SEPARATION OF THE CONTRIBUTIONS OF VOLUN- TARY AND VIBRATORY ACTIVATION OF MOTOR UNITS IN MAN BY CROSS-CORRELOGRAMS

Keidai Hirayama*, Saburo Homma*, Muneaki Mizote*,
Yasuo Nakajima*, and Shiro Watanabe**

Department of Physiology, School of Medicine, Chiba University, Chiba
**Department of Physiology, School of Medicine, Kyohrin University,
Mitaka-shi, Tokyo, Japan

Summary The relationship between vibration and human motor unit spikes elicited by reflex and voluntary actions was studied by means of cross-correlograms. Using this method motor unit spikes could be classified into two categories, locked spikes with good correlation to vibratory frequency and unlocked ones with poor correlation to vibratory frequency.

1. Inter-spike intervals of the locked spikes were integer multiples of the cyclic time of the vibration used. This suggests that the locked spikes are elicited by the firing of α-motoneurons that are activated by mono-synaptic transmission of Ia vibratory afferents.

2. Locked spikes are only elicited immediately after vibratory application. Spike frequency soon attains its maximum and frequency plateau level is then maintained.

3. Unlocked spikes are slow in appearance and a gradual increase of their spike frequency is a characteristic feature. Increase of the total motor unit spike frequency is therefore attained by the recruitment of unlocked spikes even without apparent increase in the frequency of the locked spikes. This mechanism is held to explain the gradual incre- ment of the tonic vibration reflex activity.

4. It is suggested on the basis of previous work (Homma and Kanda, 1973) that polysynaptic transmission caused by sustained Ia vibratory afferent activity elicits a slowly increasing EPSP which is directly respon- sible for the unlocked spikes.

5. Vibration superposed upon a voluntary effort elicits a considerable increase of locked spikes. These may be the sum of motor unit spikes activated by vibratory Ia impulses and other Ia impulses whose firing had become locked to the vibratory stimuli though originally driven by the

gamma loop mobilized by voluntary command.

6. It is thus maintained that the unlocked spikes are elicited either by direct voluntary α-activation or by the polysynaptic slowly rising EPSP.

7. Data collected in the present study revealed that the ratio between unlocked and γ-loop driven spikes was 1:2.4. Since alpha-gamma linkage characterises voluntary command, an α–γ co-activation ratio of 1/2.4 in a light voluntary contraction suggests that under the circumstances indirect loop-activation would be dominant.

Tonic muscle contraction can be observed during vibratory stimulation of the human muscles (SUZUKI, 1961; DE GAIL et al., 1966; HAGBARTH and EKLUND, 1966b; RUSHWORTH and YOUNG, 1966). Owing to the reflex nature of this contraction it has been called "tonic vibration reflex, TVR" (HAGBARTH and EKLUND, 1966a). Non-sequential inter-spike interval histogram tests of the motor unit spikes during the reflex revealed several peaks which are separated by a virtually fixed fraction of the cyclic time of the vibration used (HOMMA et al., 1971a, b). The relationship between firing frequency of an arbitrary motor unit (M_f) and the vibratory frequency (V_f) could be expressed by the equation.

$$M_f = \frac{1}{n} V_f,$$

n being an integer, 1, 2, 3, . . . n (HOMMA et al., 1972a).

The frequency of Ia afferent impulses corresponds to that of the applied vibration (KUFFLER et al., 1951; GRANIT and HENATSCH, 1956) and monosynaptically initiates EPSP ripples of the same frequency at the motoneuronal membrane (HOMMA et al., 1970). These EPSP ripples were regarded as vibratory EPSPs (HOMMA and KANDA, 1973). Temporal summation of the vibratory EPSPs initiated motoneuronal spikes, provided that the involved motoneuron's critical threshold level was attained. Such discharges of the tonically activated motoneuron caused a relative reduction of the Ia impulse frequency when the excitatory frequency at the input and output ends was compared. This is a consequence of the fact that the intervals of the driven spikes were separated by an integer fraction of the period of the vibratory EPSPs. The reduced ratio was termed "decoding ratio" (HOMMA et al., 1972a).

