

## The Relationship between Speed and Amplitude of the Fastest Voluntary Contractions of Human Arm Muscles\*

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**Summary.** The relationship between the speed of the fastest possible voluntary contractions and their amplitude was examined for several hand- and forearm muscles under isometric and isotonic conditions.

The consistent finding was the amplitude dependence of the speed of the fastest voluntary efforts: the larger the amplitude, the faster the contraction. The increase of the rate of rise of isometric tension or of the velocity of isotonic movements with rising amplitude was linear. The slope of this relationship was the same for three different hand- and forearm muscles examined.

The duration of the contractions measured from onset to peak was approximately constant for all amplitudes. The duration of the EMG-burst recorded from the contracting muscle was similar as the time from onset to peak of the contraction.

These results show that the skeleto-motor speed control system operates by adjusting the velocity of a contraction to its amplitude in such a way that the contraction time remains approximately constant. It is suggested that this type of speed control is a necessary requirement for the synchrony of synergistic muscle contractions.

**Key words:** Voluntary contractions – Speed control – Synergistic innervation – Open-loop movements

In the oculomotor system, saccadic and pursuit movements are regarded as products of independent control systems. In the skeleto-motor system there is no counterpart for this type of organization. Limb muscles can produce movements resembling the saccadic or the pursuit type. Since these can be transformed voluntarily and gradually into each other they should be considered as merely representing varieties along a continuum of possible performances.

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This is not the case in the oculomotor system where the different velocities of the two types of movements depend upon visual and vestibular inputs but can not be influenced voluntarily.

This difference in the voluntary control of eye and limb movements is the reason for their different accessibility to systems analysis. The study of input-output relationships has been proven to be a powerful approach for the investigation of the oculomotor system. Its application for the examination of limb movements is restricted to reflex studies. It is therefore difficult to extend the analysis of *voluntary* contractions beyond a purely descriptive level.

One possibility to escape this difficulty is the examination of self-initiated contractions whose performance is limited by the properties of the system. We have chosen such an experimental condition by studying the fastest possible voluntary contractions of human hand- and forearm muscles. These contractions are not the subject of voluntary modification with respect to further increase of velocity. It is therefore possible to investigate to what extent the limitation of their velocity is neural or mechanical in nature.

Our experiments show that the speed of the fastest voluntary contractions is not limited by mechanical factors but is adjusted by the central program to keep their rise time approximately constant no matter how strong they are. This organization is different from the oculomotor system where saccade duration increases linearly with amplitude (Robinson, 1964). The independence of the time of contraction of skeletal muscles from the final force level or angle of movement is regarded as representing a necessary condition for the synchrony of synergistic muscle action. The central regulation of maximum contraction velocity reveals the preservation of this principle for the fastest motor performances.

## Methods

### *Instructions and Experimental Procedure*

Experiments were performed on six healthy male volunteers aged from 24–40 years. One of them was left handed. Subjects sat in a comfortable chair with arm rests. A large screen digital oscilloscope (Omniskop EM 541 Elema Schonander, 12" videotube) was used for the display of the visual clues for their motor tasks. Two sets of experiments were performed: For the first, the subjects were instructed to perform isometric contractions or isotonic movements as fast as possible. The strength or angle of these contractions was not prescribed for the single trial but could be freely varied between very weak and the strongest possible contractions for the isometric, and between the smallest and largest angle movements for the isotonic condition. Isometric and isotonic contractions were examined at different sessions.

In a second set of experiments, the subjects had to achieve a given target level as fast as possible. The target force or angle was continuously displayed by one trace on the oscilloscope 10 cm above a second trace indicating the zero level for the force or movement recording. The task was to move the lower trace towards the upper as fast as possible and with an accuracy of 10% of the target range. The distance between these two traces on the oscilloscope was kept constant throughout all experiments.

The subjects were given a practise sequence to allow them to familiarize themselves with the system before starting the test sequence. In the target condition the tension was varied in 8 steps between 5 and 100% maximal voluntary contraction and the angle in 6 steps. Each experimental session included one of the four experiments on voluntary contractions (target and non-target

condition for both, isometric and isotonic contractions). The minimum interval between two subsequent trials was  $> 30$  sec. The entire experiment spread over a period of 1 week. No fatigue with respect to maximum velocity or force was observed throughout the experiment.

