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Exploring the Functional Significance of Physiological Tremor: A Biospectroscopic Approach*

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Summary. The functional significance of physiological tremor – the high frequency (8–12 Hz), low amplitude oscillation that occurs during the maintenance of steady limb postures – is not known. Often tremor, perhaps because of its pathological manifestations, is considered a source of unwanted noise in the system, something to be damped out or controlled. An examination of the phase relationship between tremor and rapid voluntary finger movement in normal subjects suggests a very different view. In four experiments in which tremor displacement and accompanying electromyographic activity were simultaneously monitored, we show a clear and systematic relationship between tremor and movement initiation. Empirically obtained frequency distributions of tremor peak-to-movement initiation time were most closely aligned to a probability density function (derived via numerical integration techniques) that assumed movements were initiated when the muscle-joint system possessed peak momentum. This relationship – evaluated by Chi-square goodness-of-fit tests – was evident regardless of whether the movements were self-paced (Experiments 1 and 2) or in response to an auditory reaction time signal (Experiments 3 and 4). The addition of a load to the finger in Experiments 2 and 4, though tending to reduce tremor frequency, did not prove disruptive, nor did a fractionated reaction time analysis reveal any significant inertial contribution to the maintenance of the phase relationship. These data are consistent with an emerging view that the motor control system is sensitive to its own dynamics, and suggest that under certain conditions normal physiological tremor is a potentially exploitable oscillation intrinsic to the motor system.

Key words: Role of physiological tremor

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Introduction

Physiological tremor is a high frequency (in the 8–12 Hz range), low amplitude oscillation that occurs during the maintenance of steady limb postures. Although first described by Horsley and Schaffer in 1886, the origin and functional significance of "normal" tremor is still unclear today (Marsden 1978; Stein and Lee 1981). A number of candidates have been proposed as causes of tremor. One view is that tremor arises as a visco-mechanical property of each muscle load system (Randall 1973; Rietz and Stiles 1974). According to this hypothesis, normal tremor is thought to represent vibration caused by continuous broad frequency-band forcing of an underdamped, second order system at, or near, its natural frequency. Another possible source of tremor may be that produced by patterns of motoneuron discharge that occur when muscles contract (Sutton and Sykes 1967). These can be further separated into three basic categories: First, the inherent firing properties of motoneurons per se; second, an instability in the stretch reflex arc associated with synchronization of motoneuron discharge at 8–12 Hz; and third, supraspinal rhythmic input to motoneurons (cf. Marsden 1978, for review). Over the years some investigators have favored one source more than another. However, in spite of differences in emphasis, no single view as to the cause of physiological tremor has emerged, a view aptly summed up in Matthews and Muir's (1980) comment that: "After prolonged debate on the origins of physiological tremor, it is

becoming increasingly accepted that tremor in the 8–12 Hz range may result from a variety of interacting mechanisms, one or other of which may predominate under any particular condition" (p. 429).

The present paper is not concerned directly with the causes of tremor, but rather addresses an equally intriguing but less frequently considered problem. What role, if any, does tremor play in the initiation and control of movement? It is fair to say that the general consensus on this issue is that tremor is a source of unwanted noise, something to be controlled rather than exploited. Such a view is evident, for example, in a preface to a recent volume dedicated to understanding the mechanisms of physiological tremor. Tremor is deemed as ". . . not useful . . . to have tremor oscillations cannot help by themselves, even indirectly, to make the motor performance faster or better" (Desmedt 1978, p. vii). Consonant with this perspective, currently popular closed-loop, servomechanism models of motor behavior with their emphasis on set points and error correction processes consider oscillatory behavior a nuisance, an unwanted source of variability (e.g., Adams 1971).

On the other hand, the potential importance of oscillatory processes in motor control is suggested not only be recent (Delcomyn 1980; Grillner 1975; Shik and Orlovsky 1965, 1976; Stein 1976) and not so recent (Brown 1914; von Holst 1935/37, translated in von Holst 1973) empirical investigations in the physiology of movement, but also by theoretical work in the emerging field of physical biology. Iberall (1972), for example, has characterized biological systems as ensembles of coupled and mutually entrained oscillators; stable organization, according to Iberall's physical theory of homeokinesis, is a consequence of the interaction of oscillatory processes at all levels of the system. Cyclicity, in the homeokinetic view, is not some epiphenomenal property of biological systems; instead, all persistent, self-sustaining mechanisms (including living things) exhibited dynamic stability by virtue of nonlinear, limit cycle processes (cf. Iberall 1977; Soodak and Iberall 1978; Yates 1979; Yates et al. 1972). Rather than being viewed as an incidental aspect of biological systems, oscillatory behavior may be a central feature of their organization (Goodwin 1970).

The approach that we adopt to the problem of tremor in this paper is that of "biospectroscopy" – the identification of cyclicities and determination of their functional significance – advocated by homeokinetic theory (for particular application to motor control and coordination see Kugler et al. 1980, 1982; and for empirically related work see Kelso et al. 1980, 1981). If it is accepted that oscillation is a fundamental dynamic property of living systems, then it seems possible that tremor is present for a reason and that under certain conditions, humans may actually use tremor to enhance motor performance. From mechanics we know that a system in continuous oscillation provided with an appropriately phased forcing function requires less energy to move than a system in static equilibrium. Is it possible then, that a systematic phase relationship exists between the initiation of movement and physiological tremor? An early study by Travis (1929) hints strongly at such a possibility. Travis (1929) observed that a large proportion of upward movements were initiated during the ascending phase of tremor. Similarly, downward movements appeared to be produced during the descending phase of tremor. However, in order to examine the relationship (if indeed one exists) over a wider range of conditions, and to determine the locus on the tremor cycle around which voluntary movements may be initiated, a quantitative approach seems warranted.

In the present set of experiments, subjects were required to maintain a steady, stable position of the index finger while tremor and electromyographic activity from the primary extensor were simultaneously monitored. In Experiments 1 and 3, subjects initiated upward ballistic movements of the index finger in a self-paced manner, or under time stress conditions in response to an auditory stimulus. The time stress experiment (basically a simple reaction time situation) was included to determine if inducement to respond as quickly as possible would override the hypothesized phasing between movement onset and tremor. The self-paced and time-stressed paradigms were used in two further Experiments (2 and 4) in which a load was also added to the finger in order to increase the inertia of the muscle-joint system. By fractionating movement initiation time into its so-called premotor (latency of signal onset to EMG onset) and motor (latency of EMG onset to movement onset) components (cf. Botwinick and Thompson 1966; Weiss 1965) we sought to evaluate a possible inertial contribution to the phase relationship. That is, a relationship between peripheral motor time and movement initiation time would suggest that mechanical lag in the muscle-joint system contributes significantly to the phasing.

