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Time control of hand movements

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Introduction

The time control of self-initiated voluntary limb movements is more difficult to assess than that in the oculomotor system, where saccadic and pursuit eye movements are regarded as products of two independent control systems. The different velocities of the two types of eye movement depend on vestibular and visual inputs as well as on movement amplitude. In contrast to these different types of eye movements, velocity control in the skeletal motor system is continuous, so that limb muscles can produce movements resembling the pursuit or saccadic type of eye movements. In spite of this continuum of possible performances, it is a widely held view that in the skeletal motor system ballistic and ramp movements represent different categories. Ballistic movements have been defined as being too short to allow sensory feedback to alter their execution. Therefore, one could compare ballistic with saccadic and ramp with pursuit movements. Such a comparison would be based on their different velocities and on the different role of sensory information for the motor performance.

A difficulty in a comparative analysis of time control in the two systems lies in their different accessibility to examination. Eye movements can be examined in response to visual and vestibular inputs and described in terms of input-output relationships. In reflex studies this is also possible for limb movements. However, the wide range of input variables and of possible performances of limb movements makes it difficult to explore the control strategies relevant for their performance.

Rapid isometric contractions

Freund and Büdingen (1978) studied the fastest possible self-paced isometric contractions because their velocity control is not subject to voluntary modification with respect to further increase. They represent the simplest motor performance not complicated by mechanical factors or the demands of sensory control. This allows the examination of the extent to which the limitation of speed is due to the motor program, the neural code or the contractile apparatus. These experiments showed for the isometric contractions that for a given muscle and subject the time to peak of the fastest voluntary contractions was approximately the same no matter how large the amplitude. This was achieved by a linear increase in the rate of rise of tension with force. In this respect the fastest possible voluntary contractions showed the same properties as those seen in muscle twitches elicited by single electric shocks applied to the muscle nerve. The times to peak of the fastest voluntary contractions were only slightly longer than those of the electrical twitch contractions (Miller et al., 1981).

Comparing different muscles showed a linear relationship between the amplitude-independent times to peak and the percentage of type I fibres of the muscle examined (Hefter et al., 1983). This correlation was shown for both electrical and voluntary contractions. The linear relation between force and rate of rise of tension constituting the basis for the amplitude-independent contraction times is therefore due to neuromuscular properties. Such a type of organization provides the simplest operational mechanism for the time control of synergistic movements: the synergistic muscles engaged in a motor act such as catching a ball can all start their contractions at the same time, irrespective of their relative force contributions.

Isotonic movements and sensory control

Isotonic movements show an increase of the time to peak with increasing amplitude. The slope of this increase depends on the mass to be moved: the increase in time can be manipulated by adding loads to the moving parts. The difference between isotonic movements and isometric contractions simply reflects Newtonian mechanics because the calculation of movement time requires 2-fold integration of acceleration.

A further factor augmenting movement or contraction times is sensory guidance. If the fastest voluntary contractions or movements are examined under target conditions requiring sensory guidance the situation is different. According to Fitts' law (1954), the duration of the fastest possible movements increases with the ratio of target size to amplitude of movement. The finer the adjustment required, the slower the movement.

Serial movements

If one considers repetitive movements instead of single movements and examines how fast they can be performed, the results are usually described in terms of frequency of movement reversals per second. As a psychological standard this is called motility. Such rapid repetitive movements are employed in a variety of everyday or artistic activities, such as stroking, typing, writing, pencil-shading or playing a musical instrument. The first measurements of the highest possible motility scores during key pressing lay between 8–9.3/sec (Ream, 1922). It is astonishing that despite a revived interest in motor physiology, psychology, psychophysics and motor control theory very little is known about this capacity. For musical instruments the fastest finger movements during the vibrato are performed at rates between 5–7.1/sec (Schlapp, 1973). For the piano Adams (1976) quotes an anecdote by Lashley (1951) that a pianist can move the fingers at a rate of 16/sec. The highest motility scores in musical performance seem to lie somewhere in the range between 5.5–16/sec. Nothing quantitative is known about interindividual differences and the effects of training.