For three target levels, a sample of 20 contraction curves was recorded at each tension or angle. Their amplitudes were in every case distributed normally about their mean value and the variance of the distribution was small ( $< 10\%$  of the contraction in the successive trials). The mean values of the same experiment repeated at different days showed no significant differences.

#### *Recording System: Tension Recording*

Tension was measured with a d.c. strain gauge bridge whose working range was 0–10 kg. The strain gauge could be rigidly mounted to either the medial, upper or lower aspect of the proximal phalanx of the forefinger for tension recording from the first dorsal interosseus/adductor pollicis, extensor or flexor indicis muscle respectively. For tension recording, the arm lay comfortable on the arm rest. The hand was fixed on the support for the strain gauge by rigid bands. The forefinger of the right hand was inserted into the hole of a plastic block which was attached to the strain gauge. The hole was adjusted by screws to enclose the finger firmly so that the tension recording was virtually isometric. This arrangement was thus different from that used in previous experiments (Freund et al., 1975; Büdingen and Freund, 1976). The output of the strain gauge was fed into a d.c. amplifier which was connected to the oscilloscope.

For the measurement of isotonic movements of the forefinger the arm and/or hand was inserted into a rigid plastic sleeve preventing any movements of the elbow and/or hand. The angle of the movement of the hand- or forefinger was measured by means of an angular position transducer centered to the wrist or proximal phalangeal joint representing the axis of rotation. For isotonic movements, only flexion and extension of the forefinger were measured. The experimental zero position of the finger was  $20^\circ$  flexion.

Isometric tension of isotonic movement were displayed on the digital oscilloscope in front of the subject.

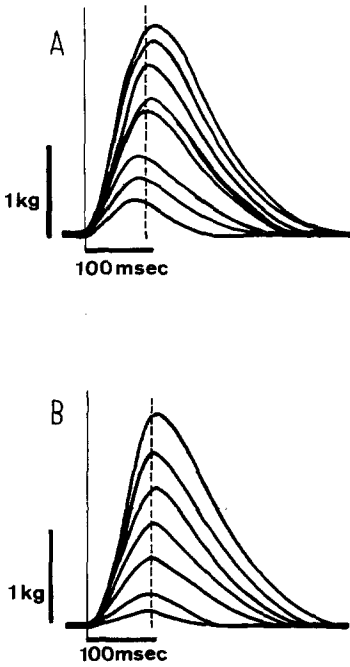
For measurement the force or movement records were fed to a digital oscilloscope (Nicolet 1090,  $100 \times 80$  mm). High gain a.-c. coupled force or displacement records were used for triggering. The midsignal trigger mode provided full display of the onset of the contractions. All records could be plotted on an X.-Y. plotter.

## **Results**

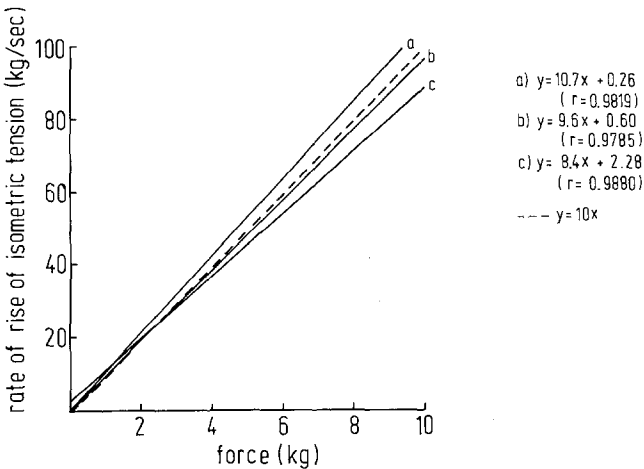
### *The Dependence of the Maximal Rate of Rise of Tension on the Strength of Contraction*

The fastest possible voluntary isometric contractions of the extensor indicis muscle (I) are shown for “free” contractions (non-target condition; see methods) in Figure 1A for 8 different force levels. The maximal voluntary contraction in this subject was 2.3 kg (upper curve) so that the contractions shown cover the whole force range of that muscle. The consistent result was the steep increase of the rate of rise of tension (RRT) at successively stronger contractions. The time between the onset and the peak of the contractions showed a slight increase with increasing amplitude.

In the target condition, in which the subjects had to achieve a given target force level as fast as possible, a similar increase of RRT with amplitude was observed (Fig. 1B). The time of the contraction remained approximately constant irrespective of its amplitude. The small variations between the contractions of different amplitude did not exceed the variance between successive trials at the same force level.