The Models

Four models were generated according to different assumptions about the time of voluntary movement initiation with respect to the physiological tremor cycle (measured as a peak-to-peak time interval). All the models used the conjoint distribution of tremor

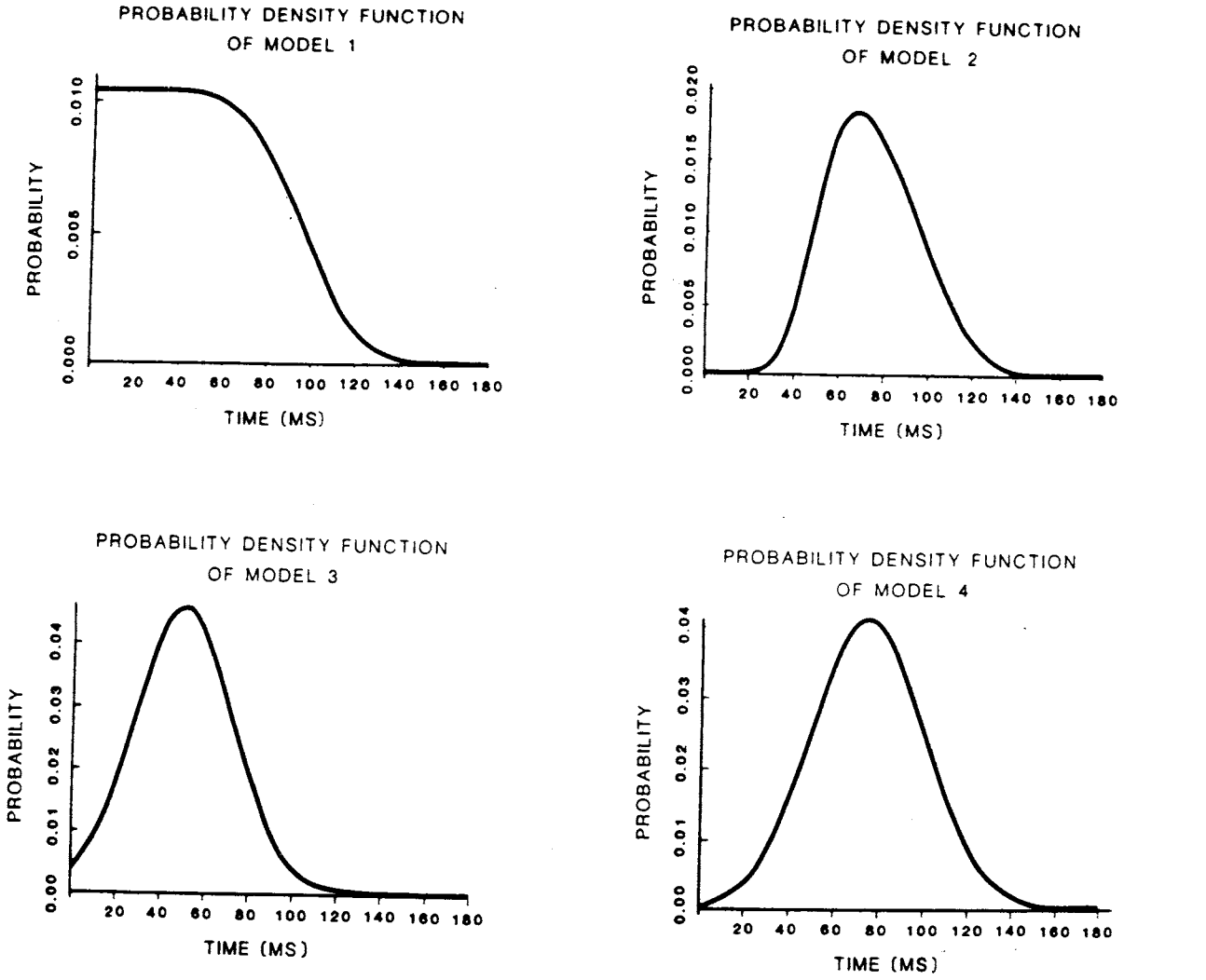

Fig. 1. Probability density functions derived from theoretical distributions based on different assumptions regarding the phase relationship between voluntary movement initiation and physiological tremor (see text and Appendix 1 for details)

peak-to-peak times and peak-to-movement initiation times to derive probability density functions for the latter. Numerical integration was used to compute the four theoretical distributions that were then compared to the actual distribution of peak-to-movement initiation times obtained from the data[1]. The details of the derivation of each model are provided in Appendix 1; Fig. 1 shows the actual theoretical distributions derived using a mean of 100 ms and standard deviation of 20 ms, as determined from pilot data.

Model 1 postulates no systematic relationship between the initiation of movement and physiological tremor. The probability of movement initiation is, therefore, uniformly distributed throughout the peak-to-peak interval, and may be described by the following probability density function:

$$f(y) = \int_{y}^{\infty} \left[\frac{1}{x} I_{[o,x](y)}\right]\left[\frac{1}{\sqrt{2\pi}\, S_x} \cdot \exp\left[-(x-\bar{x})^2/(2S_x^2)\right]\right] dx \qquad (1)$$

where x is a random normal variable of tremor peak-to-peak time, $\bar{x}$ is the sample mean, S_x^2 is the sample variance. y is a random variable defined as peak-to-movement initiation time, and $I_{[o,x](y)}$ is a rectangular function of area 1 (see Appendix 1).

1 It is important to note that the four theoretical models do not generally have solutions in closed form. Thus, numerical integration was used to evaluate the probability density functions. By taking discrete time slices from the density function it was possible to determine the number of movement initiations expected within any particular phase of the tremor cycle. The resultant distributions could then be compared directly with the data obtained from each of the experiments

Model 2 assumes that the initiation of upward movement is equally dispersed throughout the ascending phase of the tremor. Thus, the probability of movement initiation may be uniformly distributed throughout the ascending phase (from trough to peak), describable by the following probability density function:

$$f(y) = \int_{y}^{2y} \left[\frac{2}{x} I[\frac{1}{2}]_{x,x}](y)\right]\left[\frac{1}{\sqrt{2\pi}\,S_x} \cdot \exp\left[-(x-\bar{x})^2/(2S_x^2)\right]\right] dx \quad (2)$$

Model 3 assumes that the forcing function is applied when the muscle-joint system possesses maximum potential energy. Since the potential energy of an oscillatory system is proportional to its displacement, the point of maximum potential energy for an upward movement is at the trough of the tremor cycle. Hence the probability density function has the following form:

$$f(y) = \int_{x=y}^{\infty} \left[\frac{1}{\sqrt{2\pi}\,S_x} \cdot \exp\left[-(x-\bar{x})^2/(2S_x^2)\right]\right] \left[\frac{1}{\sqrt{2\pi}\,S_y} \cdot \exp\left[-(y-\bar{x}/2)^2/(2S_y^2)\right]\right] dx \quad (3)$$