We have recently conducted a systematic study of the highest motility scores that can be achieved by normal subjects for a few simple alternating movements and isometric contractions (Hefter, H., Hoemburg, V. and Freund, H.-J., unpublished data). The goal of this investigation was not only to find the highest motility scores for the different conditions tested, but also the mechanisms limiting the performance. The subjects were asked to perform an alternating finger movement starting from a slow alternating extension-flexion movement executed with the extended forefinger, and then to execute this movement at successively faster rates until the fastest possible performance was reached. The second instruction was to keep the amplitude of the movement as large as possible. Fig. 1 shows a typical amplitude-frequency relationship obtained from a normal subject. The full amplitude can only be maintained up to a rate of ≈2 Hz and

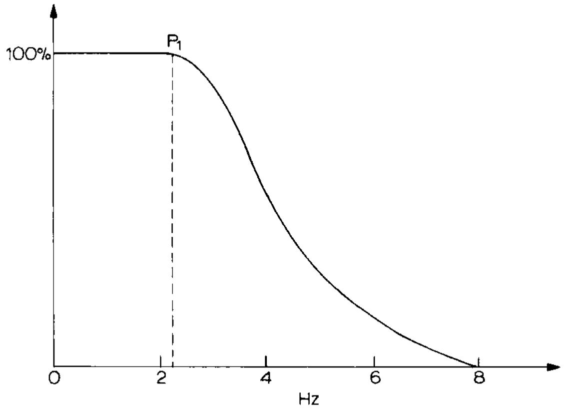

Fig. 1. Amplitude-frequency relationship of serial finger movements. Amplitude (ordinate) was measured by goniometer while the subject successively increased the rate of alternating movements trying to keep the amplitude maximal. Amplitude decreases at frequencies higher than 2 Hz (P_1).

then declines on to the highest frequency, at around 8 Hz. The decrease of amplitude with increasing frequencies was mainly the consequence of mechanical damping by means of subtraction of counteractive forces generated by the antagonistic muscles. When a similar paradigm was examined for an isometric condition, where the forefinger was fixed to a ring and the produced strength recorded by a strain gauge, a similar curve was obtained. As long as small masses have to be moved, the difference between the isotonic and isometric condition is small. This changes for larger masses, but also for different muscle groups. The turning point (P_1) of the frequency-amplitude relationship, from which onwards the amplitude decreases, is different for different muscle groups and subjects. The same is true for the maximum frequency that can be produced. As in the case of the fastest single contractions, the major determinant is the fibre-type composition of the muscles involved.

Due to their small amplitudes the fastest possible alternating movements performed voluntarily have a tremulous character. The highest possible motility scores are closely related to the peak frequency of isometric force tremor and for body parts with a small mass, such as the fingers, also to the rate of position tremor. The similarity between the fastest voluntary and involuntary movements has already been noted in a study in which the vibrato produced by a violinist had a similar frequency to that of the violinist's finger tremor (Schlapp, 1973). It is further illustrated by the fact that the decrease in tremor rate in pathological conditions is associated with a corresponding decrease in motility scores (Hefter et al., 1983).