Since each spike was triggered by vibratory Ia afferent volleys, it was locked to an arbitrary phase of the vibratory stimulus. Therefore it could be shown by a cross-correlation test that all motor unit activities during vibratory stimulation were being sorted out by the prevailing locked intervals. A special gate circuit was applied in the later stage of the present experiments. The circuit was made to pass the "locked" spikes whose firing phase correlated with the bivratory phase. The subtraction of such "locked" spikes from a total set of motor unit spikes leaves a surplus of "unlocked" spikes lacking temporal correlation with

the vibratory stimulus.

By the use of this procedure it was possible to examine whether an augmentation of motor unit spikes during TVR was recruited by "locked" or "unlocked" spikes.   Results of such experiment will be described and discussed.   The method was found very useful also for the discrimination of "locked" and "unlocked" motor unit spikes during a slight voluntary effort superposed on a TVR activity. It was furthermore possible to ascertain whether additional motor unit spikes were elicited by the direct alpha, or by the indirect gamma loop.

METHOD

Twenty normal male adults took turns sitting in a specially designed experimental chair.   Their feet were tied to a steel foot-plate with a strip of soft cloth. A Hagbarth-type motor vibrator 4 cm in diameter and 14 cm in length (HAGBARTH and EKLUND, 1966a), was fixed onto the patellar tendon by a rigid rubber band. Through small movements of a steel rod supporting the foot-plate both reflex tension and voluntary contraction were recorded almost isometrically.   A fine Teflon-insulated copper wire was inserted into the quadriceps femoris muscle through an injection needle of comparable size and was used to record motor unit spikes monopolarly or bipolarly.   In most of the experiments motor unit activity during TVR were stored in a four channel FM data recorder which also recorded vibratory cycles and stretch tension.

Processing of motor unit spikes into non-sequential inter-spike intervals was performed by a biological mini-computer, ATAC 501–20, Nihon Kohden, Tokyo. The correlation block of the computer also measured the interval between each peak of the sinusoidal excursion of the motor vibrator and the motor unit spikes and, hence, delivered a cross-correlogram between them.   When the processing of a set of TVR spikes showed a good cross-correlation the data were re-processed through the special gate whose gate time was set by t and Δt adjustments, t being an arbitrary interval from some arbitrary peak of the vibration excursion, Δt being the gate period.   Both were set according to information from the original cross- correlogram. Therefore the motor unit spikes between t and $t+\Delta t$ are the "locked" spikes mentioned above.   It was also possible to take separate records of "locked" and "unlocked" activities on a strip chart recorder as will be shown below.

RESULTS

1.   Correlation between motor unit spikes during TVR and vibration

In Fig. 1 are shown typical results of a TVR experiment studied in the quadriceps femoris muscle.   A non-sequential inter-spike interval histogram processed from the original record of Fig. 1b is shown in Fig. 1d.   Approximately four
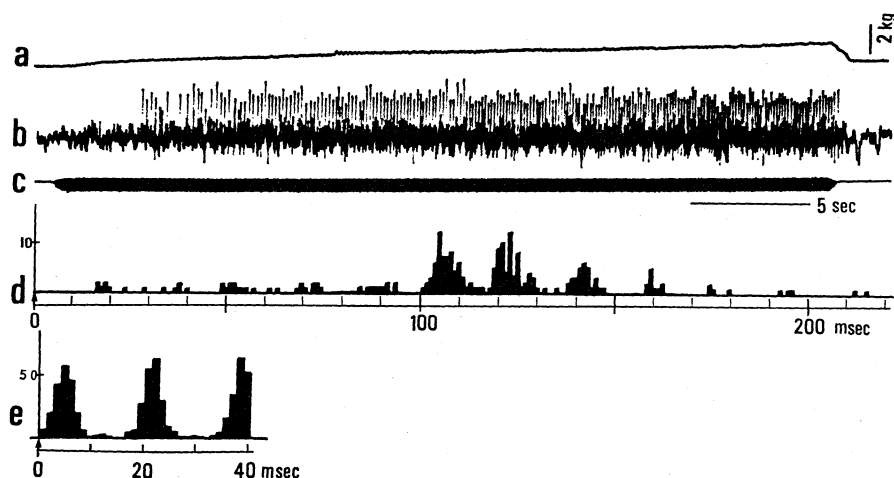
Fig. 1. Motor unit spikes during TVR of the quadriceps femoris muscle in man. a, muscle tension; b, EMG spikes; c, monitored vibration is indicated by the thick part of the line. All three parameters were recorded simultaneously. Vibratory frequency 55 Hz. d, non-sequential inter-spike interval histogram processed from the data shown in Fig. 1b. e, cross-correlogram between b and c. Record a, b, c, and d are independently calibrated as shown in the illustration.