Model 4 follows from a minimum energy hypothesis in which the forcing function is applied when the system possesses peak momentum. Since momentum is proportional to mass and velocity, and since mass is held constant in this case, the point of maximum momentum is at the inflection point of the upward phase of the tremor cycle. Therefore, the probability density function takes the following form:

$$f(y) = \int_{x=y}^{\infty} \left[\frac{1}{\sqrt{2\pi}\,S_x} \cdot \exp\left[-(x-\bar{x})^2/(2S_x^2)\right]\right] \left[\frac{1}{\sqrt{2\pi}\,S_Y} \cdot \exp\left[-(y-3\bar{x}/4)^2/(2S_y^2)\right]\right] dx \quad (4)$$

Methods

Subjects. Each experiment was limited to three subjects. The same three subjects produced movements under self-paced and time-stress conditions without a load (Experiments 1 and 3). Three different subjects performed under the same conditions with a load attached to the end of the finger (Experiments 2 and 4). The subjects were adult male volunteers who were not compensated for their participation. All subjects signed informed consent forms that described the experiments and any accompanying risks and benefits. Subjects were free to withdraw their participation at any point if they so chose.

Apparatus. A linear variable differential transducer (LVDT, Model PCA 116-100, Schaevita) 5.0 cm long by 2.1 cm in diameter, was mounted in an adjustable wooden arm such that the transducer was suspended over and above the extended finger of the subject. A 2.0 cm diameter wooden dowel served as a hand grasp and was mounted horizontally 7.6 cm above a standard height table, 12.7 cm from the table's leading edge and parallel to it.

The LVDT was coupled to an amplifier, and the resultant signal displayed on an oscilloscope and stored on FM tape. The transducer was able to detect movements as small as 0.025 mm, while the actual weight resting on the fingertip was approximately 10 g. An oscilloscope was positioned behind the table at eye level, directly in the field of vision of the subject. Two horizontal bars, centered 4 cm apart on the oscilloscope display screen served to define the acceptable field of movement. In Experiments 3 and 4 a Minisonalert (Mallory) was employed to generate an auditory stimulus. The Minisonalert was situated approximately 1 m in front of the subject and generated a high-pitched tone (approximately 2,900 Hz) for a duration of 8 ms upon switch closure by the experimenter. In Experiments 2 and 4 a 200 g metal disk (a 100 g disk was used by one of the subjects who had difficulty initiating movements with the heavier disk) of 4.2 cm diameter was taped under the distal phalangeal joint of the index finger. The load itself did not interfere with the range of motion.

Procedures. The same general procedure was employed in all four experiments. Specific procedures are detailed only insofar as they deviate from those described below. Bipolar, hooked-wire electrodes consisting of a pair of platinum-tungsten alloy wires (50 μm in diameter with isonel coating) were inserted into the extensor digitorum communis. After amplification and high-pass filtering at 80 Hz, the signals were recorded on a multichannel instrumentation tape along with the signal from the displacement transducer. The subject placed his right arm on the table, grasped the wooden dowel, then extended the right index finger and maintained it in a horizontal position. The wooden arm supporting the linear transducer was then adjusted so that the transducer was positioned directly above the center of the fingernail of the extended finger. The mid-range position of the finger was associated with a straight line tracing on the oscilloscope, centered between the two horizontal bars.

Each experiment proceeded through an initial practice session followed by the experimental session. The practice session consisted of as much time as needed for the subject to establish a sufficiently stable tremor to allow the recording session to proceed. The subject was instructed to watch the oscilloscope tracing and to maintain the position of the tracing between the two horizontal bars on the screen as well as possible. Approximately 10 min of practice were usually necessary. After making a rapid movement, the subject returned the finger to the mid-range position, held it stable for a short time and then repeated the sequence a total of 200 times. A 20 s rest was given after each set of ten trials and a 2 min rest after the 50th, 100th, 150th trials. The subject was permitted as much time as necessary to stabilize the finger between each trial and additional rest periods were taken as needed.

Data Analysis. An analogue to digital conversion was made by reading simultaneously from the displacement and EMG channels on the FM tape and saving the digital conversion in direct access files. Each signal was sampled at 5 kHz and low-pass filtered at the Nyquist limit. The displacement signal was downsampled and smoothed by means of a monotonic low-pass filter to remove frequencies over 30 Hz. The electromyographic signal, which was time locked to displacement, was rectified and integrated into 5 ms bins. A wave editing and display routine (WENDY; Szubowicz[2])

2 Szubowicz L (1977) A tutorial guide to WENDY: The Haskins wave editing and display system (unpubl. manuscript). Haskins Laboratories

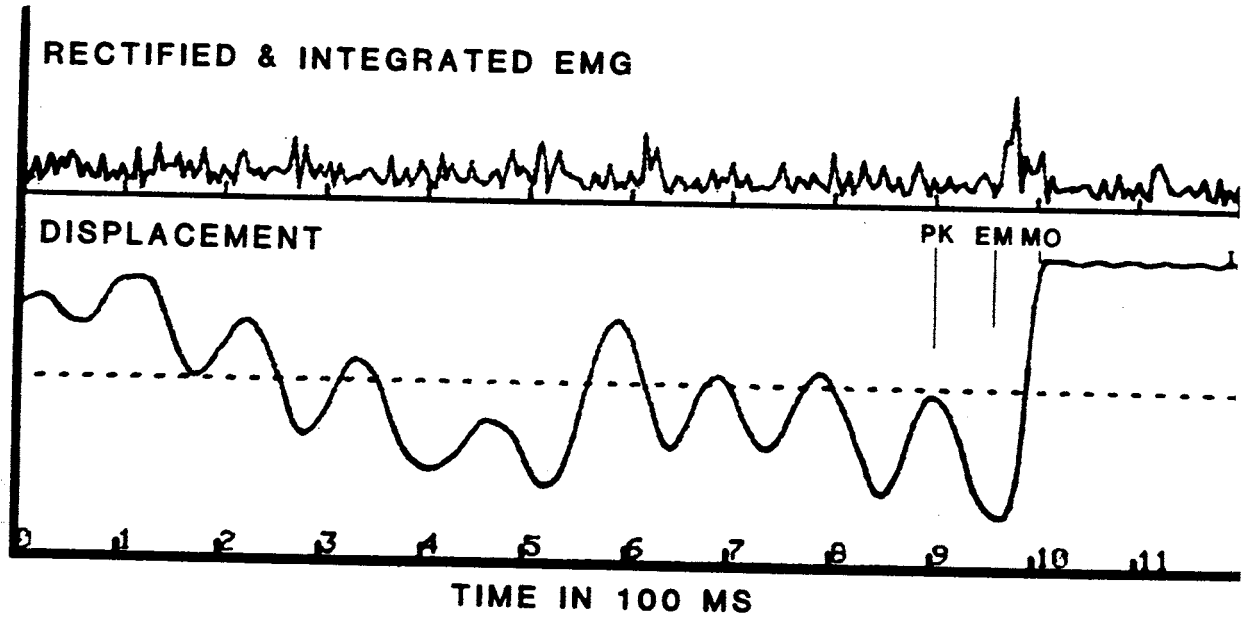

Fig. 2. Sample record of tremor displacement-time profile and associated rectified and integrated electromyographic activity from M. extensor digitorum communis. Marker labels defined as in text

was used to display and label each record as shown in Fig. 2. In Fig. 2, PK corresponds to the last clearly defined peak of tremor before the upward movement; MO indicates the time of movement onset, defined as the amplitude exceeding a predefined critical (or trigger) value[3]; and EM is the time of the first EMG activity associated with upward movement as indicated by the onset of the initial rise of activity on the rectified and integrated EMG record.