The EMG during rapid alternating movements shows an antagonistic pattern similar to that in tremor records. At slower repetition rates (below P_1) a different EMG pattern can be observed. It is the typical triphasic pattern seen in rapid single movements. This triphasic pattern reflects the biomechanical demands of moving parts, and therefore is less pronounced or absent during small-amplitude finger movements or isometric contractions. If the triphasic pattern is employed at repetition rates below P_1, the subject follows a strategy of a succession of single rapid movements with a ramp-plateau type of pattern. If the subject wants to produce a smoother sinusoidal movement at the same rate, the alternating pattern will be employed instead. Therefore, at rates slower than P_1 the subject can choose between the single move strategy associated with the triphasic burst pattern and the alternating mode, depending on the intended action. Above P_1 it is no longer possible to employ the first strategy. The decrease in amplitude demonstrates that this is due to the damping properties of the moved parts. The movement initiated by the activity of the agonistic muscles does not reach full amplitude because the antagonist activity starts too early, so that the movement in the opposite direction commences before the maximum is reached. For this reason the activation of the antagonist as a breaking mechanism is not necessary. For finger and, similarly, for hand movements the range between P_1 and maximum frequency lies between 2 and 6–12 Hz. This is the range of restrained capacity of movement performance where full amplitude movements cannot be produced.

The isochrony principle

A large number of automized everyday performances of the hand and fingers are characterized by rapid, repetitive small-amplitude movements. These movements are usually performed at frequencies higher than P_1, so that they already fall into the range of reduced amplitudes. Their temporal organization follows a similar principle to that described for the fastest voluntary isometric contractions: the time of performance is approximately constant. This had already been noticed by Katz (1948) and was recently found to apply for a wide range of manual performances. Variation of the size of letters by a factor of 5 did not change their execution time (Katz, 1948). Enoka (1983) observed that the duration of the first component of a weightlifting movement did not vary with amplitude. The tangential velocity of a pen's tip was found to be closely related to the total linear extent