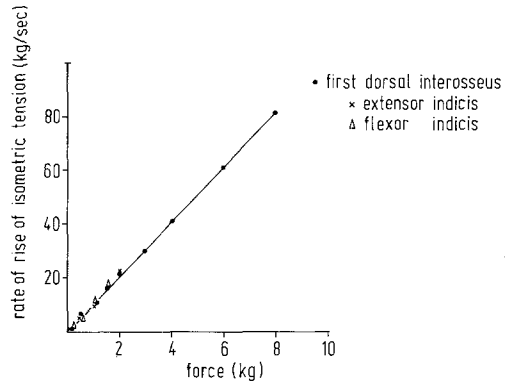


**Fig. 1.** The fastest voluntary isometric contractions of the extensor indicis muscle are shown for free (non-target) contractions in **A** and for target directed contractions in **B**. The dashed line represents the mean contraction time for each sample



**Fig. 2.** Dependence of the rate of rise of tension of the fastest possible voluntary target directed isometric contractions on the peak force level. The regression lines calculated for the experimental values obtained from the first dorsal interosseus/adductor pollicis muscles of three subjects are labelled a-c. The regression equations are given to the right of the diagram. Dashed line: theoretical regression line for a contraction time of 100 msec (see text). The rate of rise of tension was calculated for the time from onset to peak of the contraction

**Fig. 3.** Rate of rise of tension of the fastest possible voluntary target directed isometric contractions plotted against the peak force level for three different muscles: first dorsal interosseus adductor pollicis, extensor and flexor indicis



The mean contraction times of the two samples are indicated by the dashed lines in Figure 1A and B. They were  $88.3 \pm 11.7$  msec for the non-target condition and  $92.8 \pm 4.9$  msec for the target condition. This difference is not statistically significant.

In the target condition the increase of RRT associated with increasing strength of contraction is plotted in Figure 2 for 3 different subjects (a–c). The RRT was calculated for the entire contraction measured from onset to peak. The full lines are the regression lines for the values obtained for the first dorsal interosseus/adductor pollicis muscles. As revealed by the correlation coefficients, the relationship is strongly linear. Because  $RRT = \frac{f}{t}$ , a linear correlation implies that the time of the contraction remains constant:

$$\frac{f}{t} = mf + c.$$

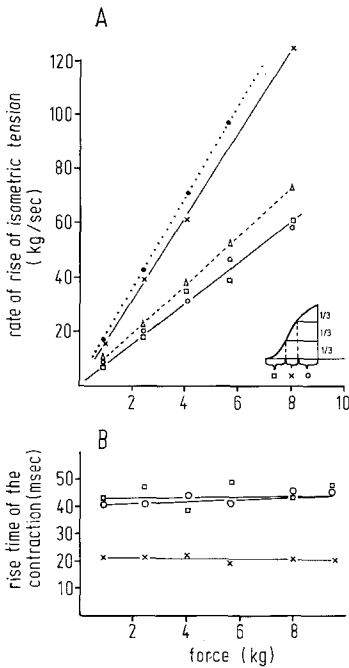
where  $f$  = isometric force and  $t$  = time.

In the case of  $m = 10$  and  $c = 0$  (dashed line),  $t = \frac{1}{10}$  sec. The values for the three regression lines (a–c) are close to this contraction time.

In the non-target condition the relationship is not linear, because the small amplitude contractions are slightly faster than in the target condition. The additional time necessary for precise target acquisition of smaller contractions was, however, very small (cf. Fig. 1A and B).

### *Comparison between Different Muscles*

The comparison between the RRT-force relationship of three different muscles of the right hand- and forearm of one subject is shown in Figure 3 for the target condition. Experiments on each muscle were performed on different days. All muscles acted on the same finger. The different force range of the three muscles can be seen from the different extent of the symbols along the regression line. In this case, each symbol represents mean values of 10 successive contractions. All three muscles show the same RRT-force relationship. This result was confirmed by experiments on the other subjects.