In addition, in Experiments 3 and 4, the onset of the auditory stimulus was labeled as RT. The latency from the signal to EMG onset allowed for the determination of so-called premotor time, and the latency of EMG onset to movement onset was indicative of the motor component of reaction time (cf. Botwinick and Thompson 1966; Weiss 1965).

Although each subject made 200 movements in each of the four experiments, the number of trials included in the final analysis was lower due to the rigorous conditions for retention of a trial. The most frequent reasons for rejection of a trial were either that there were not two clearly defined peaks of tremor just prior to movement initiation, or that the displacement record was out of range of the measuring instrument. A less frequent reason for rejection was that the EMG record was of poor quality. In addition, in Experiments 3 and 4, trials in which the reaction times were less than 70 ms or greater than 600 ms were rejected. This is a standard procedure used in reaction time studies to reduce the respective effects of anticipation and inattention (cf. Goodman and Kelso 1980).

In order to determine the best fitting theoretical distribution, a linear transformation was made so that the data could be collapsed over all subjects. Each individual subject's data were transformed such that the last peak-to-peak interval before movement onset (peak n-1) had a mean of 100 ms and standard deviation of 20 ms. The transformed data were then analyzed in a similar manner to the individual subject data to produce a frequency distribution, mean, and standard deviation. These resulting distributions for each of the four experiments were compared to the four theoretical distributions by means of Chi square goodness-of-fit test.

3 This point was chosen after much deliberation. The wandering nature of the tremor signal precludes an earlier point such as the dotted line shown in Fig. 2. Neither the first or second derivatives of the displacement signal proved helpful to indicate movement onset. The trigger value approach proved the best alternative, although it was always an overestimate (12 ms on the average)

Results and Discussion

Three aspects of the results are presented in turn. First, a reliability analysis on the measurements of interest is given followed by a summary analysis for all experiments. The last section deals with tests of the four theoretical models.

Reliability of Measures

We first conducted a reliability check on the main measures of interest, namely, the movement onset and the EMG onset. Every fourth trial of a randomly chosen subject's (S3) performance was measured a second time by a person not familiar with the purposes of the investigation. This second "measurer" was instructed to label each of the movement records given only the definition of each event as described in the previous section (i.e., PK, MO, and EM). These data were tabulated in the same manner

Table 1. Means (and SD) in ms for each of the subjects in the self-paced experiments

a) Experiment 1: Unloaded

Subject	Peak-to-peak time[a]	Peak-to-EMG onset[b]	Peak-to-movement onset
1	98.0 (20.1)	50.5 (24.7)	95.0 (26.8)
2	109.5 (14.0)	34.8 (29.8)	92.9 (27.7)
3	101.9 (18.1)	34.3 (26.3)	91.7 (26.7)

b) Experiment 2: Loaded

Subject	Peak-to-peak time	Peak-to-EMG onset	Peak-to-movement onset
4	170.1 (59.6)	59.1 (56.6)	146.8 (62.0)
5	112.5 (28.9)	32.5 (39.4)	102.9 (36.0)
6	208.1 (63.4)	62.0 (37.5)	107.7 (34.0)

[a] Interval between last two measured tremor peaks before movement onset
[b] As measured from rectified and integrated signal

as the originally measured data and were then correlated. For both movement onset and EMG onset the mean difference was within one bin width (5 ms). The reliability coefficient exceeded 0.90 for both dependent measures, a not unexpected result given the rigorous conditions for retention of a trial.

Self-Paced Experiments (1 and 2)

The results of the first two experiments involving self-paced movements with and without a load attached to the finger, are summarized in Table 1. Without loading, all subjects had a tremor rate ranging between 9.1 and 10.2 Hz, which is consistent with previous estimates (e.g. Rack 1978). The variability of the tremor cycle-to-cycle time in the unloaded condition was considerable, with an average standard deviation across subjects of 17.4 ms. As shown in Table 1a, the movement onset generally occurred in the last quarter of the tremor peak-to-peak cycle. It should be emphasized again, however, that the method of measuring movement onset time was necessarily a slight overestimate. The phasing of voluntary movement with the tremor cycle is evident in the examples of the raw data for self-paced,