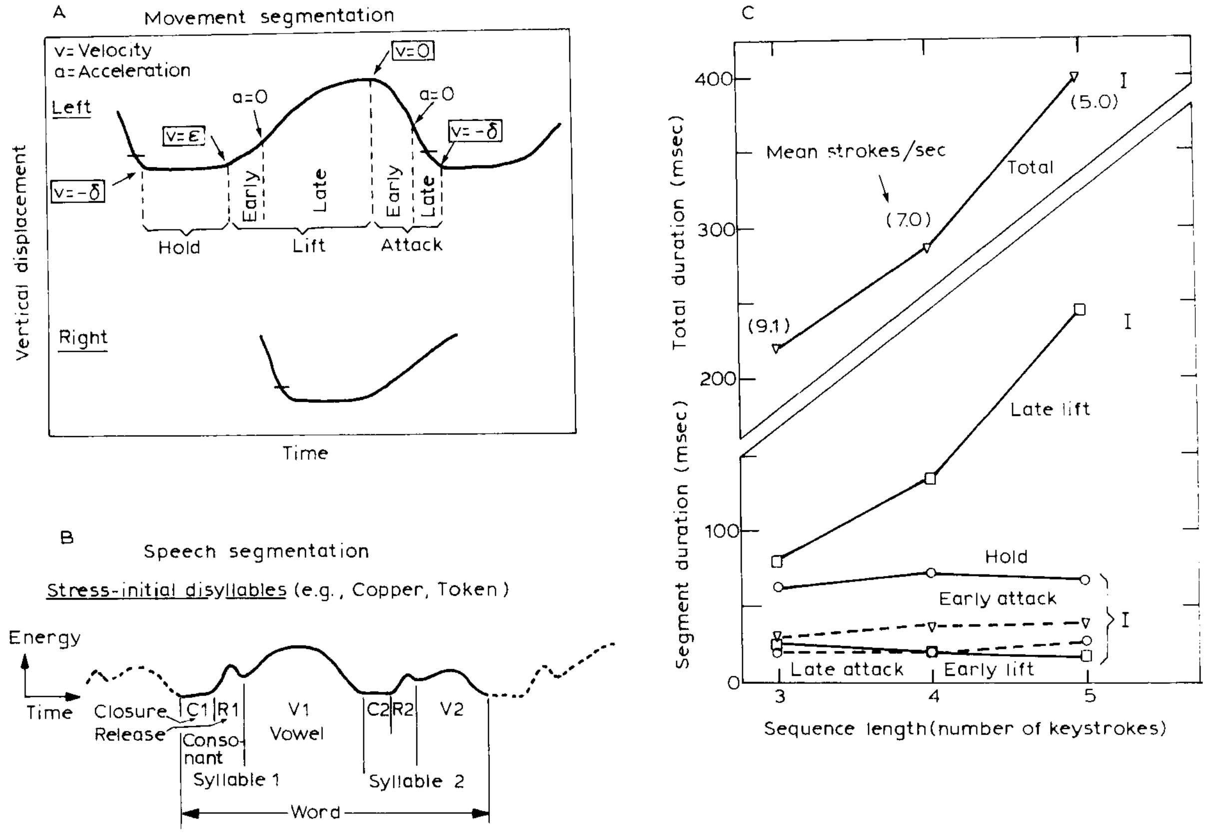

Fig. 2. Segmentation (A) of a finger trajectory during rapid typing and (B) of speech for a two-syllable word. The influence of sequence length on the duration of each segment of the finger movement is shown in C. Only the late lift phase showed major variation with sequence length. For the two-syllable word only the final, second vowel was length dependent. From Sternberg et al. (1984).

of the trajectory, keeping the execution time independent of movement size, even for complex trajectories (Viviani and Terzuolo, 1980). This relationship was found to apply to the linear extent of one cycle of movement as well as to the whole performance. These observations led Viviani and Terzuolo (1980) to formulate isochrony as a general principle in movement control. Similar observations have been made on the basis of experiments on the control of rapid action sequences in speech and typing (Sternberg et al., 1984). For typing they constructed a finger-trajectory apparatus and segmented the finger trajectory as illustrated in Fig. 2. The examination of the influence of sequence length on finger movement showed that the late lift segment was the only one revealing any substantial effect of sequence length. This was interpreted as reflecting that the control system must gain access to the next subprogram before the attack, fitting in with the idea of a retrieval process that is temporally discrete. A comparable segmentation of two-syllable spoken words into six segments also showed that all these time segments remained unaltered when the number of words was varied between two and five. Only the final, second vowel of the second syllable was length dependent. Sternberg et al. (1984) regarded this as evidence for the advanced planning of whole sequences. Their model employs an action unit containing several actions that are executed as part of the same unit, thus supporting the hypothesis of hierarchical control in the execution of two classes of rapid-action sequences. These experiments revealed that this type of time control operates at a fairly general level.

Eye-hand interaction

Although the interaction between eye and hand has been of some importance for human development it is astonishing how little is known about this issue. With respect to the temporal characteristics of eye movements, it is known that the eye will follow moving targets by means of smooth pursuit eye movements up to frequencies around 1 Hz. Further increase in frequency is associated with an increasing number of sacadic eye movements, until the ocular tracking stops completely at frequencies exceeding 2 Hz (Von Noorden and Mackensen, 1962; Mather and Putchat, 1983; Leist et al., 1986). This does not change significantly if active movements of the own hand or finger are pursued instead of an external object, although the accuracy of the tracking may improve (Mather and Putchat, 1983). The fastest hand or finger movements that can be produced lie in the range between 6–12 Hz. Hand and finger movements faster than 2 Hz are frequently employed in everyday activities. Since the eye will not pursue objects moving at frequencies above 2 Hz, these rapid hand and finger movements will not be followed by the eyes. As known from the high velocities that can be employed by the oculomotor system this limitation is not due to the motor side. This is illustrated by the ability to perform sinusoidal eye movements up to frequencies around 6–8 Hz, when the vestibulo-ocular reflex is brought into play by shaking the head as fast as possible while fixating the finger (Atkin and Bender, 1968). Leist et al. (1986) have explained the inability of the eyes to track at frequencies exceeding 2 Hz by the failure to see the target at faster frequencies even when a combination of saccades and smooth movements is used. Calculating the time spent in eye movement at 2 Hz and assuming that 20° saccades have durations between 50–60 mseconds, then 4 saccades/sec need 200–250 mseconds. This leaves less than 200 mseconds for each period of fixation, which is too short for visual perception because of the visual blanking by post-saccadic suppression. Therefore, Leist et al. arrived at the conclusion that the limitation of oculomotor tracking to frequencies below 2 Hz is visual rather than motor in nature.