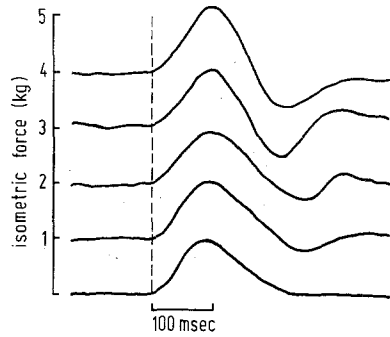
**Fig. 4.** **A** Dependence of the rate of rise of tension on target force calculated for different fractions of the contraction curve. □, × and ○ are the values calculated for each third of the peak amplitude as illustrated by the insert. The triangles represent the rate of rise calculated for the whole contraction curve and the dots the maximum rate measured from the peak of the differentiated curves. The time needed for each third is plotted in **B**

As a consequence, the rise time of the fastest possible contractions is the same for these three muscles. Since the force range of the muscles is quite different this indicates that the RRT of the muscles depends on the absolute force level. In one subject tentative experiments were performed on the calf muscles. The task was to extend the foot as fast as possible. The contraction times were also in the 80–90 msec range.

#### *Comparison between Different Parts of the Contraction Curve*

For larger rapid positional movements it has frequently been recognized that different stages can be distinguished. The distinction between a fast distance – covering and a slow homing-on-target phase has been made by Annett et al. (1958) and Welford et al. (1969). Because the initial part of the curve is as different from the steep rising slope as is the target acquisition portion we have measured the time needed to accomplish these different parts separately. For this purpose the amplitude of the isometric contractions of the first dorsal interosseus/adductor pollicis muscles of one subject (target condition) was subdivided into thirds (see insert Fig. 4A) and the average RRT was calculated for each of these segments (Fig. 4A). In addition, the time needed for each third was measured (Fig. 4B). The results show that for both the initial and terminal third about 40 msec are needed, no matter how strong the contractions are whereas the middle third takes about 20 msec. Correspondingly the RRT

**Fig. 5.** The fastest possible isometric contractions of the first dorsal interosseus/adductor pollicis muscles starting from 5 different force levels which were maintained 10 sec prior to the rapid contractions. The task was to increase force by 1 kg as fast as possible at each force level



calculated for the first and last third have similar values but are about twice as fast for the middle third (Fig. 4A). For comparison, the maximal rate of rise of tension measured from the peak of the differentiated curve ( $RRT_{MAX}$ ) is illustrated by the dotted line and the RRT calculated for the whole contraction by the dashed line. The slope  $RRT_{MAX} : f$  is 18, the contraction time calculated from this value 55 msec. This would represent the contraction time if the contraction would consist solely of its steepest part.

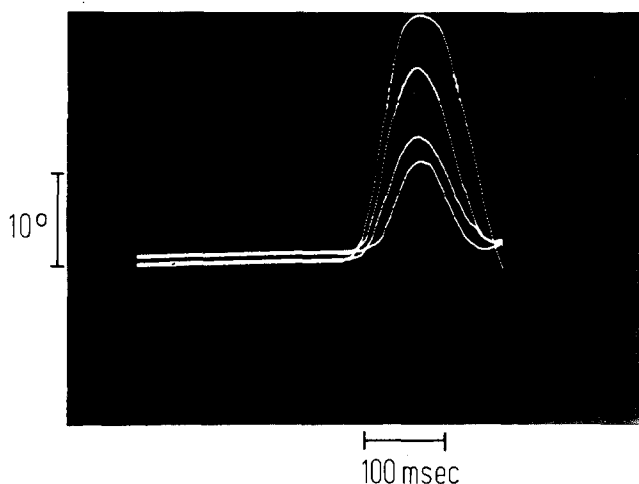
#### *The Influence of Stationary Contractions of Different Strength Maintained Prior to the Rapid Contractions*

In the experiments reported so far, the contractions always started from zero force. In the experiment shown in Figure 5 the subjects were asked to maintain a steady force level 10 sec prior to the phasic contraction. The task was to increase each of the five force levels by 1 kg as fast as possible.

The RRT and the time of contraction are similar at all force levels so that both parameters are independent of the force exerted prior to a rapid contraction.

#### *The Dependence of the Speed of Isotonic Movements on Their Amplitude*

If the maximal speed of isotonic movements was examined, analogous to the isometric contractions, a similar dependence on amplitude was observed as for the RRT. Figure 6 shows a typical sample of curves obtained for finger flexion in the target condition. Target directed movements required approximately the same time no matter how large the angle of movement. Non-target movements showed a similar small increase of the time between onset and peak of the movement with increasing amplitude as was observed for the isometric contractions. The mean values were  $84 \pm 3.6$  msec for the target and  $76 \pm 10.7$  msec for the non-target condition. Comparing isotonic movements and isometric contractions the time from onset to peak was similar in the two conditions.