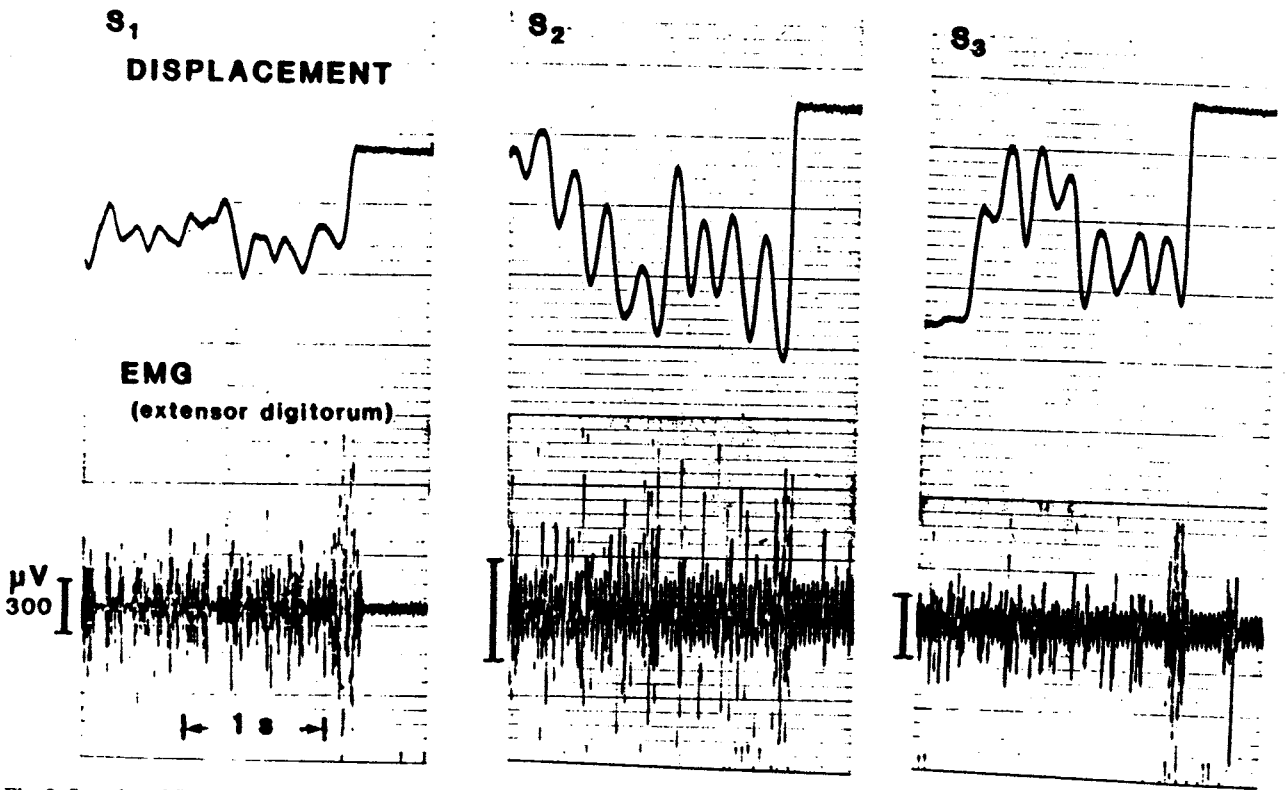

Fig. 3. Samples of finger displacement and raw EMG records (extensor digitorum communis) for each of the three subjects in Experiment 1. The movements were self-paced without a load added to the finger

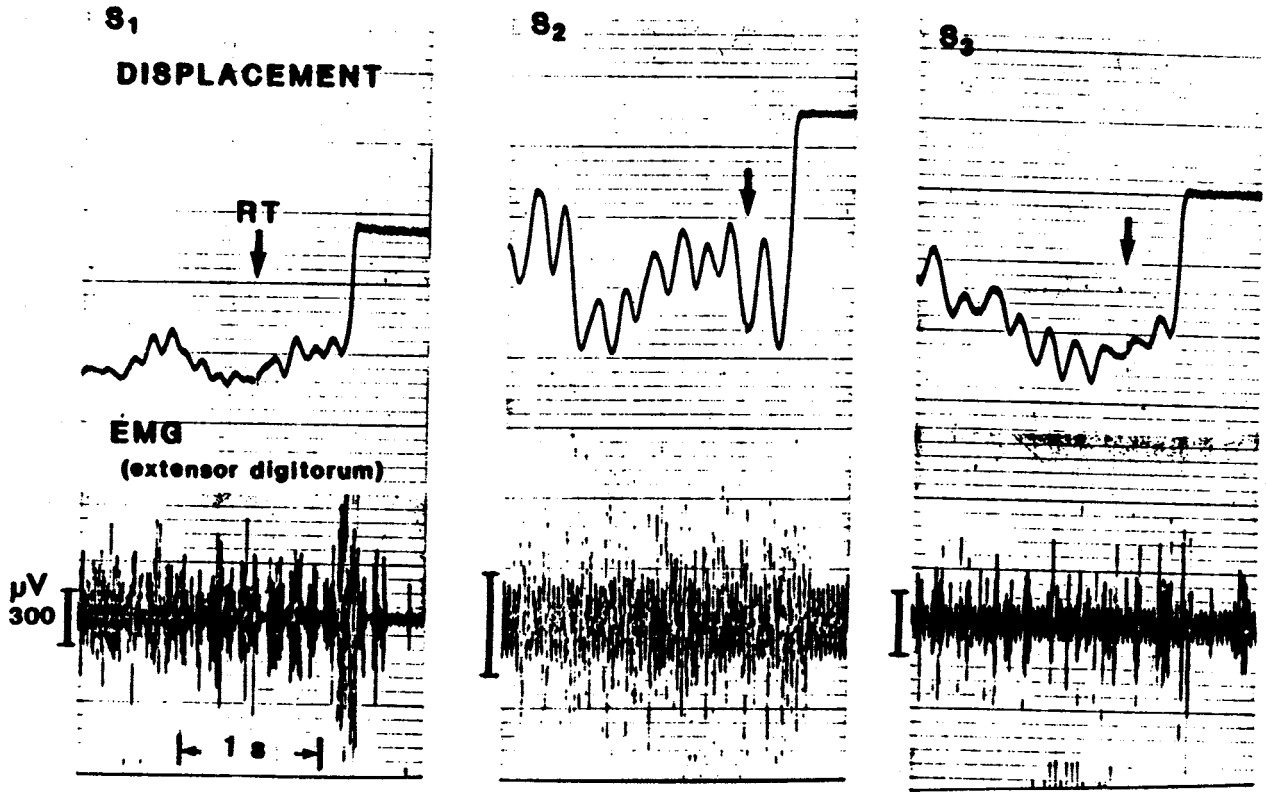

Fig. 4. Samples of finger displacement and raw EMG records (extensor digitorum communis) for each of the three subjects in Experiment 3. An auditory reaction time signal (RT in the figure) triggered subjects' movements which were produced without a load on the finger

unloaded movements shown in Fig. 3. The correlation between the onset of the rectified and integrated EMG signal and movement initiation, as defined here, was quite high (r = 0.84) and the average lag between these variables was 53 ms which is again consistent with other data (e.g., Desmedt and Godaux 1978).

Although cross-experimental comparisons are tenuous, it appears that the addition of load reduced the tremor rate in two of the subjects' data shown in Table 1b. The remaining subject (S5) had only a 100 g load attached to the finger, and his tremor rate was well within the bounds of normal physiological tremor. These data suggest that heavier loads are associated with reduced tremor rate, a notion that is consistent with other findings showing that increasing the moment of inertia of the vibrating part reduces frequency of oscillation (Stiles and Randall 1967). On the other hand, there are data showing no change in finger tremor rate with added mass of up to 100 g (Halliday and Redfearn 1956). Although the changes in tremor rate with loading were not a central aspect of the present work, they are interesting because they suggest that there may be a critical value of added mass below which tremor is unchanged and above which tremor exhibits a reduction due to visco-mechanical effects (cf. Rietz and Stiles 1974).

Time of peak-to-movement onset with respect to the tremor cycle of the loaded finger was similar to that observed under unloaded conditions for two of the subjects (S4 and S5). However, for S6, movements tended to be initiated around the midpoint of the cycle. The correlation between movement initiation and onset of EMG was again quite high (r = 0.88) with a lag time of 68 ms. This slight increase in lag time, compared to Experiment 1, is probably due to adding a load which tends to prolong the mechanical contractile latency of muscle (cf. Desmedt and Godaux 1978, for review).