Plotting the amplitude-frequency relationship for the eye movements in the same way as shown for the hand performance in Fig. 1 reveals that the larger part of the frequency range of human hand movements cannot be controlled by the eye (Fig. 3). Therefore, fast moving target and hand movements cannot be foveated. What the eye can do instead is a 'Ganzfeld-Kontrolle' (whole field control). In the context of this chapter I would like to call this control mode 'range control'. As obvious from everyday experience, the range of pencil-shading or handwriting, activities commonly executed at rates faster than 2 Hz, can be controlled well with fixed gaze, so that one can write within a demarcated area. These considerations are approximate and only valid for smooth regular movements. Grossly irregular movements may be different, because they contain a spectrum of different frequencies.

Another modality which is of major significance for the control of hand movements is somatosensory information gained from the hand. The hand is a somatosensory sense organ used for object manipulation. Tactual scanning has been compared

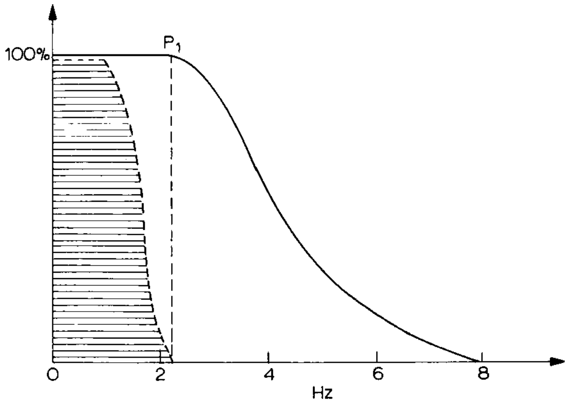

Fig. 3. Amplitude-frequency relationship of serial finger movements as shown in Fig. 1 (solid line) and of eye movements (dashed line), measured while the subject was trying to watch his moving finger.

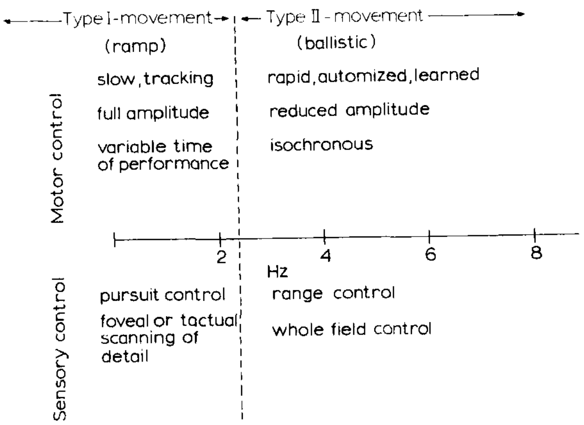

Fig. 4. Schematic illustration of the major differences between slow and rapid hand movements.

with visual scanning (Gibson, 1962), and it was assumed that the scanning procedures are closely similar for the eye and hand, as there is a high precision in cross-modal matching between the visual and somatosensory modalities. The speed of the exploratory movements of the hand is, to my knowledge, not known quantitatively. Watching the action of hand and fingers during tactile prehension and exploration of objects gives the impression that such movements are slow rather than fast. Therefore, it may be tentatively suggested that the sensory guidance of hand and finger movements, no matter whether visual, somatosensory, or both, will be restricted to the range of slower movements.