dominant peaks can be recognized, all being separated by the vibratory cyclic time of 55 Hz which was used to stimulate the quadriceps femoris muscle. Therefore it is possible to conclude that the quadriceps motoneuron fired preferentially at integer multiple intervals of the vibratory cyclic time (HOMMA et al., 1972a).

   For further investigation of the relationship between motoneuronal firing and vibration, a cross-correlation between two parameters was made. Statistical measuring was performed by a built-in fixed program of the minicomputer's correlogram section. The section measured intervals from a motor unit spike to an arbitrary phase of vibratory excursion within the surveying time span, 40 msec in this case. The correlogram was shown in Fig. 1e in which the ordinate is the count of numbers of motor unit spikes and the abscissa the measured intervals between an arbitrary phase of vibration and motor unit spikes.   Three large peaks can be seen to be related to the cyclic time of the 55 Hz vibratory stimulation. Hence it is legitimate to conclude that the interval of the second peak corresponds to the time between the motor unit spike and the top amplitude of a vibration which was one phase ahead of it, while the interval of the third peak corresponds to the time of two vibratory phases ahead of it.   Statistically, however, it would be permissible to assume that each burst of motor unit spikes occurred in some definite correlation to a vibratory excursion although the absolute latency between the motor unit firing and the vibratory phase responsible for it can not be ascertained from the correlogram.   Thus what the correlogram showed is that
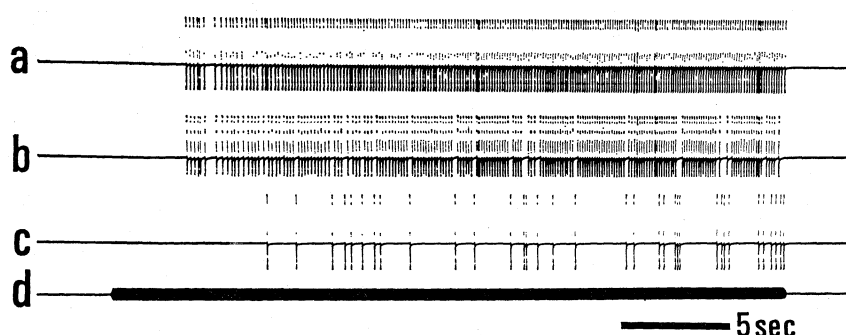
Fig. 2. Separation of "locked" and "unlocked" spikes in the TVR activity of the quadri-
ceps femoris muscle of man. a, reproduced EMG spikes of Fig. 1b processed through
an amplitude limiting circuit; b, vibration locked spikes; c, unlocked spikes; d, moni-
tored vibration. Difference in the time course of the two groups of spikes can be
clearly seen in the figure and is explained in detail in the text.

most spikes were triggered by vibratory stimulation.   These will be called "locked"
spikes. Some "unlocked" ones, however, are also present. The two types of
spike were separated by processing the special gate circuit, as described above.
Figure 2a shows the original motor unit spikes during vibratory stimulation, Fig.
2b the "locked" spikes and Fig. 2c the "unlocked" spikes.