**Fig. 6.** The fastest possible isotonic hand movements (flexion) plotted for different angles

As in the isometric condition, extension and flexion of the forefinger had similar contraction times. The mean values for the target condition were  $84 \pm 3.6$  msec for finger flexion and  $81.3 \pm 2.8$  msec for finger extension. These differences were not statistically significant.

#### *The Relationship between the Electrical and Mechanical Events during Rapid Contractions or Movements*

The electromyographic activity of the contracting muscle was recorded by surface electrodes. Its relation to the isometric contraction is shown in Figure 7 for the extensor indicis muscle. The duration of the EMG burst was the same as the duration of the contraction (80 msec). The same relationship was seen in the case of isotonic movements. More extensive and quantitative results on the correlation between the electrical and mechanical aspects of ballistic contractions will be reported in a subsequent article.

Simultaneous recordings from both the agonist and antagonistic muscles showed an almost synchronous activation. This is shown in Figure 8 for the surface recordings from the flexor and extensor muscle during an isotonic flexion of the hand. The same coactivation was found during finger movements or isometric contractions. Needle recordings confirmed that the activity was actually recorded from the antagonistic muscles. A fast extension of the hand produced a similar pattern as shown in Figure 8. Qualitatively, the two movements could not be distinguished from each other by inspection of the EMG pattern. This co-activation was found for both target and free movements. This illustrates how difficult the correlation between peripheral and central neuronal units may be when rapid movements are investigated. During slower alternating movements, the usual antagonistic innervation pattern was seen in the two muscle groups.



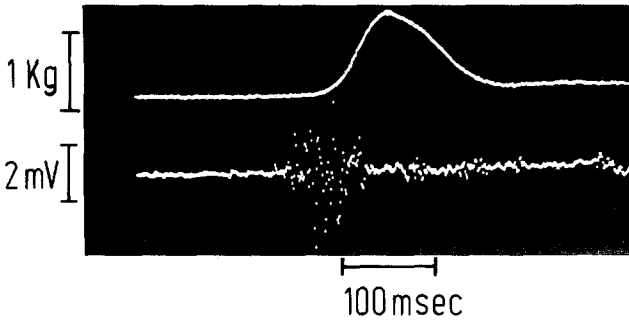


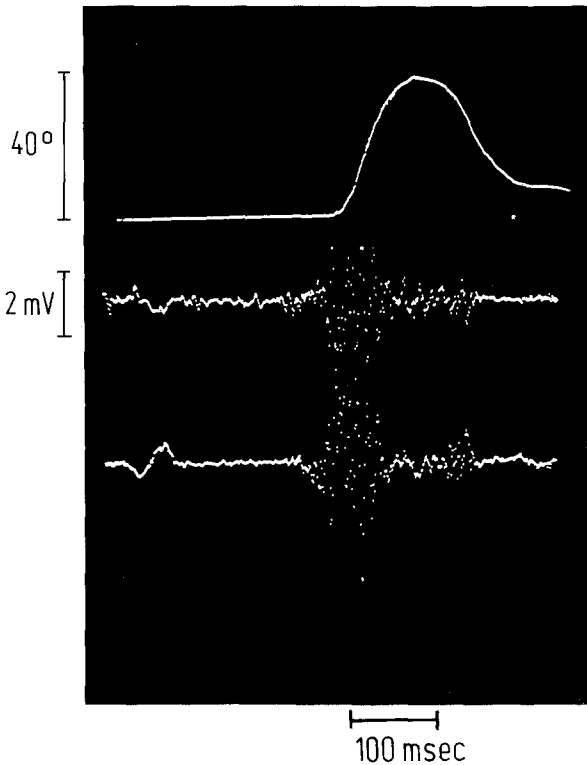
Fig. 7. Rapid isometric contraction of the extensor indicis muscle. Force record and EMG activity

## Discussion

The consistent result of this study was that the rise time of the fastest goal directed voluntary contractions is approximately the same no matter how strong they are or what angle they cover. This is achieved by a linear increase of the rate of rise of tension with increasing amplitude for the isometric and of the velocity of the movement for the isotonic condition. The speed control system therefore operates by amplitude dependent regulation of contraction velocity so that the contraction time remains constant.