Conclusions

Two modes of eye-hand interaction

The analysis of the temporal characteristics of hand movements shows a continuum of possible performances between very slow and brisk. On the basis of the evidence discussed so far, I would like to propose a model of sensory motor interaction which is based on the temporal characteristics of eye and hand movements. This model is schematically represented in Fig. 4 and consists of two classes of hand movements:

1. Type I movements: slower movements; if repetitive, below 1–2 Hz. These movements can be executed under sensory guidance based on pursuit, foveal control or on tactual scanning.
2. Type II movements: rapid single or serial movements; if repetitive, commonly performed at rates above 2 Hz. They include many skilled and learned movements. The time of their individual performance is independent of amplitude for the usual operational range. This provides the basis for a stable relationship between the spatial and temporal code addressing fixed times to the formation of distinct trajectories or action units. This may be an important determinant for motor learning. These movements can be sensory controlled but the type of sensory control is a range control rather than a fine, foveal pursuit control mode, as employed in the sensory guided movements.

The eye also employs two modes of operation when interacting with the hand: 1. Smooth pursuit eye movements used for the sensory guidance of the slower hand movements. 2. Range control — with the eyes watching the range of performance — for the fast, learned, skilled hand movements.

This concept provides a new quantitative and qualitative basis for the old idea of separating ballistic movements from ramp movements. Ballistic movements have been regarded as movements that are terminated before sensory feedback can come into action, and therefore were referred to as single rather than repetitive movements. The term ballistic was frequently under attack because of its vague definition with respect to its temporal limits and to the continuous transition from ballistic to ramp movements.

A distinction between the two types of hand movement as shown in Fig. 4 is based on different mechanisms and operational strategies and can be applied to single as well as repetitive, serial movements. In contrast to the concept of ballistic movements, type II movements frequently are performed under sensory control, but this is a whole field, a range control rather than a pursuit foveation of detail. This type of sensory control can set the border conditions and control them. Therefore, the performance of learned movements may or may not be subject to sensory range control. What is impossible is foveation or precise tactual scanning.

The two types of hand movement have both different sensory control modes and different motor capacities. Although the latter are not as different as in the oculomotor system, the slower, type I movements belong to that range of motor control that allows full amplitude performance, employment of triphasic or alternating EMG patterns in antagonistic muscles, and the generation of motor patterns is variable in time. In contrast, the type II movements cannot reach full amplitude, cannot be generated as a sequence of single movements with triphasic patterns and their execution time is amplitude independent, allowing for invariant timing in the production of motor patterns.

There is not yet enough information about the actual extent of the frequency range to which isochrony applies. The examples given so far were all rapid performances. The relation between isochrony and motor learning and their frequent association with fast motor acts remains the subject of future research. Why is it so difficult, or sometimes impossible, to reproduce the typical features of one of the best learned movements, one's own signature, at very low speed? On the other hand, a pianist can play a learned musical sequence at slow as well as at high speed.

With respect to nomenclature, the term 'ballistic' seems difficult to adapt for rapid serial movements such as writing. Since 'saccadic' would not be suitable for a fast limb movement, the most adequate terms would possibly be those reflecting their different functional role, such as sensory guided slower and intrinsically patterned faster movements. Since no single term defines the sets of properties shown in Fig. 4 unambiguously, the designation of the functional categories as type I and type II movements may be the clearest one.

As compared with the smooth pursuit and the saccadic eye movements, there are more differences than similarities. The engagement of smooth pursuit or type I movements in sensory guidance of eye or hand is similar. However, almost everything else is different, including their functional context. Moving the eye back to a new fixation point has nothing to do with the rapid production of learned motor patterns. This differs as soon as the interaction between eye and hand comes into play. Then, the perceptive and executive aspects show astonishing mutually adaptive control modes underlying the type of sensory-motor organization illustrated in Fig. 4. Not only sensory control — pursuit or range — is different but also the characteristics of the movement as listed in this figure. A closer understanding of the mechanisms underlying the matching of certain temporal demands for perception and motor control is an intriguing problem for future research.

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