In order to obtain the locked spikes, the time setting of the gate circuit was
adjusted to the period (Δt) between 1.3 and 7.7 msec from the top amplitude of
the vibratory excursion. This could be done because the original cross-correla-
tion had been found reliable, as seen in Fig. 1e.   Only motor unit spikes within
periods of such high cross-correlation were allowed to pass through the gate
circuit. These are the locked spikes shown in Fig. 2b. On the other hand
motor unit spikes beyond Δt could not pass through the gate circuit. These un-
locked spikes have no cross-correlation with the vibration and are shown in Fig. 2c.
The total number of spikes, locked plus unlocked ones, is equal to the number of
original motor unit spikes, as shown in Fig. 2a.

When the whole time course of locked motor unit spikes in Fig. 2b is con-
sidered, it is evident that during the initial phase of vibration the majority are
locked, while later on in the vibratory stimulation, the discharge is contaminated
by an increasing number of unlocked spikes.

A roughly parallel increase in the frequency of the locked and the total number
of motor unit spikes during the initial phase is seen in Fig. 2a and b.   The gradual
recruitment of locked spikes clearly showed that the number n in the decoding
ratio, $1/n$, of the involved quadriceps motoneurons likewise diminishes gradually.
To activation of polysynaptic reflex arcs was attributed the dominant role in
reducing n in cat extensors (cf. our preceding report, HOMMA and KANDA, 1973).
Intracellular study revealed that a polysynaptic augmentation of motoneuronal

depolarization gradually took place during vibratory stimulation. This depolarization was termed augmenting EPSP and it generated intermittent spikes only when the motoneuron's critical level of depolarization was attained by the EPSP. The augmenting EPSP was found responsible for the diminution of the n in the motoneuronal decoding of the impinging regular Ia afferents.

On the other hand it was noticed that, even when the maximum frequency of the locked spikes was readily attained, a gradual increase of the total motor unit discharge could still be observed. It is clear therefore that this increase was possible only by the recruitment of unlocked spikes. Although the unlocked spikes do not directly correlate in phase with the vibration, it is seen in Fig. 2c that they stop firing immediately at cessation of it. They thus presuppose some vibratory stimulation.

Generation of augmenting EPSP at the membrane makes the motoneuron attain its critical threshold of firing, as explained above, and thus a very slight depolarizing polysynaptic input can fire it. Such conditions are likely to be responsible for the unlocked motor unit activity. Cessation of the vibratory input leads to immediate disappearance of augmenting EPSP and consequent disappearance of unlocked motor unit spikes.

2. Analysis of voluntary motor unit spikes

Motor unit spike activity during voluntary command has been shown to have intervals of normal distribution (HOMMA et al., 1972b). Figure 3 shows a typical
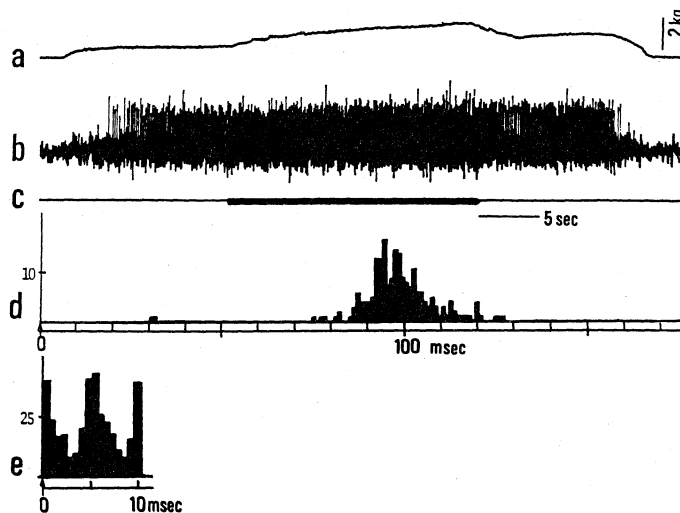

Fig. 3. Motor unit spikes during voluntary contraction and superimposed TVR in man. Explanation for a, b, c, d, and e are same as in Fig. 1. Vibratory stimulation of 167 Hz was applied in the middle of a light voluntary contraction. Dependence of spikes upon vibration is not apparent in d but clear in the corss-correlogram of e.

example of the nonsequential inter-spike interval histogram of motor unit spikes of the quadriceps femoris muscle when the muscle was slightly contracted by a voluntary effort during which vibration of 167 Hz was applied. Superposition of vibratory stimulation upon the voluntary effort facilitated the TVR as seen in the uppermost record of Fig. 3.