Time-Stress Experiments (3 and 4)

In these Experiments subjects responded as quickly as possible to an auditory signal with (Experiment 4) and without (Experiment 3) a load attached to the finger. As shown in Table 2a, the tremor rate in Experiment 3 was similar to Experiment 1 (8.8–9.7 Hz), with an average standard deviation in periodicity of 18.4 ms. Movement onset occurred, as in the

Table 2. Means (and SD) in ms for each of the subjects in the time-stress experiments

a) Experiment 3: Reaction time, unloaded

Subject	Peak-to-peak-time[a]	Peak-to-EMG onset[b]	Peak-to-movement onset	Reaction time	Premotor time	Motor time
1	113.7 (21.2)	46.4 (30.8)	97.9 (27.4)	268.9 (55.7)	217.5 (50.9)	51.4 (17.8)
2	108.7 (15.5)	42.5 (25.2)	85.1 (49.9)	241.1 (53.0)	198.4 (50.9)	42.6 (11.2)
3	102.8 (18.6)	31.7 (19.7)	86.2 (18.9)	264.5 (35.2)	210.0 (35.4)	54.5 (8.7)

b) Experiment 4: Reaction time, loaded

Subject	Peak-to-peak time[a]	Peak-to-EMG onset[b]	Peak-to-movement onset	Reaction time	Premotor time	Motor time
4	155.6 (29.6)	15.3 (30.8)	95.8 (19.6)	298.6 (46.0)	218.1 (37.0)	80.6 (16.0)
5	107.5 (18.3)	4.5 (30.8)	95.3 (27.8)	287.6 (47.8)	196.8 (48.6)	90.8 (16.2)
6	127.6 (30.1)	69.0 (30.1)	110.3 (27.5)	206.5 (44.6)	165.3 (44.4)	41.3 (11.6)

[a] Interval between last two measured tremor peaks before movement onset
[b] As measured from rectified and integrated EMG

self-paced, unloaded experiment in the last quarter of the tremor cycle. Again, the phasing is evident in the examples of the raw data shown in Fig. 4.

The results of the fractionated reaction time analyses for unloaded and loaded experiments are also given in Tables 2a and 2b. The reaction time in Experiment 3 (Table 2a; mean = 258 ms) was highly correlated to premotor time (mean = 208 ms; r = 0.97) while uncorrelated with motor time (mean = 49 ms; $r < 0.01$). The partial correlation of motor time to total reaction time (with the variance of reaction time due to premotor time parceled out) was negligible ($r < 0.01$). This independence of premotor time and motor time ($r = -0.174$) is congruent with other data (e.g., Botwinick and Thompson 1966), which also showed little or no correlation between these variables.

The results of Experiment 4, in which subjects produced reaction-time movements under loaded conditions are given in Table 2b. Tremor rates remained somewhat slower than normal for two of the subjects although S6 actually showed an increase in tremor rate, 7.8 Hz, compared to self-paced conditions (compare Tables 1b and 2b). The relative time of movement onset with respect to the tremor cycle was in correspondence with the previous experiments. The results of the fractionated reaction time analysis revealed that reaction time (mean = 264 ms) was correlated to pre-motor time (mean = 193 ms, r = 0.94), and uncorrelated to motor time (mean = 71 ms, $r = -0.02$). As in Experiment 3, the partial correlation of motor time to total reaction time was negligible ($r < 0.01$). This result concurs with other work (e.g., Kamen 1980) which has found reaction time to be related to premotor time but not motor time in both unresisted and resisted cases.

Test of Models

The basic question of interest in all the experiments was the existence and nature of the phase relationship between the initiation of movement and physiological tremor. Analysis of each separate experiment produced a frequency distribution that allowed for a comparison with each of the four theoretical models. Thus, each experiment, while analyzed separately, was treated similarly with respect to the above question. The number of movement onsets within each 10 ms interval and the consequent frequency distributions generated are shown for each of the four experiments in Fig. 5. Table 3 gives the expected cumulative proportion for those same intervals, derived from each of the theoretical distributions,

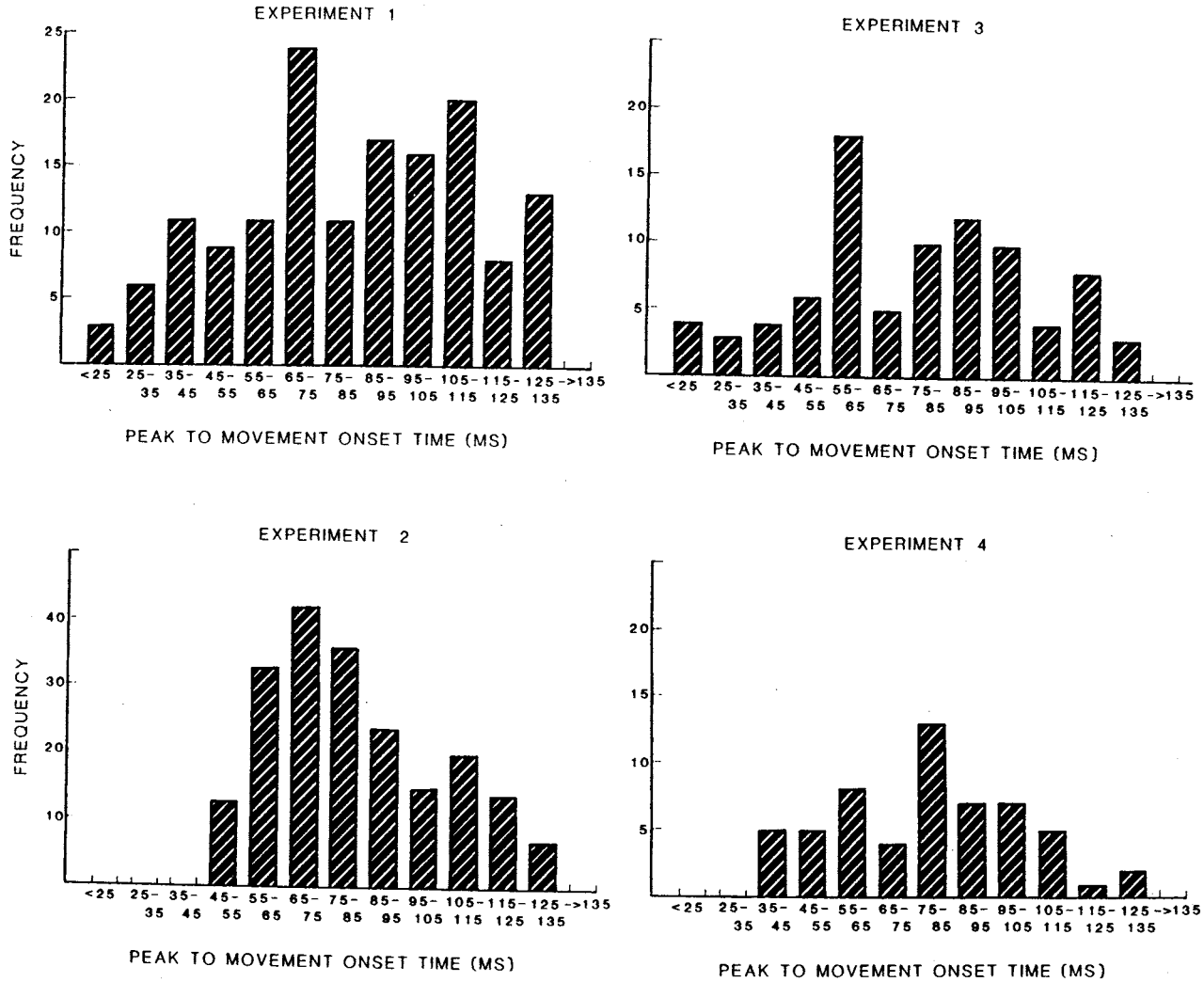

Fig. 5. Frequency distributions of transformed peak-to-movement initiation times for all four experiments. Experiments 1 and 3 correspond to self-paced and reaction time conditions for unloaded movements. Experiments 2 and 4 involve the same conditions but with a load attached to the finger