It has already been noticed from previous experimental studies on skilled movements that in many voluntary motor acts the subjects varied the speed of movement with amplitude to keep the duration relatively constant (Searle and Taylor, 1948; Taylor and Birmingham, 1948; Annett et al., 1958; Johns and Draper, 1964). Similar observations were made by Katz (1948) when measuring the time required for automatic fast writing movements of different amplitude. In these experiments, variation of the height of the letters by a factor of five did not change the duration for the performance of each letter and word significantly. The time needed for one letter was 210–300 msec so that these movements can be regarded as ballistic movements. These observations were all made on ballistic movements of less than half a second duration. It is therefore suggested that this type of regulation is not only characteristic of the fastest but also of somewhat slower movements as long as they are still ballistic. The term ballistic movement was originally used for a certain type of pathological movements in extrapyramidal motor disorders. According to present convention is also used for a category of preprogrammed open-loop movements whose execution ends before they can be modified by sensory- or feedback information. This type of movement is frequently used in every day life and fundamental for skilled motor performances, in particular for the primate hand.

The speed control system can only operate in the way described if the fastest contractions are not limited mechanically by properties of the muscle fibres. Otherwise the large amplitude contractions could not be performed many times



**Fig. 8.** Rapid isotonic movement (flexion) of the hand (upper trace). The EMG activities of the extensor (middle trace) and flexor muscles (lower trace) are shown below the movement record

as fast as small amplitude contractions. The amplitude dependent variation of the speed of muscle contractions must therefore be achieved by neural commands. The neuronal mechanisms for speed regulation are changes in recruitment and firing rate. For rapid contractions recruitment will not participate in speed regulation, because the motor units of a muscle are recruited almost simultaneously (Büdingen and Freund, 1976). The variation of the speed of rapid contractions will therefore depend on changes in firing rates.

In stimulation experiments on cat muscles the rates necessary to produce the fastest isometric contractions are considerably higher than those to achieve maximum force (Cooper and Eccles, 1930; Buller and Lewis, 1965). The same observation has been made for electrical stimulation of a human muscle (Merton, 1954). In the cat experiments the optimal stimulus interval was close to the absolute refractory period. The plateau of the active state in the sarcomeres was estimated to be below 3.3 msec for cat soleus muscle (Buller and Lewis, 1965). The highest motor unit firing rates reported during rapid voluntary contractions of human muscles were 120–150/sec (Marsden et al., 1971). Our measurements confirm that the firing rates do not exceed 150/sec during the fastest voluntary contractions

(unpublished observations). The firing rates during voluntary contractions in humans are therefore considerably below the optimal stimulus rates for electrical stimulation of cat muscles.

The neural parameter determining the time of contraction or movement is the duration of the EMG burst. It is therefore suggested that the neural mechanisms underlying the achievement of an approximately constant contraction time by amplitude dependent variation of the speed of contraction are constant burst duration and modulation of spike density.

According to Kornhuber's hypothesis (1971), the correct timing of the burst duration is accomplished by the cerebellar cortex. This is in agreement with the experimental results of Conrad and Brooks (1974) who found that the program for generating the correct amount of force for the correct amount of time was disturbed after dentate cooling. On the other hand, the impairment of the generation of accurate ballistic actions has been found to represent the basic defect in Parkinsonian movements but was not present in patients with intention tremor (Flowers, 1975, 1976). This favours the view that various parts of the motor system contribute to the elaboration of the central program for ballistic movements.

The type of organization described is clearly different from the oculomotor system, where the amplitude of the saccades depends on the duration of the oculomotor discharge (Fuchs and Luschei, 1970; Robinson, 1970; Schiller, 1970). This difference between the two systems can not be attributed to the different mechanical conditions of eye and limb movements because the speed regulation is the same for isometric and isotonic contractions. If the skeleto-motor system would be organized in a manner similar to the oculomotor system the extent of the most rapid limb movements would depend on their duration. Because almost all limb movements need co-contractions of several synergistic muscles, this would imply that all the muscles participating in synergistic movements with different effort would have to start contracting at different times. This would demand very complicated motor programs for sequential innervation of synergistic muscles. A much easier way to match the requirements of the limb muscles is to make velocity the regulated variable determined by contraction amplitude instead of duration. In this case, the peak of the contraction can always be achieved by all the muscles at the same time no matter how much they contribute.

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