A non-sequential interval histogram of the quadriceps motor unit activity during vibratory stimulation is shown in Fig. 3d which suggests a typical normal distribution with a median value around 100 msec. A cross-correlation test of the motor unit activity of Fig. 3b is shown in Fig. 3e. Two categories of spike activity can be noticed in the correlogram, one with a good correlation to vibration (the peaks), the other less well correlated (between peaks). The spikes of the latter category are likely to be the ones activated by the voluntary command that was independent of the vibration.

The gate circuit was used in order to differentiate "locked" spikes from the "unlocked" ones in Fig. 3b. In this case, the time setting of the gate circuit was adjusted to the period (Δt) between 3.8 and 7.7 msec from the top amplitude of the vibratory excursion. The outcome of this operation is shown in Fig. 4b which revealed that 83 locked spikes were recorded during a superimposed vibration of 10 sec duration. "Unlocked" spikes during the superposition phase are found in Fig. 4c to a number of 27. Addition of the two groups of motor unit spikes is shown in the record of Fig. 4a giving the total number of motor unit spikes. The effect of the slight voluntary effort before and after the superimposed phase can also be seen in the record of Fig. 3a. Motor unit activity during the periods of voluntary effort was found to be 92 spikes which were distributed within a 10 sec duration, adding pre- and post-vibration periods.

For further analysis of the significance of the varieties of motor unit activity described above, three categories of motor unit spikes have been separated.

(1) Motor unit spikes elicited solely by voluntary command may be subdivided into two groups. Those activated by the descending alpha path and the
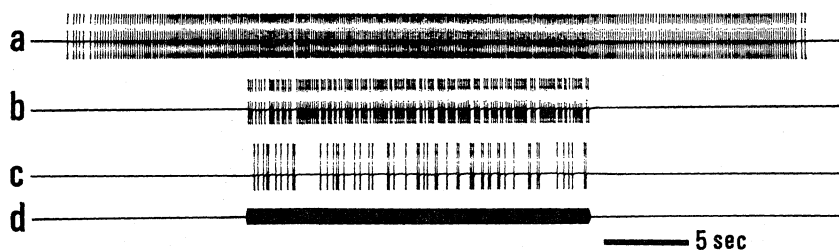

Fig. 4. Separation of locked and unlocked spikes during voluntary contraction and superimposed TVR. a, reproduced motor unit spikes of Fig. 3b through pulse limiter as used in Fig. 2; b, vibration-locked spikes; c, unlocked spikes during superimposed vibration; d, monitored vibration.

ones activated indirectly through the gamma loop and the ensuing spindle activity. The 92 motor unit spikes during the pre- and post-vibratory periods of Fig. 3 are held to belong to category (1).

(2) It has been established that Ia impulses can be driven by gamma efferents which supposedly belong to the static fusimotor fibers (CROWE and MATTHEWS, 1964; BESSOU et al., 1968). It has been suggested that almost all such Ia impulses, driven by gamma activity readily would become locked to the added vibratory stimuli and thus that their firing phase would be vibration-correlated (HOMMA et al., 1973b). It is possible therefore that the 83 locked spikes of Fig. 4b are the sum of motor unit spikes, activated directly by vibratory Ia impulses plus motor unit spikes activated by some other Ia impulses whose firing phase became locked to the vibratory stimuli.

