

times between successive pulses fluctuate randomly about a mean and are stochastically independent. Through some algebra, it was seen that another factor contributing to the interval variance is the variance of N, which was seen to be proportional to the interval mean. The size of this proportionality factor was seen to depend on the slope of the linear function relating the interval variance and mean, and this slope was observed to differ in the relaxed and stringent conditions of the experiment. Having established the above relationships, it was observed that the mean RTs in the nonzero, finite-interval conditions were inversely related to the (predicted) variance of N. Then. through a curve-fitting procedure, it was seen that this relationship could account for almost 95 percent of the variance of the mean RTs in the nonzero finite-interval conditions. The inverse relationship between the mean RT and predicted variance of N can be explained by saying that it takes longer to select a particular value of N as the range of allowable values decreases. Such a relationship can be understood in statistical terms as reflecting a decreasing likelihood of selecting an allowable value of N as the range of allowable values of N decreases. If reselection of a value of N is required when an unallowable value has been picked, the average time to select an allowable value would vary in a way consistent with the mean RT results obtained here.

It is interesting to note that the physiological basis for an alarmclock system has been demonstrated. In the cortex of the cerebellum, rows of regularly spaced neurons known as Purkinje cells are connected to other neurons in such a way that the delay between the entry of a signal into the row and the exit of a signal from the row depends on which Purkinje cell is permitted to conduct the output signal. 20,21 The process of selectively permitting a given Purkinje cell to conduct an output signal on the basis of the delay that would occur prior to that output signal is physiologically analogous to the clock-setting process proposed here.

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