and Table 4 gives the actual cumulative proportion derived from each of the experiments. A summary table of Chi-square goodness-of-fit tests is presented in Table 5, and indicates a similar pattern for the four experiments. That is, the Chi square goodness of fit was smallest when the empirical distributions obtained from each of the four experiments were compared to the theoretical distribution of Model 4. This result alone suggests that the initiation of voluntary movement is not arbitrary with respect to tremor, but rather occurs systematically in phase with it.

Additional support for the foregoing claim is provided by the large Chi square obtained by comparing the empirical distributions to the theoretical distribution of Model 1. Had there been no relationship between movement initiation and physiological tremor, a model based on movements occurring with equal probability throughout the tremor cylce would have been supported. Such was not the case: in each experiment the resultant Chi square for Model 1 was approximately three times as large as the Chi square obtained for Model 4. Model 3 can also be rejected on these grounds for each of the experiments.

The distinction between Model 2, which postulates a simple phase relationship between movement initiation and physiological tremor, and Model 4, which postulates a more exact relationship between the two variables, is not quite as clear, particularly when the appendage was loaded (Experiments 2 and 4, see Table 5). However, in all cases Model 4 had a lower Chi square than Model 2 (sometimes by a

Table 3. Expected cumulative frequency (in %) for the four theoretical distributions

	Theoretical distribution derived from			
Frequency bounds (upper limit)	Model 1	Model 2	Model 3	Model 4
25	26	0	12	2
35	37	1	24	6
45	47	6	41	12
55	58	18	58	21
65	67	35	74	35
75	77	53	85	50
85	85	69	93	66
95	91	82	95	73
105	97	91	100	88
115	100	100	100	95
125	100	100	100	98
>125	100	100	100	100

Table 4. Actual cumulative frequency (in %) for the four experiments

	Actual distributions			
Frequency bounds (upper limit)	Exp 1	Exp 2	Exp 3	Exp 4
25	2	0	5	0
35	6	0	8	0
45	13	0	13	9
55	19	6	20	18
65	26	22	40	32
75	42	43	46	39
85	49	60	57	61
95	61	72	71	74
105	71	79	83	86
115	84	90	87	95
125	89	97	97	96
>125	100	100	100	100
N[a]	149	206	87	57

[a] Actual number of observations

factor of 3) and, therefore, appears to more likely candidate.

Neither is there evidence to support the notion that the phase relationship between physiological tremor and movement initiation breaks down when a premium is placed on responding quickly. In support of this claim are the small Chi squares obtained for Model 4 in both of the experiments requiring a speeded response (Experiments 3 and 4). Although in all experiments there was a small proportion of trials in which subjects initiated a response that was not in phase with the tremor cycle (as reflected in the tails of the distributions in Fig. 5), this proportion

Table 5. Chi-square goodness-of-fit tests (and degrees of freedom) between empirical distributions from the four experiments and the theoretical models

Experiment	Model 1	Model 2	Model 3	Model 4
1	262.6 (17)	196.0 (17)	566.2 (15)	65.6 (19)
2	297.1 (12)	104.7 (14)	553.4 (10)	67.5 (15)
3	111.4 (17)	113.0 (17)	155.8 (15)	38.4 (19)
4	79.4 (14)	20.3 (16)	118.2 (17)	18.7 (17)

remained relatively constant across experimental conditions.

In summary, the data from all four experiments show a strong tendency for upward ballistic movements to be initiated in the upward phase of the tremor cycle. Moreover, the point of initiation appears to be distributed around the point in the tremor cycle at which the muscle-joint system possesses peak momentum.

General Discussion

Sidestepping the question of tremor's origins the present experiments were directed to an issue of equal puzzlement to physiologists, namely, the functional significance, if any, of normal, physiological tremor. We hypothesized, on the basis of theoretical considerations (see Introduction) that tremor may be used as a type of background facilitation for voluntary movement. The four experiments reported here offer strong support for the notion that tremor is exploitable. In all the cases examined, we observed a systematic phase relationship between movement initiation and tremor.

The present results are consistent with a general theme that is only recently receiving its due notice; namely, that the motor control system is sensitive to its own physical dynamics and is capable of taking advantage of them (Cooke 1980; Greene 1972; Kelso 1981; Kelso and Holt 1980; Kelso et al. 1980; Kugler et al. 1980, 1982). With respect to the findings here, it is worth noting that kinetic energy is greatest around the point of maximum momentum in an oscillation. Thus, on mechanical grounds alone, it would be energy-efficient for voluntary movement initiation to be distributed around the point of peak momentum (maximum angular velocity). As pointed out some years ago by Greene (1972), the use of small, rapid oscillatory movements allows for graded ("proportional") control to be exerted by highly nonlinear and discontinuous systems. For example, a rapid fluctuating signal (or dither) added to a slowly varying control signal is often useful to overcome a

threshold or "unstick" friction. Tremor could play this role by keeping the system in motion so that inertia is minimized and velocity of reactivity enhanced.

That a highly evolved system may exploit an intrinsic oscillation for the purpose of reducing the energy demands associated with movement, is supported by studies that measure the energy requirements of sustaining sinusoidal movements of a limb. Rack and his colleagues coupled the elbow joint to a machine capable of driving the joint sinusoidally and found that below 6 Hz and above 13 Hz the machine had to do work to sustain the movement; however, between 6 and 13 Hz (peaking around 10 Hz) the limb actually did work on the machine (cf. Joyce et al. 1974). Thus, the amount of energy required to drive the limb at its natural resonant frequency (coinciding with tremor) was much less than at other frequencies (see Rack 1978, Figs. 4 and 5). Although Rack's findings are consistent with the present data and help to rationalize them, they do not address the issue germane to the present studies, viz., the phasing of volitional activity and tremor.