(3) The 27 unlocked spikes of the record of Fig. 4c are independent of the vibratory period and may belong to one or several of the following three categories. i. The motor unit spikes are activated by the alpha path. ii. The spikes are activated by the Ia impulses, driven by the gamma efferent impulses during the voluntary command but remaining unlocked to the superimposed vibratory stimuli. iii. The spikes are driven by the tonic polysynaptic pathways which are mobilized by continued vibration (as in Figs. 1 and 2). These elicit unlocked motor unit spikes, 28 ± 3.7 in the average, as seen in Table 1. They are thus few in number compared with the number of "locked" spikes. It is not much of an error if for the prevention of confusion, these spikes were to be attributed to the alpha path of our category (i).

These ideas can be summarized in the following three formulae which express constituents of the motor unit spikes of three categories.

(1) voluntary spikes = α-spikes + γ-loop elicited spikes = 92/10 sec
(2) locked spikes = γ-loop elicited spikes + vibratory spikes = 83/10 sec
(3) unlocked spikes = α-spikes = 27/10 sec

On this view the number of γ-loop elicited spikes can be derived from a formula.

Table 1.

	1*	2	3	4	5	6	7	Mean$\pm$SD
(1) Voluntary spikes	92	86	92	96	92	90	100	93 ± 4.4
(2) Locked spikes	83	64	61	84	83	67	70	73 ± 9.9
(3) Unlocked spikes	27	27	31	23	25	28	34	28 ± 3.7
(4) (1)−(3) γ-loop driven spikes	65	59	61	73	67	62	66	65 ± 4.6
(5) (2)−(4) Direct vibratory spikes	18	5	0	11	14	5	4	8 ± 6.3
(6) (4)/(3) α-γ Co-activation ratio	2.4	2.2	2.0	3.2	2.7	2.2	1.9	2.4 ± 0.4

Numbers are spikes/10 sec, * is a case calculated from Fig. 4.

(4) γ-loop elicited spikes $= (1) - (3) = 92 - 27 = 65/10$ sec

The 65 spikes in formula (4) thus shows the number of motor unit spikes elicited by the γ-loop during the voluntary effort and is 2.4 times greater than the number of pure α-spikes, 27.   This ratio of 1:2.4 allows the assumption that in a light voluntary contraction alpha and indirect gamma contribution in $\alpha-\gamma$ linkage may be expressed by that ratio.   The calculated values for 7 such experiments are shown in Table 1.   The average of the ratios likewise was 2.4±0.4.   It means that participation of the gamma loop in a light voluntary contraction producing 93 motor unit spikes/10 sec was 2.4 times that of direct alpha contribution.

It was already suggested above that locked spikes are composed of γ-loop driven motor unit spikes which were correlated to the vibration and motor unit spikes directly activated by the vibration by means of the monosynaptic reflex arc.   Since the number of γ-loop motor unit spikes was known to be 65, subtraction of this number from the whole number of locked spike, 83, should give the number of motor unit spikes that was vibratorily activated.   Therefore the number of the motor unit spikes activated by vibration during the superposition phase can be held to be 18 spikes for the period of 10 sec.   The average frequency of superposed vibration motor unit spikes collected from 7 experiments was 8.4 impulses/10 sec which is fairly low compared with the normal range of other motor unit activity.

DISCUSSION

The decoding ratio of the spinal motoneuron that was primarily investigated in the cat (HOMMA et al., 1971a) was also confirmed in the present experiment since the inter-spike interval histogram was composed of integer multiples of the vibratory cyclic time.   The integer ratio between motor unit spike frequency and vibratory cycle was explained by the temporal summation of integral numbers of EPSP ripples by which the motoneuron attained the firing threshold.   The inter-spike intervals, being much dependent upon the degree of temporal summation, may be determined both by the duration of after-hyperpolarization of the motoneuron and by the duration of the recurrent inhibition from Renshaw cell (HOMMA and KANDA, 1973).   The shortest inter-spike interval during TVR in quadriceps femoris muscle was known to be around 50 msec although it slightly varied according to the vibratory frequency.   This fact means that human motor unit spikes have their preferred firing frequency around 20 Hz even if the precise frequency may differ from neuron to neuron according to their size.   The term "preferred firing frequency" of alpha motoneurons was introduced in a previous paper (HOMMA et al., 1972a).

The gradual increase of the firing frequency of the alpha motoneuron during TVR is accompanied by a parallel increase of the preferred frequency, it has been confirmed intracellularly in the cat (HOMMA and KANDA, 1973).   Slow but steady

depolarization of the cell membrane of the alpha motoneuron made the vibratory EPSPs attain the critical threshold level and, therefore, shortened the firing interval increasing the preferred frequency. This slow increment of depolarization could be abolished by an *i.v.* injection of Mephenesin without influencing the size of the vibratory EPSPs (HOMMA *et al.*, 1973a). Since the size of the monosynaptic EPSP elicited by Ia afferents did not change, although it was slowed down by the drug, the slow depolarization that was abolished by it should be considered to have an origin different from that of the vibratory EPSPs. As Mephenesin has been used for selective pharmacological blocking of the polysynaptic pathway, abolition of the slow depolarization suggests its dependence on a polysynaptic neuronal circuit.

The fact that TVR is characteristically a tonic stretch reflex has been confirmed in the study of Ia afferent impulses recorded from human nerves (HAGBARTH and VALLBO, 1968) and also by a statistical analysis of the neuronal and muscular discharge pattern (HOMMA *et al.*, 1971a). Participation of a polysynaptic neuronal circuit in the stretch reflex has long been recognized (GRANIT *et al.*, 1957; TSUKAHARA and OHYE, 1964; KANDA, 1972). In the recent study of the polysynaptic mechanism (HOMMA and KANDA, 1973) the steady depolarization was temporarily termed the "augmenting EPSP". The gradual increase of the locked spike frequency during continued vibratory stimulation is due to the algebraical summation of the monosynaptic vibratory EPSPs and the polysynaptic augmenting EPSPs. The gradual increase of the "augmenting EPSP" in vibration should allow the motoneuron to fire, even to a small input from the polysynaptic pathway and clearly the interval determined by such a firing mechanism need not conform to the integer multiple activation principle. It is therefore suggested that the unlocked spikes without cross-correlation were determined mostly by the unpredictable time course of the augmenting EPSPs.

Supporting this notion is the fact, seen in Fig. 2, that the unlocked spikes appeared with some delay after the onset of vibration and, once they appeared, were gradually augmented. This property resembled the mode of appearance of the augmenting EPSPs during vibration.

In the present report stress was placed on the cross-correlogram analysis of the voluntary motor unit spikes. It has been well established that the voluntary contraction always is executed under the control of alpha-gamma linkage (see GRANIT, 1970). This notion has been recently confirmed by the dircet recording of Ia afferent impulses during voluntary contraction of the human muscle (HAGBARTH and VALLBO, 1968).

For treatment of classified motor units a proposition has been presented that, during superposed vibration upon voluntary contraction, Ia afferent impulses driven through the gamma loop are locked to vibratory excursion (HOMMA *et al.*, 1973b).

By the several reasons discussed above it is possible to mention that the "unlocked" motor unit spikes may be the ones directly associated with the alpha path

activation and that the subtraction of the unlocked spikes from the whole amount of motor unit spikes recorded during voluntary command may simply give the number of motor unit spikes elicited by the γ-loop only.   By applying above conjecture to the present data collected in the present experiment ratio of $1:2.4$ was found between α-spikes and γ-loop elicited spikes.

REFERENCES

BESSOU, P., LAPORTE, Y., and PAGES, B. (1968)   Frequencygrams of spindle primary endings elicited by stimulation of static and dynamic fusimotor fibers.   *J. Physiol.*, **196**: 47–63.

CROWE, A. and MATTHEWS, P. B. C. (1964)   Further studies of static and dynamic fusimotor fibers.   *J. Physiol.*, **174**: 132–151.

DE GAIL, P., LANCE, J. W., and NEILSON, P. D. (1966)   Differential effects on tonic and phasic reflex mechanisms produced by vibration in man.   *J. Neurol. Neurosurg. Psychiat.*, **29**: 1–11.