The results of the experiments reported here are particularly relevant to the work of a group of Russian investigators (cf. Aizerman and Andreeva 1968; Chernov 1968). In a series of studies this group provided qualitative evidence that when the arm is held in a particular position, opposing agonist-antagonist muscles alternately pull the arm one way and then the other, producing a "tremor" of about ten cycles per second. The EMG envelopes of both muscles were observed to display "peaks" that arose each time the absolute value of joint angle velocity reached a certain threshold value. These peaks alternate in that if at one moment the peak is large for the flexor and small for the extensor, the next time the threshold value is reached, a large peak is observed for the extensor and a small one for the flexor. In this way movements in one direction or another are associated with increases in the amplitude of the EMG tremor peak of the involved muscle. In Aizerman's model, the brain is envisioned as sending the same signals to each muscle contributing to the limb's movement at the tremor frequency, while prior adjustments in the interneuronal pools allow each muscle to respond by the appropriate amount.

Our findings fit rather well with Aizerman's "threshold" concept in which "splashes" of neuromuscular activity occur in relevant muscles when the joint reaches a critical angular velocity. Moreover, the idea that there may be critical values of certain system-sensitive parameters (or in the background state of interneuronal pools) that establish optimum conditions for control, receives support in larger scale activities such as human handwriting. In an elegant model of cursive handwriting that uses coupled oscillations in horizontal and vertical directions to produce letter forms, Hollerbach (1978) has shown that letter height modulation is best accomplished by altering acceleration amplitude at the vertical zero crossing. This point occurs at the top and bottom of letter corners and would be associated (roughly) with the onset of EMG activity observed in our experiments (but see Viviani and Terzuolo 1982, for an alternative to the oscillator view of handwriting).

The present data also offer an empirical basis for the recent speculations of Hallett et al. (1977) on Parkinson patients, that ". . . some of the delay in initiating movement in patients with tremor-at-rest might come from waiting to get into the correct time of the cycle' . . ." (p. 1133). Our results concur and suggest that the "correct time" may be distributed around a point at which it is physically advantageous to initiate movements.

From a broader theoretical perspective, it is worth noting that physical biologists have recently discounted static, snapshot views of biological systems, in which the methodology dictates that periodic events are ignored (see Iberall 1972; Katchalsky et al. 1974). For persistence of function, living system must conduct energy transactions in a cyclical manner if thermodynamic requirements are to be met. Such cycling is a general and inevitable consequence of the physics of open systems that undergo energy flux (Morowitz 1979). Moreover, fluctuations in a system, according to contemporary physical theory, are a necessary precondition for the evolution and maintenance of function (Iberall 1972, 1977, 1978; Prigogine 1980; Soodak and Iberall 1978).

Up to now, however, and possibly because of a preoccupation with pathological tremors, physiologists have tended to consider low-level fluctuations as unwanted sources of noise. Physiological tremor is hypothesized to occur "as a result of instability in the servomechanism associated with the spinal stretch reflex" (cf. Stein and Lee 1981). The emphasis on "instability" and on ways to reduce tremor oscillations may have led us to overlook the possible uses of tremor. Our results, of course, suggest that tremor does indeed play an important function. More generally, they underscore the potential significance of oscillatory processes in the initiation and control of movement.

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Appendix 1

Derivation of the Models

All four models assume that tremor peak-to-peak time is a random variable x, which is distributed normally with some mean μ_x and variance σ_x^2. Then:

$$x \sim \eta(\mu_x, \sigma_x^2)$$

and the density function of x, f(x) is described as:

$$f(x) = \frac{1}{\sqrt{2\pi}\, S_x} \cdot \exp\left[-(x-\bar{x})^2/(2S_x^2)\right]$$

where $\bar{x}$ is the sample mean; S_x^2 is the sample variance.
The rationale and test of this assumption is given in Goodman (1981).

Model 1. Let y be a random variable representing the peak-to-movement initiation time. This is distributed uniformly over the peak-to-peak interval x. The conditional density function of y given x, g(y|x) is described as:

$$g(y|x) = \frac{1}{x} I_{[o,x]}(y),$$

where $I_{[o,x]}(y)$, is a rectangular function such that $\int_o^x g(y|x)\, dy = 1$.

Hence the joint distribution of peak-to-peak times and peak-to-movement initiation times is:

$$h(y,x) = \left[\frac{1}{x} I_{[o,x]}(y)\right]\left[\frac{1}{\sqrt{2\pi}\, S_X} \cdot \exp\left[-(x-\bar{x})^2/(2S_x^2)\right]\right]$$

After integrating over the limits of x, the resultant probability density function of peak-to-movement initiation time, y, is that given in equation (1) of text.

Model 2. A similar argument follows for model 2, which assumes a uniform distribution of y in the ascending phase of the peak-to-peak interval x. g(y|x) is described as:

$$g(y|x) = \frac{2}{x} I\left[\frac{1}{2}{}_{x,x}\right](y)$$

Hence the conjoint distribution of tremor peak-to-peak times and peak-to-peak-movement initiation times is distributed as:

$$h(y,x) = \left[\frac{2}{x} I\left[\frac{1}{2}{}_{x,x}\right](y)\right]\left[\frac{1}{\sqrt{2\pi}\, S_x} \cdot \exp\left[-(x-\bar{x})^2/(2S_x^2)\right]\right]$$

By integrating over the limits of x, the probability density function of peak-to-movement initiation time, y, given in equation (2) of text results.

Model 3. In model 3, y is a random normal variable distributed about $\bar{x}/2$. g(y|x) is then described as:

$$g(y|x) = \frac{1}{\sqrt{2\pi}\, S_y} \cdot \exp\left[-(y-\bar{x}/2)^2/(2S_y^2)\right]$$

Hence the conjoint distribution of tremor peak-to-peak times and peak-to-movement initiation times is distributed as:

$$h(y,x) = \left[\frac{1}{\sqrt{2\pi}\, S_x} \cdot \exp\left[-(x-\bar{x})^2/(2S_x^2)\right]\right] \left[\frac{1}{\sqrt{2\pi}\, S_y} \cdot \exp\left[-(y-\bar{x}/2)^2/(2S_y^2)\right]\right]$$

Model 4. In model 4, y is a random normal variable distributed about $3\bar{x}/4$. g(y|x) is then described as:

$$g(y|x) = \frac{1}{\sqrt{2\pi}\, S_y} \cdot \exp\left[-(y-3\bar{x}/4)^2/(2S_y^2)\right]$$

Hence the conjoint distribution of tremor peak-to-peak times and peak-to-movement initiation times is given as:

$$h(y,x) = \left[\frac{1}{\sqrt{2\pi}\, S_x} \cdot \exp\left[-(x-\bar{x})^2/(2S_x^2)\right]\right] \left[\frac{1}{\sqrt{2\pi}\, S_y} \cdot \exp\left[-(y-3\bar{x}/4)^2/(2S_y^2)\right]\right]$$

By integrating over the limits of x, the probability density function of peak-to-movement initiation time, y, given in equation (4) of text results.

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