GRANIT, R. (1970)   The Basis of Motor Control.   Academic Press, London and New York.

GRANIT, R. and HENATSCH, H. D. (1956)   Gamma control of dynamic properties of muscle spindles.   *J. Neurophysiol.*, **19**: 356–366.

GRANIT, R., PHILLIPS, C. G., SKOGLUND, S., and STEG, G. (1957)   Differentiation of tonic from phasic alpha ventral horn cells by stretch, pinna and crossed extensor reflexes.   *J. Neurophysiol.*, **20**: 470–481.

HAGBARTH, K. -E. and EKLUND, G. (1966a)   Motor effects of vibratory muscle stimuli in man. *In* Muscular Afferents and Motor Control, Nobel Symposium I, ed. by GRANIT, R.   Almqvist and Wiksell, Stockholm, pp. 177–186.

HAGBARTH, K. -E. and EKLUND, G. (1966b)   Tonic vibration reflex (TVR) in spasticity. *Brain Res.*, **2**: 201–203.

HAGBARTH, K. -E. and VALLBO, Å. B. (1968)   Discharge characteristics of human muscular afferents during muscle stretch and contraction.   *Exp. Neurol.*, **22**: 674–694.

HOMMA, S., ISHIKAWA, K., and STUART, D. G. (1970)   Motoneurone responses of linearly rising muscle stretch.   *Am. J. Phys. Med.*, **49**: 290–306.

HOMMA, S., KANDA, K., and WATANABE, S. (1971a)   Monosynaptic coding of group Ia afferent discharges during vibratory stimulation of muscles.   *Jap. J. Physiol.*, **21**: 405–417.

HOMMA, S., KANDA, K., and WATANABE, S. (1971b)   Tonic vibration reflex in human and monkey subjects.   *Jap. J. Physiol.*, **21**: 419–430.

HOMMA, S., KANDA, K., and WATANABE, S. (1972a)   Preferred spike intervals in the vibration reflex.   *Jap. J. Physiol.*, **22**: 421–432.

HOMMA, S., KANDA, K., and WATANABE, S. (1972b)   Integral pattern of coding during tonic vibration reflex.   *In* Symposium Neurophysiology Studied in Man, ed. by SOMJEN, G. G. Excerpta Medica, Amsterdam, pp. 345–349.

HOMMA, S. and KANDA, K. (1973)   Impulse decoding process in stretch reflex.   *In* Motor Control, ed. by GYDIKOV, A. A., TANKOV, N. T., and KOSAROV, D. S.   Plenum, New York, pp. 45–54.

HOMMA, S., KANDA, K., and MIZOTE, M. (1973a)   Role of mono- and polysynaptic reflex arcs during the stretch reflex.   *Electroenceph. Clin. Neurophysiol.*, **34**: 799.

HOMMA, S., MIZOTE, M., NAKAJIMA, Y., and WATANABE, S. (1973b) Muscle afferent discharges during vibratory stimulation of muscles and gamma fusimotor activities. *Agressologie.*, **13**, D: 45–53.

KANDA, K. (1972) Contribution of polysynaptic pathways to the tonic vibration reflex. *Jap. J. Physiol.*, **22**: 367–377.

KUFFLER, S. W., HUNT, C. C., and QUILLIAM, J. P. (1951) Function of modulated small-nerve fibers in mammalian ventral roots: efferent muscle spindle innervation. *J. Neurophysiol.*, **14**: 29–54.

RUSHWORTH, G. and YOUNG, R. R. (1966) The effect of vibration on tonic and phasic reflexes in man. *J. Physiol.*, **185**: 63 p.

SUZUKI, S. (1961) Human muscle contraction evoked by vibrating stimuli through the skin. *Jap. J. Phys. Fitness*, **10**: 106–114.

TSUKAHARA, N. and OHYE, C. (1964) Polysynaptic activation of extensor motoneurones from Group Ia fibers in the cat spinal cord. *Experientia*, **20**: 628–629.